2011 Arctic-Yukon-Kuskokwim Sustainable Salmon Initiative

Project Final Product[1]

Stock-specific forecast of AYK Chinook salmon

by

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ABSTRACT:

The regional-scale decline of Chinook salmon to AYK drainages indicates that the marine environment may play a critical role in production of this species in western Alaska. However, understanding marine survival, including incidental harvest, on western Alaska Chinook salmon is limited by the lack of marine life history information. We developed and applied the fundamental capacity necessary to apply genetic stock identification to investigation of marine life history of Chinook salmon. Based on our evaluation of the available genetic markers for use in studies of Chinook salmon across the entire range of the species, SNPs were chosen as they provide numerous advantages for shared databases including ease of automation and standardization. We developed the standardized baseline of 45 single nucleotide polymorphism markers for Chinook salmon from 172 populations across the species range with emphasis on Western Alaska. This baseline was used to estimate the stock composition of samples of juvenile and immature Chinook salmon collected during the U.S. BASIS cruises 2002-2007 to describe the stock distribution of Upper and Middle Yukon River stocks and other Coastal Western Alaska stocks in the eastern Bering Sea. Further analysis provided the stock composition of samples from the 2005-2006 bycatch in the BSAI pollock fishery and a limited sample from the early 2007 bycatch during tests of a salmon excluder device. Results showed that fish from coastal western Alaska dominated the bycatch samples taken in the northwest continental shelf; fish from southern populations (a large group including British Columbia, Washington, Idaho, Oregon, and California) comprised up to half of the samples collected on the southeast continental shelf. These results were used by NOAA as the best available science in the Federal Environmental Impact Statement analysis of the BSAI pollock fishery bycatch. The evaluation of scales taken in the 2005A season showed results similar to those obtained by genotyping fin clips. While the genetic results showed the breadth of populations present in the bycatch, concerns were raised that the non-random sampling strategy implemented by the NOAA Observer Program could result in downstream bias and the Science and Statistical Committee of the North Pacific Fishery Management Council recommended an overhaul of the observer sampling program. Given these concerns, development of a stock-specific cohort analysis to investigate the relationship of marine abundances to estimated returns was not possible. However, the baseline data and methods developed here provide a pathway to forecasting, and the results have been used to evaluate the potential to forecast returning Yukon River stocks using juvenile abundance. The relationship between Upper Yukon River juvenile abundance and Upper Yukon River adult returns was not constant over time and contained a level of variability similar to recent adult returns. The presence of significant variability in subsequent marine survival of juveniles will not permit accurate forecast adult returns from juvenile abundance alone and will require mortality corrections before juvenile abundance data can be incorporated into adult return forecast models.

Keywords: Chinook salmon, bycatch, migration, genetic stock identification, SNPs

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PRESS RELEASE:

Poor returns of Chinook salmon to AYK drainages prompted recent disaster declarations resulting in substantial economic and social impact. The regional-scale decline of these stocks indicates that the marine environment may play a critical role. Our understanding of marine survival as well as the effects of the incidental harvest or bycatch from trawl fisheries on AYK Chinook salmon suffers from the lack of marine life history information. In this project, we developed a DNA dataset for Chinook salmon in the Bering Sea to estimate juvenile migration routes and investigate the origins of the bycatch and to explore the use of the estimates in forecasting future returns.

We present a standardized baseline for Chinook salmon from populations across the range of Chinook salmon with emphasis on those inhabiting Western Alaska. We collected data from 45 single nucleotide polymorphism markers (SNPs) from a total of 172 populations. SNPs were chosen as they provide numerous advantages for shared databases including ease of automation and standardization. We used the DNA baseline to estimate the stock composition of samples from the NMFS BASIS cruises 2002-2007 where we describe the stock distribution of Upper and Middle Yukon River stocks and other Coastal Western Alaska stocks in the eastern Bering Sea.

We then used the baseline to determine the stock composition of samples from the 2005-2006 bycatch in the BSAI pollock fishery. Results showed that fish from coastal western Alaska dominated the bycatch samples taken in the northeast continental shelf; fish from southern populations (a large group including British Columbia, Washington, Idaho, Oregon, and California) comprised up to half of the samples collected in the southeast continental shelf. The evaluation of scales taken in the 2005A season showed results similar to those obtained by genotyping fin clips. While the genetic results showed the breadth of populations present in the bycatch, concerns were raised that the sampling strategy implemented by the NOAA Observer Program was not random and could result in downstream bias. As a result of these discussions, the Science and Statistical Committee of the North Pacific Fishery Management Council evaluated sampling considerations for genetic analyses and recommended an overhaul of the observer sampling program. Our final objective, to develop stock-specific cohort analyses and investigate the relationship of marine abundances to estimated returns, was not possible under the new guidelines. However, the baseline data and methods developed here provide a pathway to forecasting, and the results have been used in a limited forecast of returning Yukon River stocks using abundance indices of juvenile salmon.

An enormous legacy of this project is the transition of three NOAA laboratories and three additional state laboratories to the use of common SNP data for studies of migrating Chinook salmon. For example, baseline data from this project are used by the Auke Bay Laboratories for analysis of contemporary bycatch in the BSAI pollock fishery and by Alaska Department of Fish and Game for inseason updates on passage in the Yukon River.

PROJECT EVALUATION:

Introduction

Unanticipated poor returns of Chinook *Oncorhynchus tshawytscha* and chum salmon *O. keta* to AYK drainages prompted 15 separate disaster declarations by the State of Alaska and federal agencies during the last two decades. Concomitant restrictions in both commercial and subsistence fisheries resulted in substantial economic and social impact. Causes of the poor salmon returns to AYK river systems are not known; however, the regional-scale decline of these stocks indicates that the marine environment may play a critical role. Ocean conditions, particularly in the first few months after the salmon leave fresh water, are known to significantly affect salmon survival (Holtby and Healey 1990; Beamish et al. 2004). Climate variability in the Bering Sea ecosystem is often cited as playing a substantial role in these fluctuations (Ruggerone et al. 2009).

In addition, salmon survival rates in the Bering Sea are affected by incidental harvest or bycatch from trawl fisheries for walleye pollock (*Theragra chalcogramma*) (Gisclair 2009). Western Alaska stocks of Chinook salmon likely make up more than 50% of this incidental harvest (Myers and Rogers 1988; Myers et al. 2009). Information is needed to evaluate the effects of the bycatch which reached historic levels in recent years (Figure 1). Furthermore, it is important to better understand the marine distribution of western Alaska stocks in the bycatch to properly evaluate any benefit of proposed alternatives to reduce bycatch such as Chinook salmon savings areas, rolling "hot spot" closures, or bycatch caps (see NPFMC 2009).

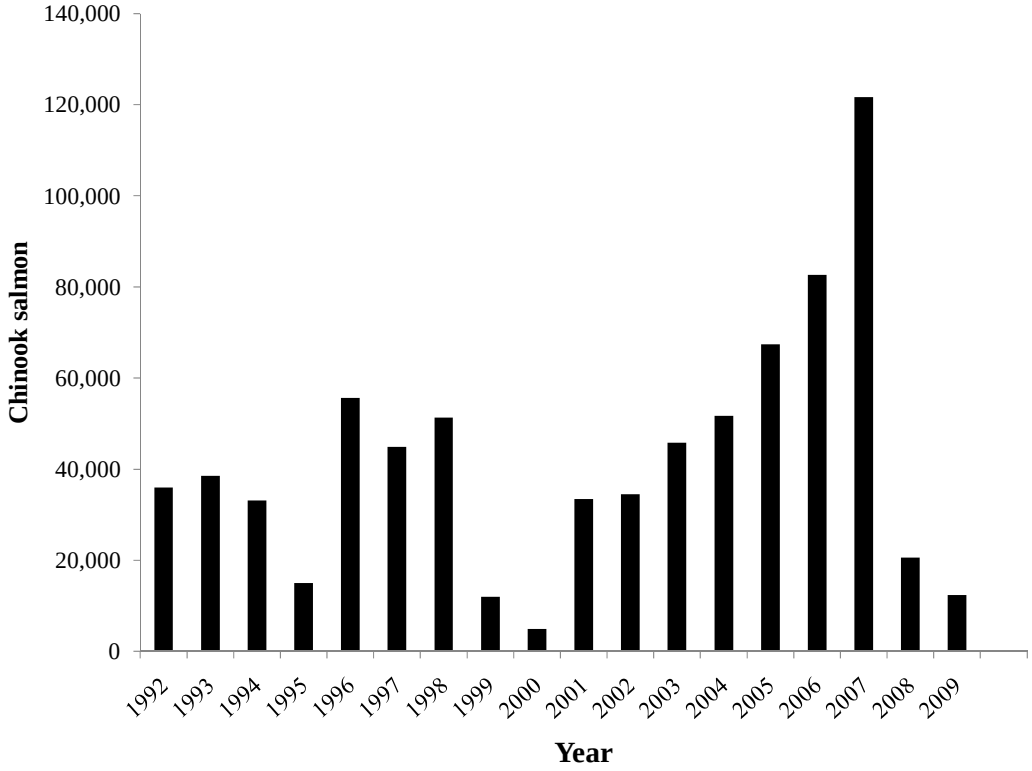


Figure 1. Chinook salmon mortality in Bering Sea Aleutian Island pollock directed fisheries, 1992–2009 (Source: http://www.alaskafisheries.noaa.gov/sustainablefisheries/inseason/chinook_salmon_mortality.pdf).

Our understanding of marine survival of the eastern Bering Sea salmon suffers due to the lack of marine life history information on western Alaska and other stocks of salmon. To address this need, the North Pacific Anadromous Fish Commission (NPAFC) began an internationally coordinated research program on salmon in the Bering Sea called the Bering-Aleutian Salmon International Survey (BASIS). Studies conducted to date under the BASIS program include information on distribution, diet, and stock of origin of juvenile Chinook salmon in the Bering Sea (see reviews in Farley et al. 2009). Other pertinent research efforts include those of Myers et al. (2009) who used scale pattern analysis to estimate the age and stock composition of Chinook salmon in samples of the bycatch from the Bering Sea and Aleutian Island (BSAI) walleye pollock fishery and evaluated the potential effects of the BSAI bycatch on Yukon River Chinook salmon. Researchers from the National Marine Fisheries Service (NMFS), Ocean Carrying Capacity (OCC) program have conducted fall surveys on the eastern Bering Sea shelf to provide key ecological data for eastern Bering Sea salmon stocks during their juvenile life-history stage with the goal of understanding mechanisms underlying the effects of environment on distribution, migration, and growth of juvenile salmon on the eastern Bering Sea shelf (Farley et al. 2007).

Concurrent with these initiatives, considerable efforts have been devoted to improving stock identification techniques via the use of genetic markers. Pacific Rim-wide databases based upon genetic markers have shown considerable success in estimating the composition and origins of complex mixtures of Pacific salmon (e.g., Seeb and Crane 1999; Beacham et al. 2008; Habicht et al. 2010). Since the 1990s, geneticists from around the Pacific Rim have collaborated to collect a common and standardized set of genetic loci and alleles to estimate the origin of chum, sockeye, and Chinook salmon intercepted on the high seas and in mixed stock fisheries. Early efforts were based on protein (allozyme) markers, but large multinational efforts are underway to use DNA markers (Seeb et al. 2007).

In this project we proposed to evaluate DNA markers and develop a DNA dataset for Chinook salmon present in the Bering Sea bycatch. Further, we proposed to use these data to develop a run reconstruction model for Chinook salmon that would combine ecological and genetic techniques to provide a valuable forecast tool based on stock-specific information.

Evaluation of Objectives

The goals of this study included addition of population data to a standardized database to enable studies of the origins of the bycatch of Chinook salmon in the Bering Sea fishery for walleye pollock. Two data types were to be evaluated: SNP DNA and microsatellite DNA. Coupling bycatch analyses, by cohort, with abundance information was then to be used to develop run reconstruction methods to forecast western Alaska Chinook salmon runs. To accomplish these goals, the following objectives were attempted:

1. *Develop a comprehensive and standardized baseline for Chinook salmon from western Alaska by adding approximately 25 populations to the existing Pacific Rim standardized DNA baseline. Evaluate genetic markers that provide useful resolution for Bering Sea mixture analyses.*

This objective was successfully completed and reported in Smith et al. (2007; Appendix 1) and Templin et al. (2011; Appendix 2). Microsatellite and allozyme data are available from ADF&G (http://www.adfg.alaska.gov/index.cfm?adfg=home.main), and all SNP data are deposited in a public access database (Dryad: doi: 10.5061/dryad.8063).

This objective was complicated by the changing landscape of DNA databases and could only be completed with the addition of substantial resources from ADF&G and collaborating projects funded at ADF&G. As originally proposed in 2005-6, we initiated this project by analyzing 25 populations for 15 microsatellite and 30 SNP polymorphisms, planning to add to the existing DNA microsatellite database supported by NMFS Northwest Center. At that time it was anticipated that the analysis of 25 populations, funded by this project, would raise the total to 114 populations in the standardized baseline dataset for use in bycatch analyses. However progress by the scientific community soon showed that standardizing microsatellite DNA data could be problematic (Seeb et al. 2007). Our lab and others began to compare the attributes of DNA markers, eventually determining that SNPs possess crucial advantages for standardized data sets for Chinook salmon(e.g., Smith et al. 2005; Smith et al. 2007; Narum et al. 2008; Clemento et al. 2011).

Concurrent with this study, we evaluated both SNPs and microsatellites in Chinook salmon for the same individuals from 14 populations originating from the Copper River, Alaska (Seeb et al. 2009). The results between the two marker sets were very consistent for all the population genetic measures estimated including diversity, spatial, and mixture analyses. Based on these results and the many desirable properties of SNPs compared to microsatellites, we focused solely on expanding and developing SNP markers in this study. We increased the SNP count from 30 to 45 to improve accuracy of estimates (e.g., Narum et al. 2008), and we increased the population count from 114 to 172 to better insure coverage of western Alaska populations found in the bycatch (Templin et al. 2011; also see objective 3 below).

2. *Determine the stock composition of samples from the NMFS BASIS cruises 2002-2006 using markers from the standardized baseline.*

   This objective was successfully completed and reported in Murphy et al. (2009; Appendix 3). The scope of analysis was expanded to include data from the 2007 cruise. We found that juvenile Chinook salmon stock proportions in the northern shelf region (north of 60°N) were: 44% Upper Yukon, 24% Middle Yukon, 31% Coastal Western Alaska, and 1% other western Alaska stock groups. Juvenile Chinook salmon stock proportions present in the southern shelf region (south of 60°N) were: 95% Coastal Western Alaska, 1% Upper Yukon, and 4% other western Alaska stock groups. We believe that these stock mixtures do not support significant northward migration of stocks from the southern shelf and reflect limited mixing of salmon from the two production regions during their first summer at sea

3. *Determine the stock composition of Chinook salmon from the 2005-2006 bycatch by age class to facilitate possible forecast model and to provide immediate insight into the number of AYK Chinook salmon in bycatch. Evaluate if scales archived from historical bycatch collections can be used to lengthen the stock-composition time series.*

We successfully determined the stock composition of the samples of Chinook salmon that were collected from the 2005-2006 bycatch (NPFMC 2009; Appendix 4). Results showed that fish from the coastal western Alaska group dominated the bycatch samples taken in the northwest continental shelf; fish from southern populations (a large group including British Columbia, Washington, Idaho, Oregon, and California) comprised up to half of the samples collected in the southeast continental shelf and adjacent to the Gulf of Alaska. The evaluation of scales taken in the 2005A season showed results similar to those obtained by genotyping fin clips taken for DNA analysis.

However, this objective was modified after discussions with the Salmon Bycatch Workgroup and the Scientific and Statistical Committee at North Pacific Fishery Management Council (NPFMC) meetings in 2007. While the genetic results for the composition of the samples showed the breadth of populations present in the bycatch, concerns were raised that the sampling strategy implemented by the NOAA Observer Program was not random, and downstream analyses of these data could have unpredictable effects on the apparent origins of the bycatch An examination of the 2005B season in fact showed that the fish sampled for genetics analysis were larger and taken later in the season than the average for the bycatch (Jim Ianelli, National Marine Fisheries Service, personal communication.) Nevertheless, these raw data were presented within the final environmental impact statement evaluating alternative measures to minimize the impacts of bycatch (NPFMC 2009). However, as result of these discussions, the Science and Statistical Committee evaluated sampling considerations for genetic analyses (Pella and Geiger 2009) and recommended an overhaul of observer program guidelines in order to provide systematic sampling by time and size.

These 2008 discussions emerged at the same time that complementary funding was provided by the Gordon and Betty Moore foundation to add additional years to the bycatch analyses and to broaden the use of standardized SNP data bases by other laboratories. Project investigators, in discussion with ADF&G and NOAA scientists, agreed to not attempt run reconstruction with potentially biased data, but rather to use these funds produce an improved and expanded baseline data set for later use with the systematic samples collected by NOAA observers after 2009.

4. *Develop run reconstruction methods to forecast western Alaska Chinook salmon runs based on stock-specific information originating from collections from juvenile surveys and the trawl bycatch.*

While we were successful in developing the methods for forecasting Chinook salmon runs to western Alaska, these methods remain to be tested. Accomplishment of Objective 4 was to be determined by successfully developing stock-specific cohort analyses for AYK Chinook salmon and investigating the relationship of marine abundances to estimated returns. The baseline data and methods developed here provide a pathway to forecasting, but these could not be tested because of potential bias in the historical observer samples. In addition to the potential bias present in sampling prior to 2009, NOAA was not able to provide matched scale and DNA samples for cohort analysis. We believe these issues to have been both corrected by implementation of the guidelines described in Pella and Geiger (2009).

However, we did investigate the potential use of the abundance indices and the stock composition of juvenile samples available from trawl surveys in the Bering Sea to forecast the return of Upper Yukon Chinook salmon (reported here). We found that marine survival of Upper Yukon juvenile Chinook salmon was not constant over time and contained a level of variability similar to the variability present in adult returns. We conclude that it is not possible to accurately forecast returns with just juvenile abundance and corrections for subsequent marine mortality will be required before juvenile data can provide insight to future adult returns.

Methods

Baseline and Mixture Sampling

Archived tissue samples from spawning Chinook salmon were available for genetic analysis for inclusion in the rangewide baseline described in Templin et al. 2011 (Appendix 2). These populations were concentrated in Western Alaska, but included representative populations from Russia and the Gulf of Alaska.

Collections of fin clips from juvenile Chinook salmon originated from U.S. BASIS cruises as described in Murphy et al. (2009) (Appendix 3).

Genetic tissue samples and scales were collected from Chinook salmon caught in the 2005 and 2006 bycatch by NMFS observers onboard Bering Sea/Aleutian Island (BSAI) walleye pollock fishery vessels. Axillary processes were collected from Chinook salmon captured as bycatch during the 2005 B season and both the A and B seasons in 2006. Additional samples were available from Chinook salmon captured during tests of a salmon excluder device during the A season in 2007. When scales were used, we used two scales per fish to obtain sufficient DNA for stock composition analysis.

Locus Selection

We considered 66 genetic markers for use in this study, 13 microsatellites standardized for use in Genetic Analysis of Pacific salmon (GAPS) analyses (Seeb et al. 2007) as well as the 53 SNPs available for use in Chinook salmon. Not all loci were necessary to achieve the resolution desired for estimates of mixture composition (see discussion in Smith et al. 2007; Narum et al. 2008). The available loci were surveyed to select a subset of the loci for use in the marine samples. First, groups of populations were defined that were potentially useful for management and research and were genetically identifiable using the full set of loci. Next, a reduced set of loci was determined that provided the same group identification with a predetermined acceptable level of precision and accuracy. Several concurrent studies were in the process of selecting loci for specific applications following this general procedure.

Laboratory analyses

Laboratory analysis of all Chinook salmon samples followed the methods described in Templin et al. (2011; Appendix 2). The genetic data collected were individual diploid genotypes for each locus. Genotype data were stored in an Oracle database (LOKI) and on a network server maintained by ADF&G computer services.

Age Analysis

Scale samples were prepared and aged using the general laboratory procedures described by Davis et al. (1990). One non-regenerated scale per fish was selected and mounted on a gummed card. Acetate impressions of the scales were made using a heated hydraulic press. The ages of Chinook salmon in the observer samples were determined by counting the number of freshwater and ocean annuli on magnified scale impressions. Scales that were too regenerated to determine a freshwater or an ocean age or are otherwise unusable were removed from the final data set used to estimate age compositions. Samples stratified by age group may have contained both immature and maturing fish. Procedures for stratifying samples and estimating age composition were the same as those used in previous studies (Myers and Rogers 1988; Myers et al. 2004).

Mixture Analysis

Reporting groups were defined based on a combination of genetic similarity, geographic features, and management applications following the recommendations and procedures used by ADF&G and described in Templin et al. (2011; Appendix 2). Testing of the accuracy and precision of these reporting groups for mixed stock analysis is described in Appendix 2. Mixed stock analysis of the juvenile samples from the BASIS surveys is described in Murphy et al. (2009; Appendix 3). Mixed stock analysis of the samples from the BSAI pollock fishery bycatch followed the methods described in Appendix 2.

Run Reconstruction

The abundance of several stock-age cohorts of western Alaska Chinook salmon was to be determined during the 2002-2006 Bering Sea juvenile salmon trawl surveys and in the BSAI trawl bycatch in 2005-2006 and 2006-2007. These abundances potentially reflected the year-class strength of five cohorts (2000-2004 broods) of western Alaska Chinook salmon. For example the cohort from the 2000 brood year occurred as age 1.0 during the 2002 Bering Sea juvenile survey and as age 1.3 during the fall of the 2005 BSAI trawl fishery. To test the feasibility of using indicators of the ocean abundance to forecast future runs of western Alaska Chinook salmon, it was necessary to assess the year-class strengths (i.e., return per spawner) of the five cohorts that occurred as 0-ocean in the BASIS samples and as 2- and 3-ocean immatures in the BSAI bycatch samples. These abundances could be combined with stock assessments of western Alaska Chinook runs to reconstruct historical runs by age for the Kuskokwim and the Yukon rivers and potentially include the Nushagak River for comparison. These assessments could be used to estimate escapement-return and sibling-age-return relationships for these stocks.

A juvenile abundance index was constructed for Upper Yukon Chinook salmon from the Yukon River using the relative abundance and stock origins of juvenile Chinook from surface trawl surveys in the northern Bering Sea shelf region. The surface trawl surveys are described in Murphy et al. (2009; Appendix 3). Due to the relatively low sample sizes of genetic samples collected during some years, a heirarchical Bayesian approach was used to estimate annual contributions of Upper Yukon Chinook salmon in the northern Bering Sea shelf (adapted from Okuyama and Bolker 2005).

The surface trawl surveys were based on a systematic spatial survey design and relative abundance of Chinook salmon was estimated for each spatial stratum using an area swept calculation as:

$$N_R = \sum_{j=1}^{S} \sum_{i=1}^{n_j} C_{i,j} \frac{A_j}{a_{i,j}},$$

where N_R is relative abundance, $C_{i,j}$ is the catch at the i^{th} station in stratum j, $a_{i,j}$ is the area swept at the i^{th} station in stratum j, and A_j is the unit area of the sample grid in stratum j. Corrections for incomplete or irregular sampling were applied by stratum when required. Abundance confidence intervals were generated through bootstrap resampling the average density by stratum. Abundance estimates are relative to total abundance by the trawl catchability. Trawl catchability is unknown and includes multiple factors such as capture efficiency of the trawl, boat and net avoidance, herding effect by trawl doors, and the proportion of Upper Yukon Chinook salmon present in the survey or sampling area. Brood-year returns of Upper Yukon River Chinook salmon (JTC 2011) were rescaled to juvenile year based on ocean age and divided by the juvenile abundance to generate the index of marine survival. Confidence intervals of marine survival were generated from confidence intervals of juvenile abundance.

Results

Baseline and Mixture Sampling

Analysis of tissues sampled from spawning Chinook salmon for the baseline was conducted on 172 populations (Figure 2). While these populations were concentrated in Western Alaska, 86 were from underrepresented regions of the Bering Sea and Gulf of Alaska; the full baseline did include representatives from throughout the range of Chinook salmon. A more complete description can be found in Templin et al. (2011; Appendix 2).

Collections of fin clips from juvenile Chinook salmon were available from NMFS Ocean Carrying Capacity BASIS cruises, described in Murphy et al. (2009; Appendix 3). Genetic tissue samples (axillary processes) and scales were collected from approximately 2,600 Chinook salmon caught in the bycatch by NMFS observers onboard BSAI walleye pollock fishery vessels during the 2005 B season and both the A and B seasons in 2006. Additional samples were available from Chinook salmon captured during a test of a salmon excluder device during the A season in 2007. The feasibility of using scale samples for genetic analysis of Chinook salmon in the bycatch was tested with scale samples from individuals taken from the 2005 bycatch.

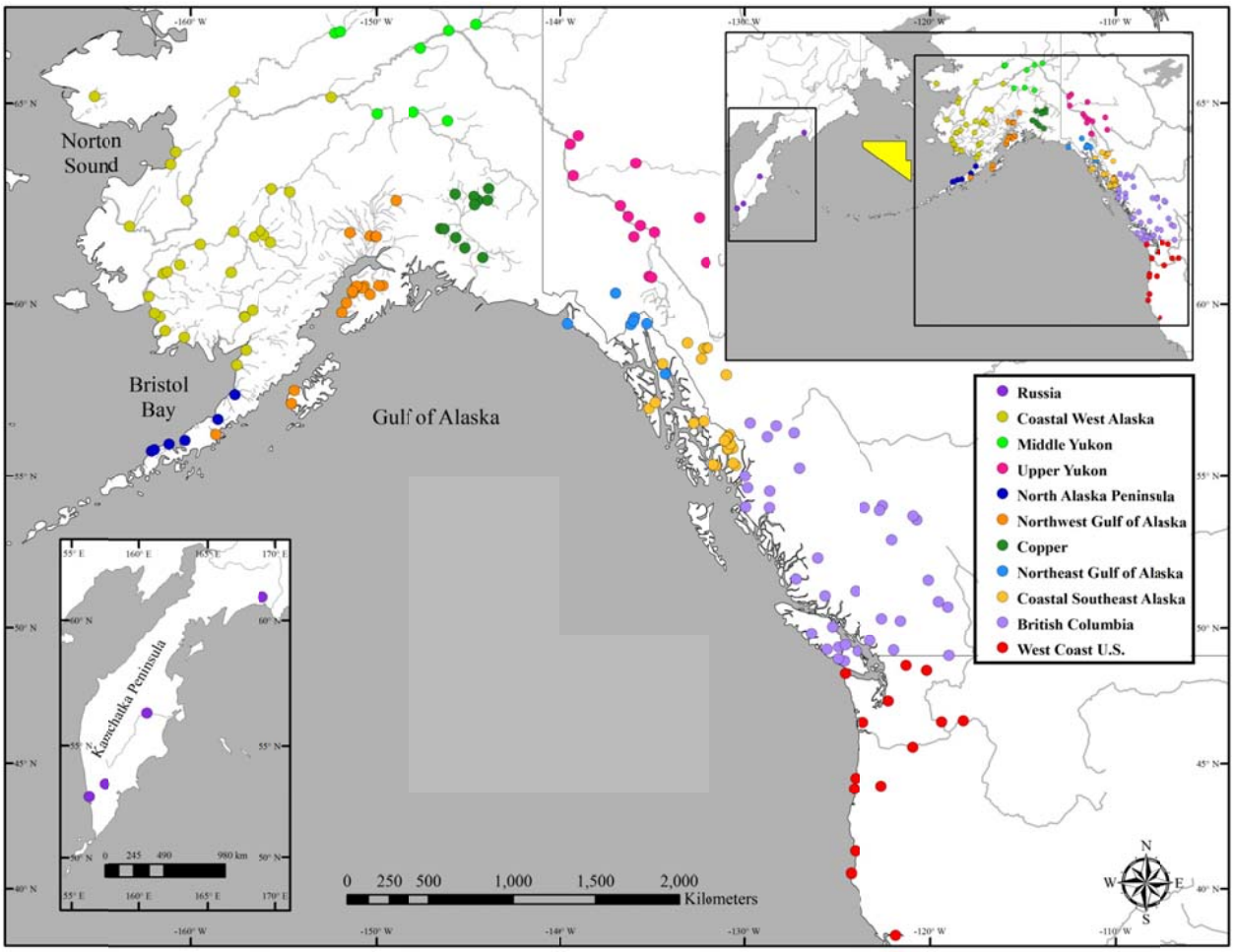


Figure 2. Collection locations for populations of Chinook salmon represented in the rangewide baseline. Numbers on the map are identical to the population numbers listed in Templin et al. (2011; Appendix 2). The location of the bycatch samples from the Bering Sea pollock fishery is indicated by the yellow polygon in the inset.

Locus Selection

Selection of a marker type for use in this study was successfully completed and reported in Smith et al. (2007; Appendix 1). This project analyzed 25 populations for 15 microsatellite and 30 SNP polymorphisms with the intent to add to the existing DNA microsatellite database supported by NMFS Northwest Center. However, selection of a marker type was complicated by the changing landscape of DNA databases and successful completion required additional resources from ADF&G and collaborating projects funded at ADF&G (e.g. Seeb et al. 2009). Across multiple analyses, the results between the two marker sets were very consistent for all the population genetic measures estimated including diversity, spatial, and mixture analyses (Figure 3). Based on these results and the many desirable properties of SNPs compared to microsatellites, we focused solely on expanding and developing SNP markers in this study including an increase of the SNP count from 30 to 45 to improve accuracy of estimates (e.g., Narum et al. 2008).

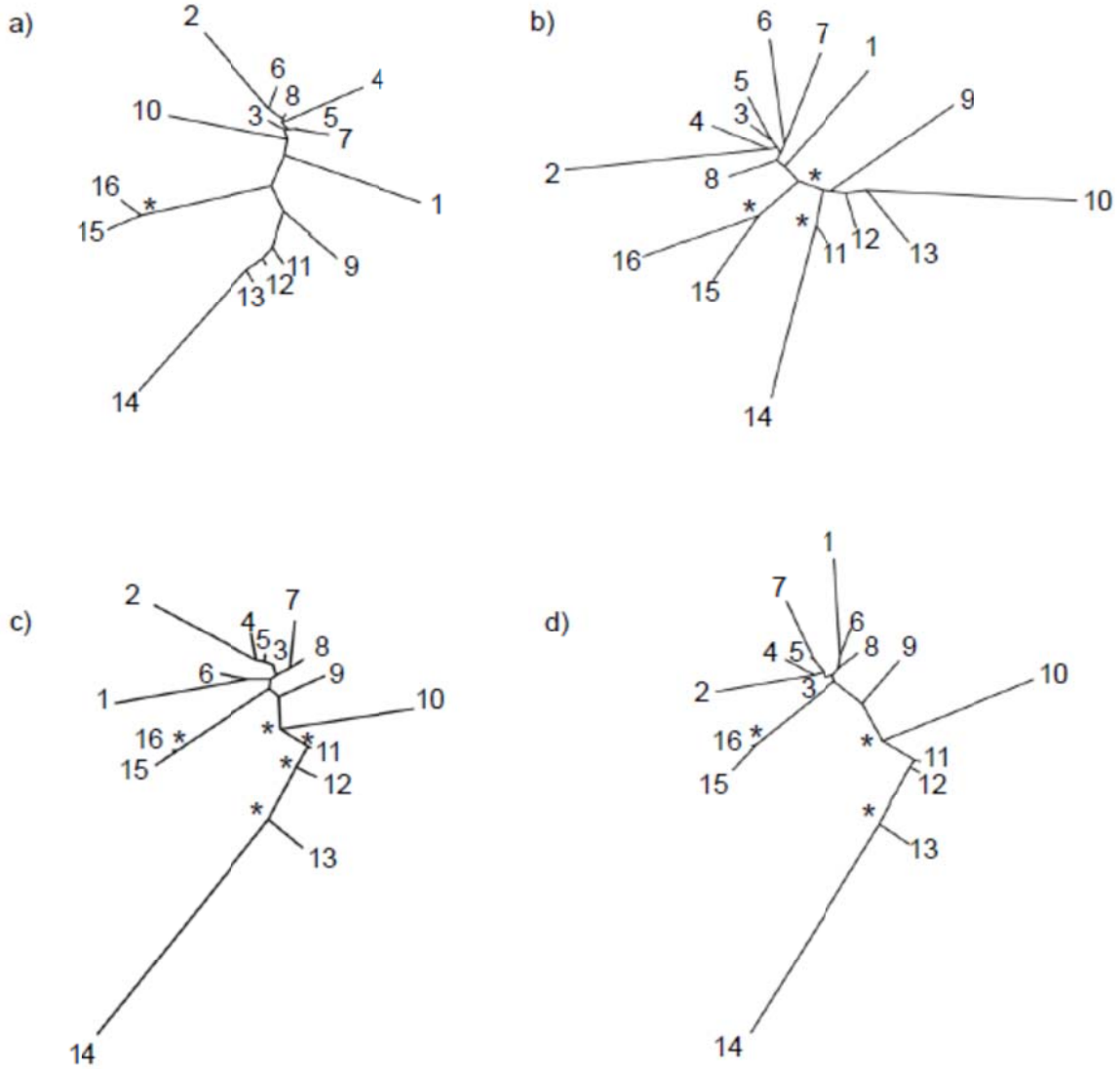


Figure 3. Neighbor joining dendrograms for Chinook salmon based on chord distances calculated from four different sets of genetic markers. The marker sets were a) 22 allozymes, b) 9 STRs, c) 39 SNPs, and d) 31 SNPs (the subset of those used for b for which neither of the criteria used here suggested increased likelihood of selection). Nodes supported by ≥70% are marked with "*". Collection numbers are 1) Bistraya River, 2) Stoney River 3) Togiak River, 4) Kuskokwim River, 5) Nushugak River, 6) Ayakulik River, 7) Moose Creek, 8) Kenai River, 9) Tahini River, 10) King Salmon River, 11) Andrew Creek, 12) Unuk River, 13) Chickamin River, 14) Deschutes River , 15) Methow River, 16) Johnson Creek. From Smith et al. (2007; Appendix 1).

Laboratory Analysis

The diploid genotypes for 45 SNP loci were assayed in 23,269 individuals for inclusion in the baseline and 4,219 individuals from ocean mixtures. The results of laboratory analysis for the baseline samples and the scale-sample feasibility study are further described in Templin et al.

(2011; Appendix 2). Of the individuals sampled for axillary processes in the 2005 and 2006 bycatch, multi-locus genotypes were successfully assayed in 2,220 individuals.

Mixture Analysis

Based on a combination of genetic similarity, geographic features, and management applications, 11 broad-scale and 44 fine-scale reporting regions were defined following the procedures described in Templin et al. (2011; Appendix 2). Testing of the accuracy and precision of these reporting groups for mixed stock analysis is described in Appendix 2. Mixed stock analysis of the juvenile samples from the BASIS surveys (Figure 3) is described in Murphy et al. (2009; Appendix 3).

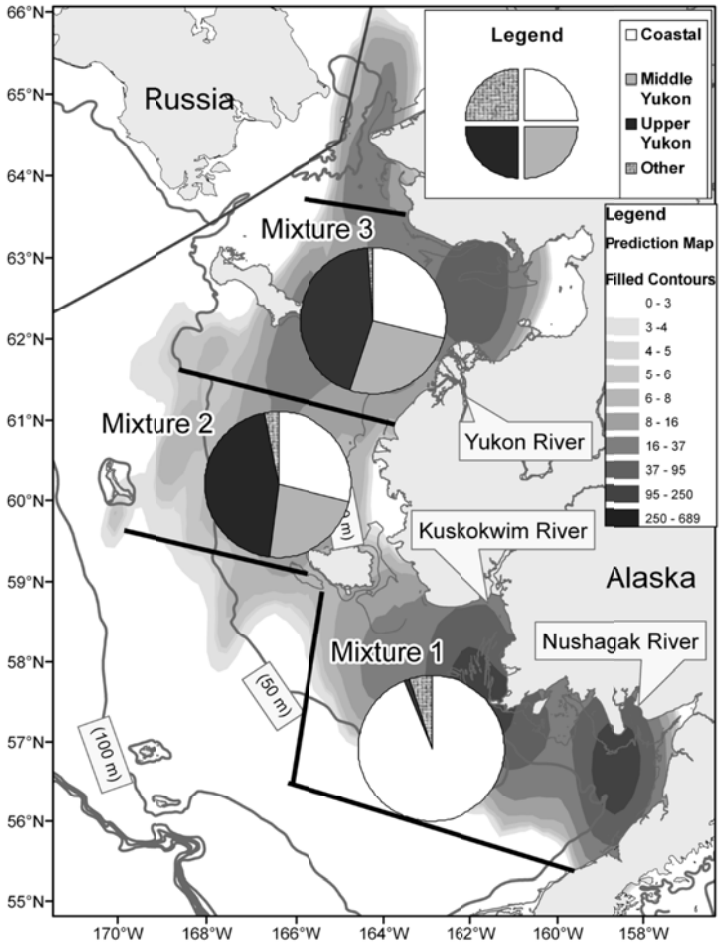


Figure 4. Genetic stock mixtures of juvenile Chinook salmon (Coastal Western Alaska, Middle Yukon, Upper Yukon, and 'other' stock groups) captured during U.S. BASIS surface trawl surveys on the eastern Bering Sea shelf (mid August to early October), 2002–2006. Mixtures are overlaid on a map of juvenile Chinook distribution and black bars identify the spatial extent of samples used for each mixture. Genetic mixtures are overlaid on the CPUE prediction surface from a Kriging spatial model. Contours are shaded at geometric intervals of the prediction surface. From Murphy et al. (2009; Appendix 3).

Mixed stock analysis of the samples from the BSAI pollock fishery bycatch also followed the methods described in Appendix 2 using the time/area strata defined in the Final Environmental Impact Assessment (FEIS) of the BSAI Pollock fishery bycatch on Chinook salmon (NPFMC 2009; Appendix 4). Estimates of the stock composition were successfully obtained from the samples from the bycatch in the 2005 "B" and 2006 "A" and "B" seasons as well as the samples from the excluder device tests during the 2007 "A" season (Appendix 4).

The estimated stock composition of the 2005 and 2006 "B" season samples showed consistent spatial patterns in the distribution of individual stocks. During each year approximately 80% of the samples from the Northwest region were from Coastal West Alaska and the middle and upper Yukon River. At the same time, samples from the Southeast region contained larger proportions of Chinook salmon from British Columbia and the west coast of the U.S.

Samples from the "A" season bycatch in the BSAI pollock fisheries during 2006 and 2007 were not spatially stratified. The largest contributing reporting group to both of these samples was Coastal West Alaska, followed by the North Alaska Peninsula group. Populations from British Columbia and the west coast of U.S. contributed 26% of the sample in 2006 and about 2% of the 2007 sample. The disparity between these samples is potentially due to the extremely restricted area and unrepresentative fishing gear from which the 2007 samples were taken.

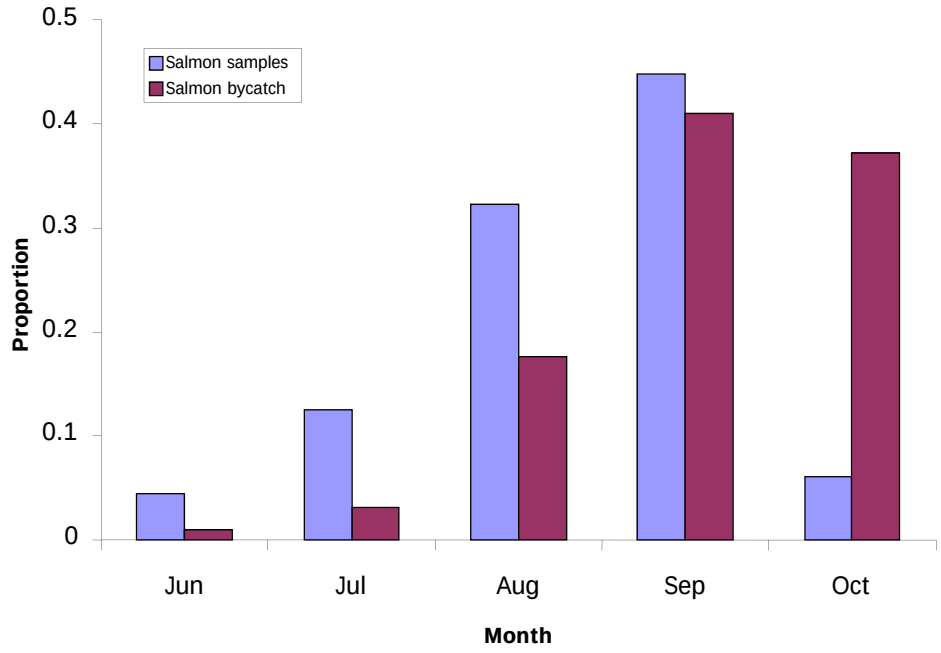
While stock composition was successfully estimated, there was concern about how well the available samples represent the actual bycatch (Appendix 4). Obtaining genetic samples from Chinook salmon was an additional task for the onboard observers and samples probably were not taken in a representative manner. A comparison of the length distribution of the genetic samples to the lengths of all Chinook salmon in the bycatch showed that the genetic samples were generally biased toward larger individuals (Figure 5a). In addition, the samples were also taken in a way that did not reflect temporal variation in the incidental catch (Figure 5b). These concerns led to two results. First, it was decided that the samples of immature and maturing Chinook salmon from the BSAI bycatch should not be used in the run reconstruction. Second, the sampling methods for Chinook salmon in the BSAI bycatch should be reviewed and a more comprehensive program should be designed and implemented. This review and sampling design is presented in Pella and Geiger (2009).

Although the samples may not provide unbiased estimates of the stock composition of the bycatch, the results were used as the "best available science" in the FEIS (NPFMC 2009).

Age Analysis and Run Reconstruction

We were successful in developing the necessary capabilities to carry out the run reconstruction, but the reconstruction could not proceed as planned. This analysis required successfully developing stock-specific cohort analyses for AYK Chinook salmon and investigating the relationship of marine abundances to estimated returns. The baseline data and methods developed here provide a pathway to forecasting, but these could not be tested because of potential bias in the historical observer samples. In addition to the potential bias present in sampling prior to 2009, NOAA was not able to provide matched scale and DNA samples for cohort analysis. We believe these issues to have been both corrected by implementation of the guidelines described in Pella and Geiger (2009).

a.



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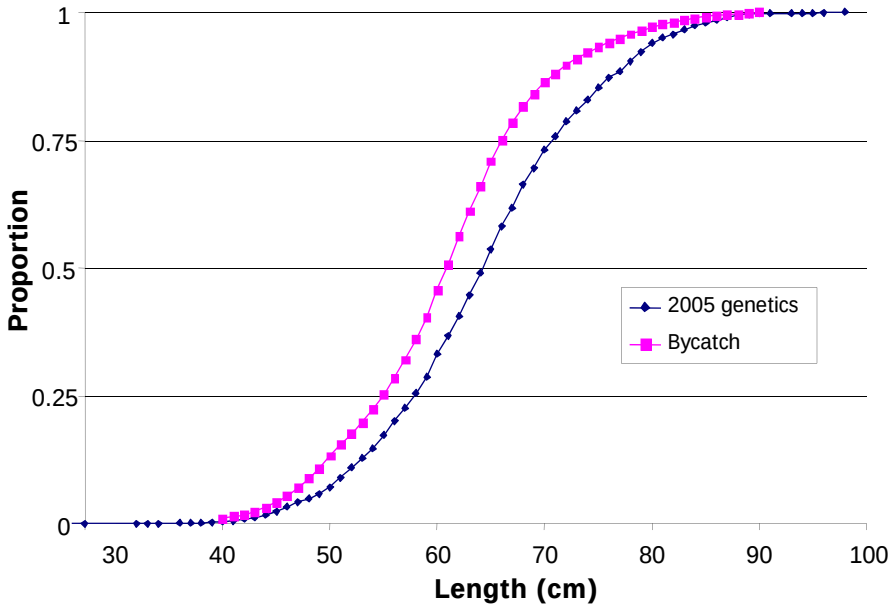

Figure 5. a) Proportion of Chinook salmon samples collected for genetics compared to the proportion of bycatch by month for 2005 "B"-season. b) Cumulative proportion of Chinook salmon samples at length collected for genetics samples compared to the same cumulative proportion of the bycatch for 2005 "B"-season. From J. Ianelli and presented by Seeb and Templin to the NPFMC in February 2007.

Most of the variability in the Upper Yukon juvenile index was the result of variable juvenile abundance. The juvenile abundance index ranged from a low in 2006 of 1,179,321 and a high of 4,079,217 in 2003, with an overall coefficient of variability (CV) of 41% (Table 1). The proportion of Upper Yukon Chinook salmon in the northern Bering Sea shelf region ranged from 43% in 2003 to 52% in 2004, with a CV of 6%. However, the overall average stock composition

was used in 2002 and 2005 due to nonsystematic sampling and this contributed to the low overall variability in stock composition. The expansion from catch to relative abundance was large with an average grid area of 2,795 km^2 and an average area swept of 0.24 km^2, making estimates of relative abundance particularly sensitive to estimates of area swept and catch.
A slightly lower level of variability was present in the estimate of Upper Yukon River Chinook salmon abundance (CV of 36%), but the abundance pattern was similar to the overall juvenile index in the northern Bering Sea with a low of 538,949 in 2006 and a high of 1,737,746 in 2003 (Figure 6). Significant variability was present in juvenile survival of Upper Yukon Chinook salmon, with a low of 5% in 2004 and a high of 11% in 2005 (Figure 7). The CV of survival was 30% and was only slightly lower than the CV present in adult returns (34%).

Table 1. Relative abundance of juvenile Chinook salmon in the northern Bering Sea shelf, genetic estimates of Upper Yukon River Chinook salmon, adult returns of Upper Yukon River Chinook salmon, and relative survival of Upper Yukon Chinook salmon by juvenile year.

Juvenile Year	Juvenile Abundance	Upper Yukon Proportion	Upper Yukon Abundance	Upper Yukon Return[1]	Marine Survival
2002	2,439,123	0.47[2]	1,146,388	109,672	0.10
2003	4,079,217	0.43	1,737,746	105,574	0.06
2004	2,063,918	0.52	1,063,950	54,972	0.05
2005	1,913,256	0.47[2]	899,230	96,852	0.11
2006	1,179,321	0.46	538,949	51,082	0.09
2007	2,796,238	0.48	1,338,000		

[1] Personal communication, Katie Howard, ADF&G
[2] Overall mean used due to nonsystematic sampling of genetic material.

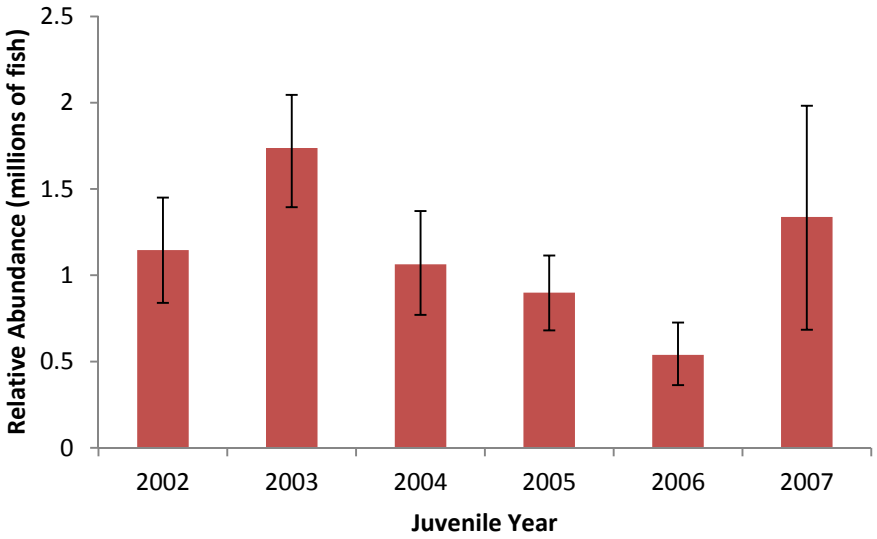

Figure 6. Relative abundance estimates of Upper Yukon River juvenile Chinook based on surface trawl surveys in the northern Bering Sea shelf, 2002-2007. The northern Bering Sea shelf is defined as the area of the eastern Bering Sea shelf north of 60N and south of the Bering Strait.

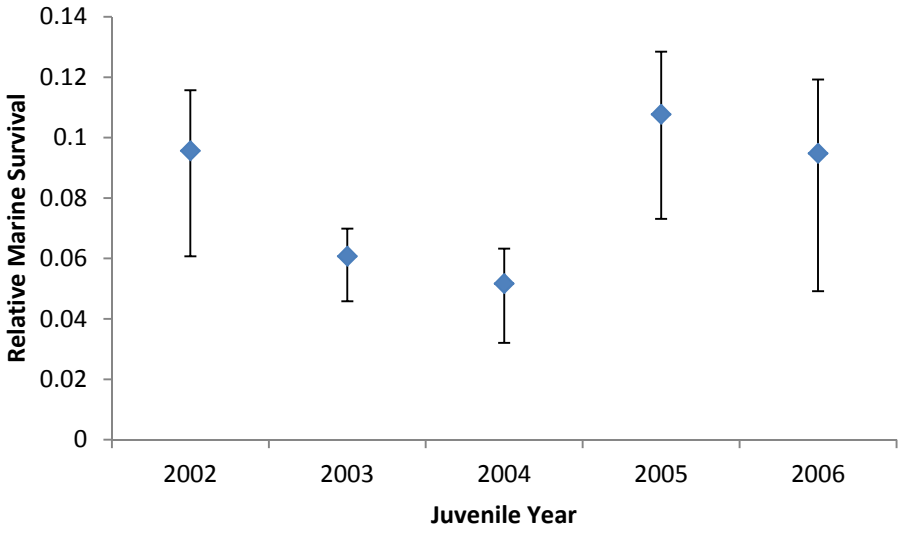

Figure 7. Relative marine survival estimates of Upper Yukon River juvenile Chinook salmon based on juvenile abundance estimates in the northern Bering Sea shelf and subsequent adult returns to the Yukon River. Marine survival is relative to true survival by the trawl catchability for juvenile Chinook salmon in the northern Bering Sea shelf.

Discussion

In this project we assembled the basic information necessary to develop and evaluate the integration of genetic information into studies of Chinook salmon in Western Alaska. After evaluating the relative merits of various DNA markers, we determined that using SNPs would be the most efficient means to interrogate the genetics of Chinook salmon (Smith et al. 2007; Appendix 1). Following this, we developed a baseline of allele frequencies for 45 SNP markers surveyed in a comprehensive set of populations throughout the range of the species. The capabilities of this baseline were then tested through simulations and applied to a sample of Chinook salmon present in the Bering Sea bycatch demonstrating the utility of genetic information for mixed stock analysis (Templin et al. 2011; Appendix 2). Mixed stock analyses were then performed on samples of juvenile Chinook salmon sampled from the 2002-2007 BASIS cruises in the Bering Sea (Murphy et al. 2009; Appendix 3) and samples taken from Chinook salmon intercepted in the BSAI pollock fisheries in 2005 and 2006 and an experimental fishery in 2007 (NPFMC 2009; Appendix 4).

Further, we had proposed to use these data to develop a run reconstruction model for Chinook salmon that would combine ecological and genetic techniques to provide a valuable forecast tool based on stock-specific information. While we were successful in developing the methods necessary for run reconstruction and forecasting of Western Alaska Chinook salmon runs, these methods remain to be tested. The baseline data and methods could not be tested because of potential bias in the historical observer samples. In addition to the potential bias present in sampling prior to 2009, NOAA was not able to provide matched scale and DNA samples for

cohort analysis. We believe these issues to have been both corrected by implementation of the guidelines described in Pella and Geiger (2009).

Further investigation into the use of information from juveniles sampled from marine trawl surveys demonstrated that marine survival of Upper Yukon juvenile Chinook salmon was not constant over time and contained a level of variability similar to the variability present in adult returns. Although a large percentage of their total mortality had occurred, year-class strength was not established well enough to produce forecasts of adult returns from juvenile abundance alone. It is possible to stabilize survival by incorporating marine ecosystem covariates of survival, however, ecosystem covariates clearly result in a process-based forecast model. Process-based forecast models are inherently unstable due to the dynamic nature of natural mortality and are prone to spurious correlations due to the high degree of cross-correlation in ecosystem covariates, limiting inferences that can be generated through simple correlation analysis. This is particularly true in short time series like the juvenile index presented here. However, all forecast models are fundamentally process-based. Even if an accurate forecast of adult returns could be generated from juvenile abundance, the underlying processes controlling subsequent marine mortality must remain the same if the forecast model is to be used. Ultimately the value of juvenile research is process driven (not harvest management), as it provides insight into the underlying production dynamics of a stock, stock-group, or species. The value of juvenile research to harvest management is limited to pre-season harvest strategies, not the principal harvest decisions that are made in-season. Application to preseason harvest decisions clearly depends on the accuracy of juvenile models relative to other pre-season forecast models such as sibling and stock-recruitment models.

An enormous legacy of this project is the transition of three NOAA laboratories and three additional state laboratories to the use of common SNP data for studies of migrating Chinook salmon. For example, baseline data from this project are used by the Auke Bay Laboratories for analysis of contemporary bycatch in the BSAI pollock fishery and by Alaska Department of Fish and Game for inseason updates on passage in the Yukon River.

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SNP III Workshop, March 2010

Templin, W. D., J. E. Seeb, and L. W. Seeb. SNPs for Chinook salmon migratory studies. Presented at the SNP III Workshop, SNP Development in Non-Model Organisms, Blaine, WA, March 23, 2010

PROJECT DATA

The data collected in this project consist of genetic assays of alleles at loci within the Chinook salmon genome. These data are stored in the form of diploid genotypes for individuals and allele frequencies for populations. Microsatellite and allozyme data are available from ADF&G (http://www.adfg.alaska.gov/index.cfm?adfg=fishinggeneconservationlab.publications). SNP data are deposited in the public-access database, *Dryad* (http://datadryad.org/; reference number: doi: 10.5061/dryad.8063). All inquiries about these data can be directed to: William Templin, Gene Conservation Laboratory, Alaska Department of Fish and Game, 333 Raspberry Road, Anchorage, Alaska 99518, phone: (907) 267-2234, fax: (907) 267-2442, email: bill.templin@alaska.gov.

APPENDICES

Appendix 1: Impacts of Marker Class Bias Relative to Locus-Specific Variability on Population Inferences in Chinook Salmon: A Comparison of Single-Nucleotide Polymorphisms with Short Tandem Repeats and Allozymes

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[Article]

Impacts of Marker Class Bias Relative to Locus-Specific Variability on Population Inferences in Chinook Salmon: A Comparison of Single-Nucleotide Polymorphisms with Short Tandem Repeats and Allozymes

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Abstract.—Single-nucleotide polymorphisms (SNPs) exhibit several attributes that make them appealing as a class of genetic markers for applications in ecology and evolution. Two commonly cited limitations of SNPs in this capacity are that ascertainment bias and natural selection may shape allele frequencies of these markers, thus biasing estimates of population structure. The impacts of ascertainment bias and selection on estimates of population parameters have been demonstrated in a few model species, but their impacts relative to locus-specific variability and other potential complications on structure inferences in wild populations are unclear. We examined 22 allozymes, 9 short tandem repeats (STRs), and 41 SNPs in approximately 1,300 Chinook salmon *Oncorhynchus tshawytscha* representing 16 collections. We used plots of the genetic differentiation index F_{ST} versus heterozygosity and sequence criteria to identify SNPs that might be under natural selection. We then calculated several measures of population structure based on the three marker sets and a subset of the SNPs from which loci identified as likely targets of natural selection had been removed. Correlation of genetic distances between collections was stronger between allozymes and SNPs than between either of these markers and STRs, suggesting that the influences of marker class bias (e.g., selection and ascertainment bias) were smaller than impacts of locus-specific effects. Divergence estimates between SNP ascertainment populations were not significantly higher when based on SNPs than when based on other markers. Overall divergence (F_{ST}) was higher for SNPs than for allozymes; however, the choice of F_{ST} estimator influenced the relative values for STRs and SNPs. Estimates of within-population diversity based on allozymes and STRs correlated better with each other than with estimates based on SNPs; such estimates based on SNPs were relatively low for collections from populations outside the geographic coverage of the SNP ascertainment sample.

Population genetic analyses have increased our understanding of a broad range of evolutionary and ecological processes. Expanding numbers and classes of available genetic markers have afforded more flexibility in choosing tools for use in any given study (Schlötterer 2004). One class of genetic markers that has received recent attention for its potential in ecological and evolutionary studies is single-nucleotide polymorphisms (SNPs; Brumfield et al. 2003; Morin et al. 2004). Several attributes of SNPs (including density in the genome, relatively well-understood evolutionary properties, and small number of alleles per locus) have led to the use of these markers for mapping and association studies in model genetic species (e.g., Kruglyak 1997). Consequently, several high-throughput SNP genotyping platforms and chemistries were developed over the past decade (reviewed by Kwok 2003). Despite optimism regarding the potential applications of SNPs in wild populations of nonmodel organisms, it is possible that SNP markers are detrimentally affected by ascertainment bias (Brumfield et al. 2003; Morin et al. 2004) and natural selection of alleles (Luikart et al. 2003; Heath et al. 2006).

Wright (1951) identified four forces that shape allele frequencies at a locus as selection, mutation, drift, and

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migration (N_em). If one assumes that the influences of selection and mutation are very small relative to those of drift and migration, then allele frequencies can be explained in terms of balance between drift and migration. Population genetic analyses using allozymes, short tandem repeats (STRs), and other marker classes often make several assumptions, including negligible selection and mutation. Because SNP markers in nonmodel organisms are often developed based on expressed sequence tags or sequences of genes with known functions, neutrality assumptions for these may be more questionable than for markers developed by sequencing random shotgun clones from a genomic library. Measurement and modeling of selection are extremely complicated and impractical in many cases, so one technique that researchers use is to identify outlier loci and remove them prior to population analyses (Beaumont and Nichols 1996). However, the question remains as to how much influence selected loci will have on analyses of wild populations of an organism, especially if large numbers of neutral loci are also included in the analyses. Luikart et al. (2003) summarized results from studies of several species and found that inclusion of a small proportion of selected loci did not, in most cases, influence biological inferences or management recommendations. Parallel analyses of allozymes and STRs have indicated that the two marker classes reveal highly concordant population structures in sockeye salmon *Oncorhynchus nerka* (Allendorf and Seeb 2000) and chum salmon *O. keta* (Scribner et al. 1998). Divergence estimates between populations will be influenced by the evolutionary properties and locus-specific history of any genetic marker; however, the studies described above lead us to expect that analyses of reasonable numbers of either allozymes or STRs will lead to accurate inference of population structure.

Ascertainment bias is the effect of using genetic markers that are chosen or developed in a way that makes them nonrepresentative of genetic variation in the population(s) of interest to infer various aspects of population structure. In developing SNP markers, for example, researchers generally examine DNA sequences of several loci in a small number of individuals. This group of individuals is sometimes referred to as the "ascertainment panel" or "panel." After sequence analysis, the researcher will develop assays that genotype a nonrandom portion of the SNPs observed in the panel. Finally, the assays are applied to a larger and broader collection of individuals drawn from one or more populations. It is obvious from this process that (1) the number of individuals in the panel, (2) the selection of those individuals from the larger population, and (3) the choice of which observed SNPs are targeted for assay development will potentially bias the amount and pattern of diversity observed in the broader population study.

Because the probability of SNP detection is proportional to the frequency of the SNP's minor allele in the panel, one effect of ascertainment bias is that low-frequency SNPs will be missed (not assayed; Nielsen and Signorovitch 2003). Polymorphisms that exist at low frequencies in the population(s) from which the panel was drawn will be missed, as will polymorphisms that exist exclusively outside the panel populations. Failure to detect or account for these polymorphisms will result in an underestimation of interpopulation divergence (and thus overestimation of migration), which should be increasingly pronounced in populations with increasing phylogenetic distance from the panel population(s).

While it seems likely that ascertainment bias and selection will influence population inferences in nonmodel species, it is unknown whether these sources of bias will be notably more pronounced in SNPs than other markers. Further, the influence of these sources of bias relative to marker-specific variation present in all classes of genetic markers is unclear. Assessment of these issues will require side-by-side comparisons of population inferences from SNPs and other markers on the same samples (Brumfield et al. 2003). By comparing data for allozymes, STRs, and SNPs in a common set of populations, it should be possible to test predictions that natural selection and ascertainment bias acting on a set of SNPs will lead to inference of a different structure than that inferred using allozymes or STRs. Here, we examine how patterns and levels of population divergence in Chinook salmon *O. tshawytscha* collections differ both broadly and with respect to panel populations when based on allozymes, STRs, and SNPs.

Methods

Genomic DNA was extracted from 1,324 Chinook salmon representing 16 collections taken from a broad section of the species' range (Figure 1) using a DNeasy 96 Tissue Kit (QIAGEN, Valencia, California). The DNA eluted from the columns (1 μL for each STR; 0.1 μL for each SNP) was used as template for polymerase chain reaction (PCR) amplification.

Allozyme analysis for collections 1–13 was described by Teel et al. (1999). We did not have allozyme tissue samples from collections 14–16, so we substituted published allele frequencies for geographically proximal collections (Waples et al. 2004; available: www.nwfsc.noaa.gov/publications/).

Nine STR loci were amplified in three PCR multiplexes (Table A.1): (1) primers *One7* (0.15 μM), *Ots1* (0.15 μM), and *Ots2* (0.04 μM); (2) primers

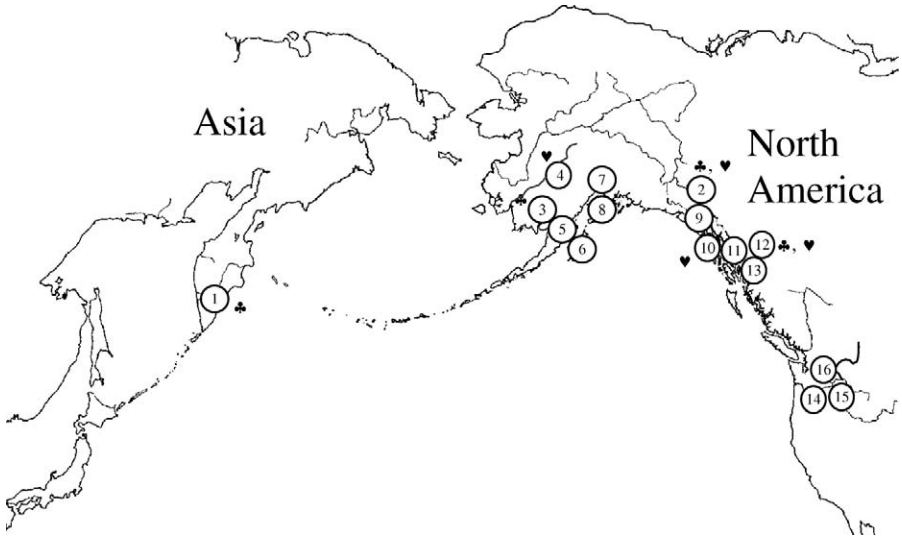

FIGURE 1.—Chinook salmon sample locations (sample sizes for short tandem repeats [STRs] and single-nucleotide polymorphisms [SNPs] in parentheses after each location): (1) Bistraya River, Russia (96, 96); (2) Stoney River, Alaska (91, 96); (3) Togiak River, Alaska (96, 96); (4) Kuskokwim River, Alaska (93, 95); (5) Nushugak River, Alaska (96, 96); (6) Ayakulik River, Kodiak Island, Alaska (90, 94); (7) Moose Creek, Alaska (50, 51); (8) Kenai River, Alaska (91, 96); (9) Tahini River, Alaska (52, 68); (10) King Salmon River, Alaska (90, 96); (11) Andrew Creek, Alaska (94, 96); (12) Unuk River, Alaska (88, 96); (13) Chickamin River, Alaska (50, 56); (14) Deschutes River, Oregon (92, 96); (15) Methow River, Washington (36, 50); and (16) Johnson Creek, Washington (30, 46). Clubs (♣) denote panel collections for 10 loci known a priori to be polymorphic in Chinook salmon (i.e., collections 1–3, and 12), and hearts (♥) denote panel collections for the remaining SNPs (i.e., collections 2, 4, 10, and 12).

One102 (0.10 μM), *Ots107* (0.06 μM), and *uSat73* (0.06 μM); and (3) primers *One13* (1.20 μM), *One9* (0.04 μM), and *Ots100* (0.25 μM). Short tandem repeat amplification was carried out in 10-μL reaction volumes consisting of 10 mM of tris-HCl, 50 mM of KCl, 0.2 mM of each deoxynucleotide triphosphate, and 0.5 units of *Taq* DNA polymerase (enzyme number 2.7.7.7, IUBMB 1992; Promega, Madison, Wisconsin) using an MJ research PTC-225 thermal cycler. The $MgCl_2$ concentration was 2.0 mM in multiplexes 1 and 2 and 2.5 mM in multiplex 3. Reactions proceeded as follows: an initial denaturation of 92°C for 2 min; seven cycles of 92°C for 1 min, annealing temperature (multiplex 1 = 53°C; multiplex 2 = 54°C; multiplex 3 = 60°C) for 2 min, and 72°C for 20 s; and 20 cycles of 92°C for 30 s, annealing temperature for 2 min, and 72°C for 20 s. All thermal cycling was conducted at a ramp speed of 1°C/s. Amplification products were size fractionated on 5% denaturing polyacrylamide gels using an ABI377 DNA sequencer (Applied Biosystems, Foster City, California). Alleles were identified and sized using the internal lane sizing standard and local Southern sizing algorithm in GeneMapper (Applied Biosystems).

To identify novel SNP markers, we used the methods and ascertainment panels described by Smith et al. (2005a; ascertainment collections are denoted by hearts in Figure 1).

Forty-one SNP genotyping assays (Table A.1) were applied to all samples. Genotyping assays were run in 384-well reaction plates; four wells in each plate served as negative (no-template) controls. Reactions consisted of 5 μL of 1× TaqMan PCR Mastermix (Applied Biosystems), 900 nM of each PCR primer, and 200 nM of each probe (probes for novel SNP assays are listed in Table 1). Thermal cycling was performed on an AB9700 thermal cycler using an initial denaturation of 10 min at 95°C followed by 50 cycles of 92°C for 15 s and 60°C for 1 min. All cycling was conducted at a ramp speed of 1°C/s. After amplification, end point reads of all plates were performed on an AB7900 real-time sequence detection system. Scoring of individual genotypes was performed using Sequence Detection Software (Applied Biosystems) to generate scatterplots that graphically depicted the amount of each allele-specific probe that bound to the PCR product of each individual.

Departures from Hardy–Weinberg equilibrium and genotypic equilibrium.—We used Genepop (Raymond and Rousset 1997) to perform exact tests (Guo and Thompson 1992) for genotypic ratios that departed from Hardy–Weinberg equilibrium (HWE) expecta-

TABLE 1.—Details for 10 novel Chinook salmon single-nucleotide polymorphism genotyping assays (F = forward; R = reverse). Each oligonucleotide probe was labeled on its 5′ end with either VIC (Applied Biosystems) or 6-carboxyfluorescence; (6-FAM) and bore a minor groove binder and a nonfluorescent quencher on its 3′ end.

Locus name, marker name, and GenBank accession number	Oligonucleotide sequences (5′–3′)
Phenylalanine-tRNA synthetase-like gene, alpha subunit *Ots_FARSLA-220* (DQ908919)*	F: GTTCGTGGGATTGTTCAATGTTCAT R: CTTGGACAGGCTCACATTACCATA VIC-CCTTGGATGGGATGTG FAM-CCTTGGATAGGATGTG
Pi-class glutathione *S*-transferase gene *Ots_GST-207** (DQ908920)	F: GGAGAACATGCATCACCATTCAAG R: TCAGCAAACGAAGGCTATGTAGAAT VIC-ATGAGAGAGTCTTTCTCTGTT FAM-ATGAGAGAGTCTTTTTCTGTT
Pi-class glutathione *S*-transferase gene *Ots_GST-375** (DQ908920)	F: CAGCCCGTCCCAAAATCAAG R: CAGGAATATCACTGTTTGCCATTGC VIC-TTTCTTGTAGGCGTCAGAG FAM-TCTTGTAGGCATCAGAG
Heat-shock 90-kDa protein gene *Ots_HSP90B-100** (DQ908921)	F: CACCTTAGTTCCACGCAACATG R: CTGCGTGTATTGTAGTGGTGACA VIC-TCTATGGTGTGATTCATT FAM-TTCTATGGTGTAATTCATT
Heat-shock 90-kDa protein gene *Ots_HSP90B-385** (DQ908921)	F: CCCTCTCAGCCACCAGGTA R: CTAGGCTGGAGCTGACATCTC VIC-ACCCACGCCAAACT FAM-AAACCCACACCAAACT
Leukocyte elastase inhibitor *Ots_LEI-292** (DQ908922)	F: CACCTGAACCTCCACTGTGT R: GCTGCTGACCTATGAGAAAATTGTG VIC-CATCATGTCAGGCCTG FAM-ATCATGTCAAGCCTG
Proteasome (prosome, macropain) subunit, beta-type 1 gene *Ots_PSMB1-197** (DQ908923)	F: AGAATGTCTAGAGTTGCCTTGAAACC R: GCAATCCAACAGCACAATATGACT VIC-AATAATACATCACTTTTTTCTC FAM-ATACATCACTATTTTCTC
Antithrombin gene *Ots_SERPINC1-209** (DQ908924)	F: CTAAGTTCTTCCTGCCTAATGTGGAT R: CCAAGATTGAGACTTACTATACATTTACAAGTACA VIC-CATTCAGCTTTTTTTC FAM-ATTCAGCATTTTTTC
Heterogeneous nuclear ribonucleoprotein L-like gene *Ots_hnRNPL-533** (DQ914957)	F: TCTTTGATATTGAGCTCATAAAAGCAAGGT R: TCCTTGTTCATCCATCAGGCATAAAA VIC-CATTTACCAGTTCTCACACAC FAM-TTTACCAGTTCACACACAC
Glycoprotein hormone alpha-subunit-like gene *Ots_GPH-318** (DQ914958)	F: GGTGATAACAGGTGTTGCACCAA R: TCAGGTGGTGGTGGACAAC VIC-ATCAAGCTGACGAACCA FAM-CAAGCTGACAAACCA

tions and Fisher's tests for genotypic linkage disequilibrium between each pair of loci across samples. Critical values for both tests were adjusted for multiple comparisons using the Bonferroni method (Rice 1989). Loci exhibiting significant genotypic disequilibrium were phased into haplotypes using the Excoffier–Laval–Balding algorithm (Excoffier et al. 2003) implemented in Arlequin (Excoffier et al. 2005). The resulting phased genotypes were used in all subsequent analyses.

Detection of loci under the influence of natural selection.—Two criteria were used to identify loci at which allele frequencies were potentially influenced by natural selection. The first was simply a determination of whether an SNP was nonsynonymous. The second was to use the method of Beaumont and Nichols (1996) to identify "outlier loci" from a plot of heterozygosity versus F_{ST} (estimated as β; Cockerham and Weir 1993). This was done in the program FDIST2 (M. A. Beaumont, University of Reading, UK) by generating a distribution of F_{ST} based on 20,000 replicates of the SNP and allozyme data and then plotting the 0.005 and 0.995 quantiles (between which 99% of the data points are expected to lie). Loci lying above or below these lines were designated as being under selection (Figure 2). Short tandem repeat loci were added to the figure for completeness; however, it was noted that (1) the null distribution was generated using an infinite allele

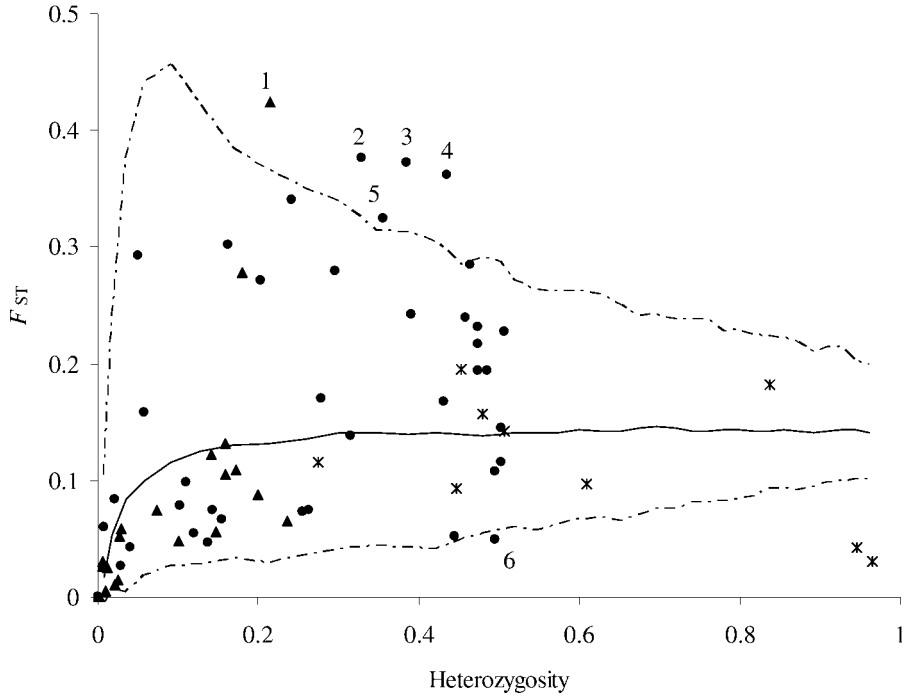

FIGURE 2.—Genetic differentiation index F_{ST} values estimated from 22 allozyme loci (▲), 9 short tandem repeat (STR) loci (∗), and 39 single-nucleotide polymorphism (SNP) loci (•) plotted against heterozygosity in Chinook salmon. Dashed lines represent 0.005 and 0.995 quantiles. Numbers denote loci outside the boundaries: (1) *sMEP-1**, (2) *Ots_u211-85**, (3) *Ots_FARSLA-220**, (4) *Ots_Tnsf**, (5) *Ots_MHC2**, (6) *Ots_P53**; two (non-numbered) STR loci had heterozygosity values of about 1.

model (which may be less appropriate for these markers than a stepwise model), and (2) loci with very high heterozygosity values have low maximum F_{ST} values (Hedrick 1999).

Comparison of structure based on different marker types with and without selected single-nucleotide polymorphisms.—To evaluate the contribution of natural selection to population structure indicated by the present SNPs, we created a second set of SNP data from which we removed loci that met either of the above criteria. This set of putatively neutral SNPs (nSNPs) was included as a fourth data set in the neighbor-joining and divergence analyses outlined below.

The first aspect of concordance between marker sets examined was the pattern of intercollection divergence. Chord distances (Cavalli-Sforza and Edwards 1967) were calculated for each pair of collections for each marker type and were used to construct neighbor-joining (Saitou and Nei 1987) dendrograms using PHYLIP (Felsenstein 1989). Consistency among markers used to generate each dendrogram was assessed by using 1,000 bootstrap replicate data sets to generate chord distances and neighbor-joining dendrograms. Correlations between the pairwise chord distance matrices generated using each marker class were calculated and tested using a permutation procedure (Mantel 1967). Our hypothesis was that greater correlation between allozymes and STRs than between either type and SNPs would be indicative of a bias acting on the SNP data.

The second aspect of concordance examined was the amount of intercollection divergence indicated by the different marker types. Overall F_{ST} among collections was estimated as the coancestry coefficient θ (Weir and Cockerham 1984), β (Cockerham and Weir 1993), population differentiation index G_{ST} (Nei 1973), and standardized genetic differentiation index G'_{ST} (Hedrick 2005) based on allele frequencies observed for each marker. Mean values of each statistic were calculated for each marker type, and 95% confidence intervals (CIs) of each mean were calculated from the *t*-distribution based on locus-specific estimates. For each locus, we calculated the within-subpopulation inbreeding coefficient F_{IS} (following Weir and Cockerham 1984) and the overall inbreeding coefficient F_{IT} (as $1 - \{[1 - F_{IS}] \times [1 - \theta]\}$). Partitioning of variance within and among collections for each marker type was performed using an analysis of molecular variance (AMOVA) framework (Excoffier et al. 1992). Differences among marker sets were assessed based on

nonoverlapping 95% CIs. As allozyme data for the southernmost three collections consisted of only collection allele frequencies, these collections were excluded from AMOVA.

Definition of ascertainment panels.—The SNPs examined in this study were developed using two different ascertainment panels (Figure 1). One ascertainment panel was used to develop 10 SNPs described by Smith et al. (2005b). This subset of SNPs is referred to here as SNPap1, and the ascertainment collections are denoted by clubs in Figure 1. The remaining assayed SNPs were developed using the ascertainment panel described by Smith et al. (2005a); this subset is designated SNPap2, and the ascertainment collections are denoted by hearts in Figure 1. A further complication is that the SNPs in SNPap1 were developed using sequences that were known a priori to be broadly polymorphic in Chinook salmon, while those in SNPap2 were chosen more arbitrarily (see Smith et al. 2005a for details).

Effects of ascertainment bias on interpopulation inferences.—To examine whether the SNP data made the ascertainment collections appear disproportionately divergent from one another, we ordered pairs of collections based on smallest to largest pairwise chord distance. This was done for each marker set (allozymes, STR, SNPap1, and SNPap2), giving us four columns that were each 120 ([16 × 15]/2) rows tall. Each column contained the same set of pairwise comparisons, but the order of pairs in each column was based on the chord distances generated using the corresponding marker set. Spearman's rank correlation coefficient (ρ_s) was calculated as a measure of concordance between each pair of columns. We then removed all pairwise comparisons between panel collections and recalculated ρ_s. Overlap between 95% CIs was used to determine whether the inclusion versus exclusion of panel collections affected ρ. If ascertainment bias is inflating relative divergence among ascertainment panel collections, then we expect that (1) ρ_s will be higher between allozymes and STRs than between either of these markers and SNPs and (2) removal of the ascertainment collections will increase ρ_s between SNPs and the other two markers.

Effects of ascertainment bias on intrapopulation inferences.—A second aspect of ascertainment bias examined was whether within-collection diversity was upwardly biased for the panel collections based on SNPs. Within-collection diversity H_s (Nei 1973) was estimated for each collection based on each marker type (allozyme, STR, or SNP). Correlations (r^2) were calculated for all pairs of marker types. If ascertainment bias is inflating within-collection diversity estimates for collections represented in the panel, then allozymes and STRs will correlate better with each other than with SNPs.

Results

Number of observed alleles, estimates of heterozygosity, and *F*-statistics for each locus are listed in Table A.1 (allele frequencies for allozymes, STRs, and SNPs are available at www.genetics.cf.adfg.state.ak.us/publish/publish.php). The STR data exhibited approximately twice as many alleles (167) as did allozymes (98) and SNPs (81). All markers exhibited multiple alleles, although nearly half of the allozymes (*sAAT-1,2**; *mAAT-1**; *GPIA**; *HAGH**; *LDHB-2**; *LDHC**; *sMDHA-1,2**; *PEPD-2**; and *PGDH**) and one SNP (*Ots_PSMB1-197**) had major allele frequencies greater than 0.950 in all collections. While fixed allele frequency differences were not observed among collections, the SNP *Ots_FARSLA-220** exhibited a 0.983 frequency difference between two adjacent collections (14 and 15).

Departures from Hardy–Weinberg Equilibrium and Genotypic Equilibrium

Tests for departures from HWE yielded significant ($\alpha = 0.05$) results for seven of the nine STR loci examined. Six of these loci deviated from HWE for one to three collections each, and generally the deviations occurred in different collections for each locus (only collection 14 exhibited departures from HWE two loci). The seventh STR locus (*One13*) exhibited departures in every collection. One significant result involved a negative F_{IS} estimate (*Ots2* in collection 5), while the 24 other significant results involved positive F_{IS} estimates. No departures from HWE were detected at any of the allozyme or SNP loci.

Genotypic disequilibrium was not detected at any of the allozyme or STR loci. The two *Ots_GST** SNPs (*Ots_GST-207** and *-375**) were significantly linked to each other in several collections, as were the two *Ots_HSP90B** SNPs (*Ots_HSP90B-100** and *-385**). Phasing the alleles at these loci yielded three alleles at *Ots_GST** and four alleles at *Ots_HSP90B**. *Ots_Prl2** and *Ots_SWS1op-182** yielded a significant result in the King Salmon River (Alaska) collection but appeared unlinked in all other collections.

Detection of Loci under the Influence of Natural Selection

Based on the plot of F_{ST} versus heterozygosity (Figure 2), we noted that four loci (*Ots_FARSLA-220**, *Ots_MHC2**, *Ots_Tnsf**, and *Ots_u211-85**) fell above the upper 0.995 quantile and that one locus (*Ots_P53**) fell below the lower 0.005 quantile. A single allozyme locus (*s-MEP-1**) also fell above the 0.995 quantile.

TABLE 2.—Summary of genetic markers examined in 16 Chinook salmon collections (see Figure 1). Note that 41 single-nucleotide polymorphism (SNP) assays were run; however, two pairs of assays were phased to create haplotypes, which reduced the number of loci to 39. Neutral SNPs (*n*SNPs) were a subset of SNPs, excluding the loci exhibiting evidence of selection. Migration estimates (N_em) were calculated as $([1/F_{ST}] - 1)/4$ (Wright 1951) based on the upper and lower 95% confidence limits of F_{ST}.

Variable[a]	Allozyme	Short tandem repeat	SNP	*n*SNP
Number of loci examined	22	9	39	31
Number of observed alleles	98	167	81	65
Mean θ (95% CI)	0.077 (0.043–0.111)	0.121 (0.083–0.159)	0.170 (0.134–0.206)	0.146 (0.116–0.177)
N_em	2.0–5.6	1.3–2.8	1.0–1.6	1.2–1.9
Mean β (95% CI)	0.078 (0.037–0.120)	0.118 (0.080–0.155)	0.170 (0.135–0.205)	0.148 (0.115–0.181)
N_em	1.8–6.6	1.4–2.9	1.0–1.6	1.1–1.9
Mean G_{ST} (95% CI)	0.076 (0.044–0.108)	0.120 (0.084–0.157)	0.167 (0.133–0.201)	0.144 (0.115–0.173)
N_em	2.1–5.5	1.3–2.7	1.0–1.6	1.2–1.9
Mean G'ST (95%CI)	0.087 (0.049–0.125)	0.332 (0.230–0.435)	0.230 (0.184–0.275)	0.204 (0.162–0.245)
N_em	1.7–4.9	0.3–0.8	0.7–1.1	0.8–1.3
Variance among collections (%)	8.38	11.19	13.30	12.02

[a] Variables are the coancestry coefficient (θ); genetic differentiation index (β); population differentiation index (G_{ST}); and standardized genetic differentiation index (G'_{ST}).

Previous sequence analyses had indicated that three SNPs were nonsynonymous (*Ots_GH2**, *Ots_HGFA**, and *Ots_Ikaros-250**). We produced a subset of the SNP data (i.e., nSNPs) that excluded these eight loci (Table 2).

Comparison of Structure Based on Different Marker Types with and without Selected Single-Nucleotide Polymorphisms

Comparisons of pairwise population chord distance matrices resulted in significant ($P < 0.001$) positive correlations in each case, suggesting broad similarities in patterns of collection divergence based on the different marker types. Correlation coefficients were slightly higher between allozymes and SNPs (0.791) than between allozymes and STRs (0.634) or SNPs and STRs (0.703). Removal of the eight SNPs designated as being under selection increased the correlation between STRs and SNPs (0.734) but decreased the correlation between allozyme and SNPs (0.773). The neighbor-joining dendrograms (Figure 3) provide a graphical representation of the relative similarities of collections based on the different marker sets. The SNP and allozyme dendrograms appear to share the most similarities. The STRs and SNPs placed the upper Yukon and Kuskokwim River drainages (Alaska; collections 2 and 4) together, but allozymes did not. Single-nucleotide polymorphisms paired the Bistraya River, Russia (collection 1), with Ayakulik River, Kodiak Island, Alaska (collection 6), but allozymes and STRs did not. The SNPs paired the Cook Inlet collections (7 and 8; Moose Creek and Kenai River, Alaska) together, but allozymes and STRs did not. When the eight SNPs were removed, the remaining nSNPs no longer paired the Cook Inlet collections. Inspection of the allele frequencies revealed that these two collections shared similar allele frequencies for two of the selected SNPs (*Ots_Tnsf** and *Ots_MHC2**). The only pair of populations with 70% or greater bootstrap support in all data sets was the Methow River and Johnson Creek, Washington (collections 15 and 16).

Mean values of θ, β, and G_{ST} provided nearly identical estimates of F_{ST} (and thus, N_em) within each marker class, while estimates of G'_{ST} were generally higher (Table 2). Comparison of 95% CIs indicated that G'_{ST} was only significantly higher than the other estimators for STRs. All three estimators of F_{ST} varied depending on the marker class used. Mean values of θ, G_{ST}, and G'_{ST} were higher for SNPs than for allozymes (nonoverlapping 95% CIs), and G'_{ST} was higher for STRs than that for allozymes or nSNPs. Mean estimates of each statistic were lower for the nSNP subset than for all SNPs; however, 95% CIs overlapped for each estimator.

The AMOVA based on the 13 collections for which we had genotype data indicated that the mean (SE) percentage of variation among collections was 8.38% (1.71%) for allozymes, 11.19% (1.97%) for STRs, and 13.30% (1.58%) for SNPs. When the analysis was repeated with all 16 collections, the percentage of variation was 12.16% (1.97%) for STRs and 17.06% (1.84%) for SNPs. Although both point estimates were higher for SNPs than for STRs, the 95% CIs overlapped, and thus we did not observe significantly different patterns in the partitioning of variation for these marker types.

Effects of Ascertainment Bias on Interpopulation Inferences

The ρ_s-values between the orders of pairwise chord distances for the marker sets examined here revealed

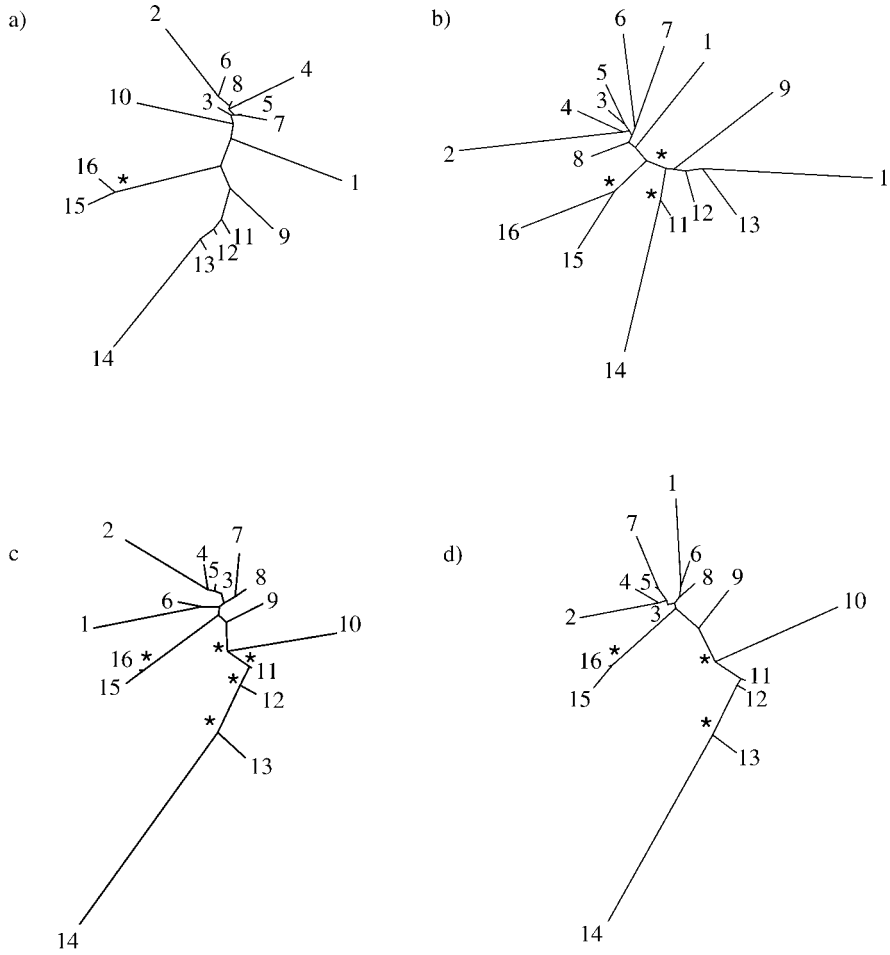

FIGURE 3.—Neighbor-joining dendrograms based on chord distances calculated from four sets of genetic markers in Chinook salmon (collection numbers are defined in Figure 1). The marker sets were **(a)** 22 allozymes, **(b)** 9 short tandem repeats (STRs), **(c)** 39 single-nucleotide polymorphisms (SNPs), and **(d)** 31 putatively neutral SNPs (a subset of those in [c]). Asterisks indicate nodes with 70% or greater bootstrap support.

TABLE 3.—Spearman's rank correlation coefficients (ρ_s; with 95% CI) between orders of pairwise chord distances for genetic markers in 16 populations of Chinook salmon (STR = short tandem repeats; SNP_{ap1} and SNP_{ap2} = single-nucleotide polymorphism ascertainment panels 1 and 2, respectively) for all samples and for only those samples that were not included in ascertainment panel collections.

	ρ_s	
Marker pair	All samples	Ascertainment collections removed
Allozyme and STR	0.71 (0.53–0.88)	0.71 (0.53–0.88)
Allozyme and SNPap1	0.78 (0.60–0.95)	0.78 (0.54–1.00)
Allozyme and SNPap2	0.68 (0.50–0.86)	0.70 (0.46–0.95)
STR and SNPap1	0.60 (0.42–0.77)	0.61 (0.37–0.86)
STR and SNPap2	0.73 (0.55–0.91)	0.60 (0.36–0.84)

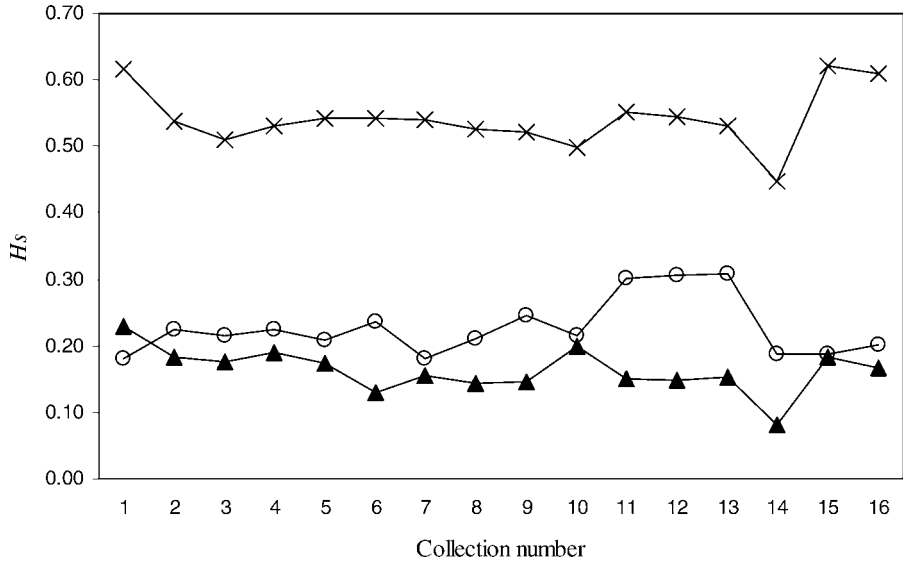

FIGURE 4.—Estimates of within-collection variation H_s for 16 Chinook salmon collections (see Figure 1) including those used in the SNPap2 discovery panel (2, 4, 10, and 12; see text). Three marker sets were used: allozymes (▲), short tandem repeats (STRs; ×), and single-nucleotide polymorphisms (SNPs; ○). Estimates based on STRs and allozymes correlated better with one another ($r^2 = 0.34$) than with estimates based on SNPs (SNP–STR $r^2 = 0.02$; SNP–allozyme $r^2 = 0.04$).

little evidence of ascertainment bias (Table 3). The highest ρ_s observed was between allozymes and SNPap1 (0.78), and the lowest was between STRs and SNPap1 (0.60). Correlation between SNPs and the other two marker classes did not appear to improve when the SNP ascertainment collections were removed from this analysis. Overlap between 95% CIs suggested that none of the differences between marker classes or between comparisons with or without the ascertainment collections were significant (Table 3).

Effects of Ascertainment Bias on Intrapopulation Inferences

The plot of within-collection diversity (Figure 4) was examined for evidence that collections with high diversity based on allozymes and STRs were less diverse based on SNPs. We observed a stronger correlation between allozymes and STRs ($r^2 = 0.34$) than between either of these marker classes and SNPs (allozyme–SNP $r^2 = 0.04$; STR–SNP $r^2 = 0.02$). Examination of Figure 4 suggests a discrepancy among the three marker classes as indicators of the relative diversity of collections outside the SNPap2 ascertainment range (i.e., outside of collections 2–12). To determine whether this caused the large discrepancy in r^2 values, we recalculated r^2 between paired marker classes based only on the ascertainment collections (2–12). In this case, the correlation between allozymes and STRs was reduced ($r^2 = 0.28$) and the correlation of SNPs with the other markers increased (allozyme–SNP $r^2 = 0.11$; STR–SNP $r^2 = 0.17$).

Discussion

The collections examined here were chosen to represent a broad sample of genetic diversity in Chinook salmon, so it is not surprising that considerable polymorphism was observed. The 0.983 allele frequency difference observed for the SNP *Ots_FAR-SLA-220** between collections 14 and 15 is extreme; however, an ancient lineage break has previously been described between the corresponding populations (Waples et al. 2004), and randomly amplified polymorphic DNA (Rasmussen et al. 2003) and STR (Narum et al. 2004) markers with similar resolving power for these groups have been reported.

Departures from Hardy–Weinberg Equilibrium and Genotypic Equilibrium

Departures from genotypic ratios expected under HWE can be caused by (1) departures from the evolutionary model assumed for HWE, (2) pooling of populations into one collection (i.e., Wahlund effect), or (3) technical errors leading to miscalled genotypes. Of the 70 markers examined here, 7 exhibited departures from genotypic frequencies expected under HWE conditions. All seven were STRs, and most departures were due to homozygote excess (indicated by positive F_{IS} estimates). Because the statistical power

to detect departures from HWE in a given sample is inversely related to the number of alleles at a marker (i.e., for a fixed sample size, a greater number of categories means lower counts per category) and because we only detected departures from HWE in the marker class with the largest number of alleles per locus, genotyping errors seem a likely explanation for our results. Null alleles (those with a mutation in the PCR priming site) and allelic dropout (preferential amplification of shorter alleles) are two common explanations for such results in STR data sets. We observed a genotypic linkage between *Ots_Prl2** and *Ots_SWS1op-182** in collection number 10 that was absent from all other collections; therefore, the linkage is probably attributable to population history or selection (discussion in Ohta 1982) rather than physical linkage.

Detection of Loci under the Influence of Natural Selection

Our power to detect which of the 38 nuclear SNP loci were under the influence of natural selection was limited. Based on a null hypothesis of neutrality and the fact that we started with 60 loci (38 nuclear SNPs + 22 allozymes), we would expect approximately one locus to lie outside the 0.005–0.995 quantiles. The model used here predicts that the four loci above the 0.995 quantile (*Ots_FARSLA-220**, *Ots_MHC2**, *Ots_Tnsf**, and *Ots_u211**) are subject to directional selection, while the locus under the 0.005 quantile (*Ots_P53**) is subject to balancing selection. Two of the four loci above the 0.995 quantile have previously been identified as targets of natural selection in Chinook salmon (Miller et al. 1997; Ford 2000). One potential problem with using the Beaumont and Nichols (1996) test on the present data set is that it assumes equal migration between populations, and violations of this assumption could lead to type I errors (i.e., labeling neutral loci as under selection). Because our objective was to remove loci that were potentially under selection, however, we do not suspect that this caused a problem for our downstream analyses. While it would be unsound to conclude that all loci outside the 99% quantiles or all loci coding nonsynonymous substitutions are strongly influenced by natural selection, we expect that exclusion of these loci removed the targets of the strongest selection and thus rendered our remaining SNP set (nSNPs) nearly neutral.

Comparison of Structure Based on Different Marker Types with and without Selected Single-Nucleotide Polymorphisms

The overall concordance that we observed in the chord distance matrices and neighbor-joining trees based on the three marker types revealed a broad-scale population structure that was independent of the marker class used. The higher correlation between allozymes and SNPs than between either marker class and STRs suggests that the influence of biases acting only on SNPs (e.g., ascertainment bias and selection) was small relative to other sources of variation (e.g., locus sampling effects and marker class evolutionary rates) affecting the relative chord distances between collections. Anderson et al. (2005) observed that geographic distance in malarial parasites had a higher correlation with genetic distance when based on 10 nSNPs than when based on 10 selected SNPs. A comparable analysis here would be complicated by the unequal number of SNPs in each category; however, because we identified loci as selected based on F_{ST} outliers, we expect that population structure based solely on these loci would be biased. The selection vectors on these loci may be different between different collections, and the large number of unlinked loci examined was probably enough to override selection acting in a particular direction in one or a few collections.

The four F_{ST} estimators used to quantify divergence between collections indicated comparable levels of among-collection variation for the three marker classes. The difference in G_{ST} values between STRs and allozymes was probably an artifact of the large number of alleles and concomitant high heterozygosity at STR loci (Hedrick 1999). Although θ and its simplified form, β, are analogous to Wright's (1951) F_{ST} and can be used to infer a balance between migration and drift, G'_{ST} is expected to reflect differences in mutation rate to a large extent and population inferences based on this statistic are less clear. We used G'_{ST} to facilitate comparison of divergence estimates regardless of the heterozygosity differences between markers; in this respect, it has proven useful. Of the three marker types examined here, SNPs provided the most consistent estimates of F_{ST} (and thus, $N_e m$) across methods. Aside from limitations based on numbers of alleles, comparisons of F_{ST} based on SNPs and STRs are limited by the different evolutionary properties of the two marker classes. The results presented here are concordant with those of other salmonid studies that found comparable overall estimates of θ based on allozymes and STRs despite a large amount of variation among specific loci (Scribner et al. 1996; Allendorf and Seeb 2000). The overlap in estimates based on STRs and SNPs suggest that such trends hold for SNPs as well.

Within- and among-collection variance proportions were similar for all three markers in the 13 collections and similar for STRs and SNPs within the entire data set (Table 1). Point estimates of among-collection

variance were highest for SNPs, but 95% CIs for all marker types overlapped. The 95% CIs also included the published estimates based on allozymes within British Columbia (8.7%; Teel et al. 2000) and south of British Columbia (12.3%; Utter et al. 1989).

Effects of Ascertainment Bias on Intrapopulation Inferences

An apparent effect of ascertainment bias was observed in our examination of within-collection diversity. In this case, a stronger correlation was observed between our two control data sets (allozymes and STRs) than between either set and SNPs. Studies of humans (Mountain and Cavalli-Sforza 1994) and fruit flies *Drosophila* spp. (Schlötterer and Harr 2002) have revealed that estimates of interpopulation diversity in ancient populations can be biased downward when based on SNPs that are ascertained in relatively derived panel populations. Given the relatively ancient divergence between collections 14 and 15–16 (Waples et al. 2004) and the fact that none of these populations were represented in the ascertainment panels, it is not surprising that the SNPs examined here did not reveal the greater diversity indicated by allozymes and STRs for collections 15–16 (Figure 4).

Conclusions

Biases affecting allele frequencies at a single marker seem unlikely to change the overall structure observed when the number of markers examined is large. Even biases affecting several markers (e.g., under the influence of natural selection) might be of little consequence as long as the selection vectors are different. This, or the possibility that selection coefficients were small relative to migration and drift for the present loci, may explain why selection did not appear to shape branching order (the relative placement of individuals in the neighbor-joining analysis), divergence estimates, or variance partitions. The impact of a few selection-influenced markers on population structure inferences cannot yet be generalized. However, empirical comparisons such as the one presented here advance our understanding. In any case, routine screening of loci for the potential influence of selection prior to structure estimation, followed by estimation of structure with and without the outlier loci, is easy to do and seems well advised (Luikart et al. 2003).

Because SNPs are often ascertained in batches, ascertainment bias probably acts in conjunction across several loci. The effects of ascertainment bias on inferences of some population parameters can be minimized by careful selection of the source and size of the ascertainment panel (Akey et al. 2003), and this concept has been used to guide SNP discovery projects (e.g., Cappuccio et al. 2006). The fact that we did not observe any impact of ascertainment bias on branching order, overall divergence, variance partitioning, or estimation of divergence among panel collections may be partially due to our relatively large and diverse panel. Additional comparative data sets will be required before we can make general statements about the effect of ascertainment bias on branching order and divergence. However, assuming a large, diverse ascertainment panel is used, the effect will be negligible in many cases. For comparisons of panel populations with nonpanel populations, we expect the results to vary quite a bit depending on which nonpanel collections are examined; even large, diverse panels might not be able to prevent such variability. Our Chinook salmon data support the inadvisability of estimating within-population diversity based on SNPs developed in ascertainment panels from derived populations.

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Appendix: Chinook Salmon Loci Surveyed

TABLE A.1.—Loci surveyed in 16 collections of Chinook salmon. The annealing temperature and $MgCl_2$ concentration associated with each short tandem repeat (STR) multiplex are given in Methods. Diversity and structure indices are within-collection diversity (H_s), within-subpopulation inbreeding coefficient (F_{IS}), overall inbreeding coefficient (F_{IT}), coancestry coefficient (θ), genetic differentiation index (β), population differentiation index (G_{ST}), and standardized differentiation index (G'_{ST}).

Locus	STR multiplex	Number of alleles	H_s	F_{IS}	F_{IT}	F_{ST} θ	F_{ST} β	F_{ST} G_{ST}	F_{ST} G'_{ST}	Source[a]
					Allozyme					
*sAAT-1,2**		4	0.018	0.004	0.025	0.021	0.025	0.023	0.024	1
*sAAT-3**		4	0.150	0.004	0.118	0.114	0.088	0.110	0.130	1
*mAAT-1**		5	0.011	0.005	0.013	0.008	0.005	0.011	0.012	1
*ADA-1**		5	0.115	0.004	0.143	0.140	0.132	0.134	0.152	1
*sAH**		5	0.147	0.004	0.124	0.120	0.109	0.115	0.136	1
*GPIA**		4	0.017	0.004	0.023	0.019	0.010	0.021	0.021	1
*HAGH**		5	0.028	0.004	0.059	0.055	0.058	0.055	0.056	1
*sIDHP-1**		9	0.160	0.005	0.120	0.116	0.105	0.112	0.135	1
*LDHB-2**		4	0.005	0.004	0.030	0.026	0.030	0.028	0.028	1
*LDHC**		4	0.012	0.004	0.028	0.024	0.027	0.026	0.027	1
*sMDHA-1,2**		4	0.001	0.001	0.004	0.004	0.000	0.004	0.004	1
*sMDHB-1,2**		6	0.024	0.024	0.004	0.118	0.014	0.017	0.017	1
*mMDH-2**		3	0.143	0.005	0.233	0.229	0.277	0.220	0.259	1
*sMEP-1**		4	0.138	0.005	0.340	0.337	0.424	0.323	0.379	1
*sMEP-2**		2	0.121	0.005	0.140	0.136	0.123	0.131	0.151	1
*MPI**		5	0.202	0.004	0.081	0.077	0.065	0.075	0.095	1
*PEPA**		5	0.064	0.004	0.082	0.078	0.075	0.076	0.081	1
*PEPB-1**		5	0.149	0.005	0.063	0.058	0.056	0.058	0.069	1

TABLE A.1.—Continued.

Locus	STR multiplex	Number of alleles	H_s	F_{IS}	F_{IT}	F_{ST} θ	F_{ST} β	F_{ST} G_{ST}	F_{ST} G'_{ST}	Source[a]
*PEPD-2**		3	0.001	0.005	0.021	0.016	0.000	0.019	0.019	1
*PGDH**		3	0.001	0.004	0.005	0.001	0.000	0.005	0.005	1
*TPI-3**		4	0.028	0.005	0.057	0.052	0.051	0.052	0.054	1
*TPI-4**		5	0.076	0.004	0.057	0.053	0.048	0.054	0.058	1
				STR						
One7	1	2	0.382	0.043	0.231	0.197	0.196	0.192	0.319	2
Ots1	1	8	0.55	0.039	0.133	0.098	0.097	0.099	0.229	3
Ots2	1	21	0.432	−0.024	0.137	0.157	0.142	0.154	0.278	3
One102	2	2	0.393	0.012	0.097	0.086	0.093	0.086	0.146	4
Ots107	2	36	0.898	0.048	0.091	0.045	0.043	0.048	0.497	5
uSat73	2	5	0.382	−0.006	0.155	0.160	0.157	0.156	0.259	6
One13	3	15	0.671	0.446	0.545	0.179	0.183	0.178	0.564	2
One9	3	3	0.222	0.130	0.249	0.136	0.115	0.134	0.174	2
Ots100	3	75	0.925	0.025	0.057	0.033	0.031	0.037	0.526	7
				Single-nucleotide polymorphism						
*Ots_E2-275**		2	0.39	−0.045	0.162	0.198	0.195	0.192	0.323	8
*Ots_arf-188**		2	0.008	0.150	0.201	0.060	0.060	0.063	0.063	8
*Ots_AsnRS-60**		2	0.418	0.028	0.079	0.052	0.052	0.055	0.097	8
*Ots_C3N3**		2	0.107			0.309	0.302	0.303	0.342	9
*Ots_FARSLA-220**		2	0.249	0.097	0.435	0.374	0.373	0.363	0.491	Table 1
*Ots_FGF6A**		2	0.338	0.092	0.293	0.222	0.240	0.216	0.333	10
*Ots_E2-275**		2	0.39	−0.045	0.162	0.198	0.195	0.192	0.323	8
*Ots_GH2**		2	0.237	−0.068	0.118	0.174	0.170	0.169	0.225	9
*Ots_GnRH-271**		2	0.048	−0.020	0.153	0.170	0.158	0.166	0.175	8
*Ots_GPDH-338**		2	0.159	0.065	0.122	0.061	0.067	0.064	0.077	8
*Ots_GPH-318**		2	0.234	0.098	0.168	0.078	0.073	0.080	0.106	Table 1
*Ots_GST-207**		3[b]	0.166	0.011	0.365	0.358	0.340	0.346	0.420	Table 1
*Ots_GST-375**										
*Ots_HGFA-446**		2	0.041	0.095	0.360	0.293	0.292	0.284	0.297	8
*Ots_hnRNPL-533**		2	0.37	0.021	0.222	0.206	0.194	0.200	0.325	Table 1
*Ots_HSP90B-100**		4[b]	0.363	−0.048	0.184	0.222	0.231	0.215	0.346	Table 1
*Ots_HSP90B-385**										
*Ots_IGF-I.1-76**		2	0.356	−0.005	0.171	0.175	0.168	0.171	0.272	8
*Ots_Ikaros-250**		2	0.109	0.051	0.146	0.101	0.098	0.101	0.114	8
*Ots_il-1racp-16**		2	0.362	0.013	0.230	0.220	0.217	0.214	0.343	8
*Ots_LEI-292**		2	0.046	0.040	0.076	0.038	0.043	0.042	0.044	Table 1
*Ots_MHC1**		2	0.408	0.022	0.203	0.185	0.228	0.179	0.311	9
*Ots_MHC2**		2	0.222	0.045	0.396	0.367	0.325	0.356	0.464	9
*Ots_ZNF330-181**		2	0.021	−0.103	−0.006	0.088	0.084	0.088	0.090	8
*Ots_LWSop-638**		2	0.098	0.050	0.119	0.073	0.078	0.074	0.083	8
*Ots_SWS1op-182**		2	0.434	−0.024	0.095	0.116	0.108	0.114	0.207	8
*Ots_Ots2**		2	0.258	0.077	0.199	0.132	0.139	0.131	0.179	9
*Ots_P450**		2	0.308	−0.008	0.230	0.236	0.242	0.229	0.337	9
*Ots_P53**		2	0.469	0.035	0.083	0.050	0.049	0.053	0.103	9
*Ots_PSMB1-197**		2	0.001	0.001	0.001	0.000	0.000	0.005	0.005	Table 1
*Ots_Prl2**		2	0.453	−0.021	0.074	0.093	0.116	0.092	0.174	9
*Ots_ins-115**		2	0.03	−0.038	−0.013	0.024	0.026	0.028	0.029	8
*Ots_RFC2-558**		2	0.143	0.035	0.301	0.276	0.271	0.267	0.314	8
*Ots_SClkF2R2-135**		2	0.431	0.015	0.148	0.135	0.144	0.132	0.239	8
*Ots_SERPC1-209**		2	0.133	0.169	0.222	0.064	0.074	0.066	0.077	Table 1
*Ots_SL**		2	0.336	−0.016	0.272	0.284	0.284	0.275	0.423	9
*Ots_Tnsf**		2	0.265	−0.007	0.343	0.347	0.362	0.336	0.465	9
*Ots_u202-161**		2	0.209	0.031	0.311	0.289	0.279	0.280	0.358	8
*Ots_u211-85**		2	0.177	0.004	0.403	0.401	0.376	0.389	0.478	8
*Ots_U212-158**		2	0.114	−0.027	0.032	0.057	0.055	0.059	0.067	8
*Ots_u4-92**		2	0.131	−0.085	−0.037	0.044	0.047	0.047	0.055	8
*Ots_u6-75**		2	0.251	0.030	0.100	0.072	0.074	0.073	0.100	8

[a] Sources for running conditions and oligonucleotide sequences are as follows: (1) Aebersold et al. (1987); (2) Scribner et al. (1996); (3) Banks et al. (1999); (4) Olsen et al. (2000); (5) Nelson and Beacham (1999); (6) Estoup et al. (1993); (7) Nelson et al. (1998); (8) Smith et al. (2005a); (9) Smith et al. (2005b); and (10) Linda Park, National Oceanic and Atmospheric Administration, Northwest Fisheries Science Center, personal communication.

[b] Number of unique haplotypes predicted by the Excoffier–Leval–Balding algorithm method (Excoffier et al. 2003). This number accounts for the blank cells below it.

Appendix 2: Genetic differentiation of Alaska Chinook salmon: the missing link for migratory studies

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SNP GENOTYPING AND APPLICATIONS

Genetic differentiation of Alaska Chinook salmon: the missing link for migratory studies

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Abstract

Most information about Chinook salmon genetic diversity and life history originates from studies from the West Coast USA, western Canada and southeast Alaska; less is known about Chinook salmon from western and southcentral Alaska drainages. Populations in this large area are genetically distinct from populations to the south and represent an evolutionary legacy of unique genetic, phenotypic and life history diversity. More genetic information is necessary to advance mixed stock analysis applications for studies involving these populations. We assembled a comprehensive, open-access baseline of 45 single nucleotide polymorphisms (SNPs) from 172 populations ranging from Russia to California. We compare SNP data from representative populations throughout the range with particular emphasis on western and southcentral Alaska. We grouped populations into major lineages based upon genetic and geographic characteristics, evaluated the resolution for identifying the composition of admixtures and performed mixed stock analysis on Chinook salmon caught incidentally in the walleye pollock fishery in the Bering Sea. SNP data reveal complex genetic structure within Alaska and can be used in applications to address not only regional issues, but also migration pathways, bycatch studies on the high seas, and potential changes in the range of the species in response to climate change.

Keywords: Alaska, population structure, *Oncorhynchus tshawytscha*, Chinook salmon, mixed stock analysis, SNP

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Introduction

Chinook salmon *Oncorhynchus tshawytscha* are the largest of the Pacific salmon (*Oncorhynchus* spp.), sometimes attaining a weight of 45 kg. Chinook salmon inhabit coastal river drainages ranging broadly across the Pacific Rim from the Kamchatka Peninsula, through the Bering Sea, to central North America (Healey 1991). With their large size comes charisma: they are highly prized in both sport and commercial fisheries and are an important subsistence and ceremonial fish for native fishers.

Chinook salmon are anadromous and semelparous and exhibit a high degree of life history variation (Healey 1991; Waples *et al.* 2004). Much of the information about life history originates from studies of populations from the West Coast USA, western Canada and southeast Alaska; many of these studies investigate freshwater life history and the genetic diversity associated with it. There are two major life history types that have been defined by the amount of time spent in freshwater before moving to marine environments. Subyearling (or ocean-type) Chinook salmon migrate to saltwater during the first year after hatching, while yearling (or stream-type) reside in freshwater for at least 1 year. Differences among populations have also been observed in marine migration patterns, timing of return to freshwater to spawn and timing of spawning (Halupka *et al.* 2003; Quinn 2005). The rich genetic diversity associated with life history divergence in populations from the West Coast USA and western Canada has been extensively documented over the last three decades (e.g. Utter *et al.* 1989; Teel *et al.* 2000; Seeb *et al.* 2007).

Less is known of the diversity and life history of Chinook salmon from western and southcentral Alaska drainages than for those more southern populations (reviewed in Utter *et al.* 2009). However, Gharrett *et al.* (1987), based upon allozyme data, observed that western Alaska populations were closely related to one another but discrete from populations to the south. Waples *et al.*

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(2009) points out that the Chinook salmon from western Alaska represent an evolutionary legacy composed of unique genetic, phenotypic and life history diversity. For example, the 3000-km migration of Chinook salmon up the Yukon River to spawn in Canadian headwaters is the longest of any freshwater migration of Pacific salmon (Evenson *et al.* 2009). Myers *et al.* (2009) review results from scale pattern analyses to show that western Alaska stocks are a dominant component of cohorts migrating in the eastern Bering Sea, although they also report strong seasonal differences in their spatial distribution.

Of recent importance both to management and conservation is the increasing harvest of western Alaska Chinook salmon, as well as Chinook salmon from throughout the range, as bycatch (not the targeted species) in the Bering Sea Aleutian Island (BSAI) fishery for walleye pollock *Theragra chalcogramma* (Stram & Ianelli 2009). The BSAI pollock fishery, the largest and most lucrative fishery in North America (Morell 2009), intercepts a mix of populations of Chinook salmon and up to 60% of this bycatch has been found to originate from western Alaska (Myers & Rogers 1988; Myers *et al.* 2009). During the last decade, a dramatic increase in Chinook salmon bycatch occurred, with a peak catch of 121 909 fish in 2007 (Fig. 1), igniting social and economic conflict between the pollock fleet and the subsistence and cultural stakeholders in western Alaska (Gisclair 2009). This increase occurred at a time of consecutive years of low Chinook salmon returns to the Yukon River. These low returns resulted in a disaster declaration by the USA Department of Commerce in 2010 (http://www.commerce.gov/news/press-releases/2010/01/15/commerce-secretary-gary-locke-announces-fishery-failure-determination). Research to accurately estimate the origin of the catch and its effect on various regions and conservation units is needed.

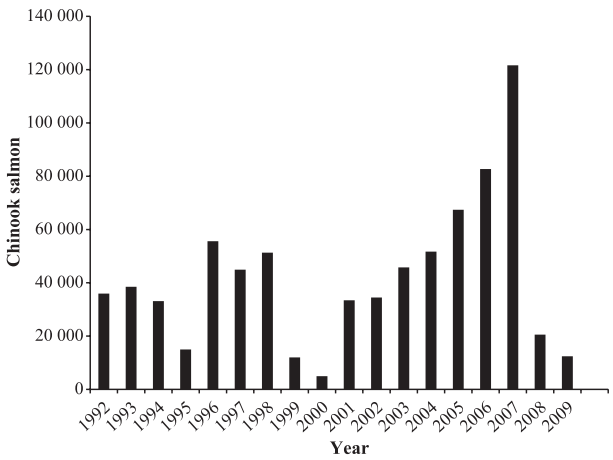

Fig. 1 Chinook salmon mortality in Bering Sea Aleutian Island pollock directed fisheries, 1992–2009 (Source: http://www.alaskafisheries.noaa.gov/sustainablefisheries/inseason/chinook_salmon_mortality.pdf).

Comprehensive genetic data have been integral to defining population structure and studying high-seas migration of chum *Oncorhynchus keta* and sockeye salmon *Oncorhynchus nerka* in this region (Seeb *et al.* 2004, 2011b; Habicht *et al.* 2010), but studies on Chinook salmon are limited. Existing studies in this region typically focus only on a single drainage (e.g. Smith *et al.* 2005a; Templin *et al.* 2005; Beacham *et al.* 2008). Beacham *et al.* (2006), in an analysis of the population structure of Chinook salmon around the Pacific Rim, include no populations in the range between the Yukon River and southeast Alaska. Efforts to standardize such data among drainages and among laboratories into a comprehensive data set have faced numerous challenges (Seeb *et al.* 2007). There is a critical need for a standard data set for the entire range of Chinook salmon to enable mixed stock analyses to investigate stock-specific distribution and harvest on the high seas.

Such a data set that includes a focus on the diversity of populations from western and central Alaska would also have substantial value for identifying the composition of harvests in other fisheries. Freshwater fisheries in the Yukon River and near-shore fisheries throughout southeast Alaska harvest mixtures of populations originating both from the USA and Canada; these fisheries are regulated by provisions of the Pacific Salmon Treaty (Noakes *et al.* 2005) where DNA data may provide important insight into nation of origin. Allocation conflicts also occur between commercial stakeholders, fishing in salt water and subsistence or sportfishing stakeholders, who fish in freshwater as salmon migrate upriver to spawn (e.g. Hamazaki 2008). In addition, the data set will foster research on juvenile migration in the Bering Sea and Pacific Ocean (e.g. Murphy *et al.* 2009) through the North Pacific Anadromous Fish Commission.

Single nucleotide polymorphisms (SNPs) have become the DNA marker of choice for studies on population structure and applications to fishery management because of their many advantages (reviewed in Vignal *et al.* 2002; Morin *et al.* 2004). SNPs are ideal for developing shared data sets because unambiguous scoring circumvents many of the errors and challenges associated with standardization of fragment-based markers such as microsatellites (contrast Stephenson *et al.* 2009). The transparency and transportability of SNP data as well as the ability to resolve both broad- and fine-scale population structure for Chinook salmon have been well documented (Smith *et al.* 2005a, 2007; Narum *et al.* 2008).

Here, we present a comprehensive and open-access data set based on 45 SNPs that includes 172 populations ranging from Kamchatka Peninsula to the Sacramento

River. We include data from representative populations throughout the species range with particular emphasis on those originating from western and central Alaska and western Canada. We assembled the populations into major lineages based upon genetic and geographic characteristics, and we further evaluated mixed stock analysis resolution for identifying these lineages in admixtures by testing *ad hoc* compositions that might occur in the Bering Sea bycatch or in nearshore fisheries in the Bering Sea or northern Gulf of Alaska. Finally, we perform mixed stock analysis on scale samples from Chinook salmon caught incidentally in the walleye pollock fishery in the Bering Sea. This data set provides immediate opportunities for Bering Sea bycatch and other fisheries applications as well as providing a basis for growth as laboratories working on Pacific Salmon Treaty and North Pacific Anadromous Fish Commission activities add data from additional loci and populations.

Methods

Tissue collections

Tissue samples for this analysis were collected from adult Chinook salmon spawning populations (Appendix I; Fig. 2). These populations provide comprehensive representation of known spawning locations within the State of Alaska and broad representation of major genetic groups from the rest of the range. Samples from some populations used in this baseline were included in other studies that were restricted to regions (e.g. southeast Alaska – Guthrie & Wilmot 2004; Yukon River – Smith *et al.* 2005b; Templin *et al.* 2005; Beacham *et al.* 2008; Copper River – Seeb *et al.* 2009b; southeast Alaska to California – Seeb *et al.* 2007; Narum *et al.* 2008). Target sample size for populations was 100 individuals across all years to achieve acceptable precision for the allele frequency

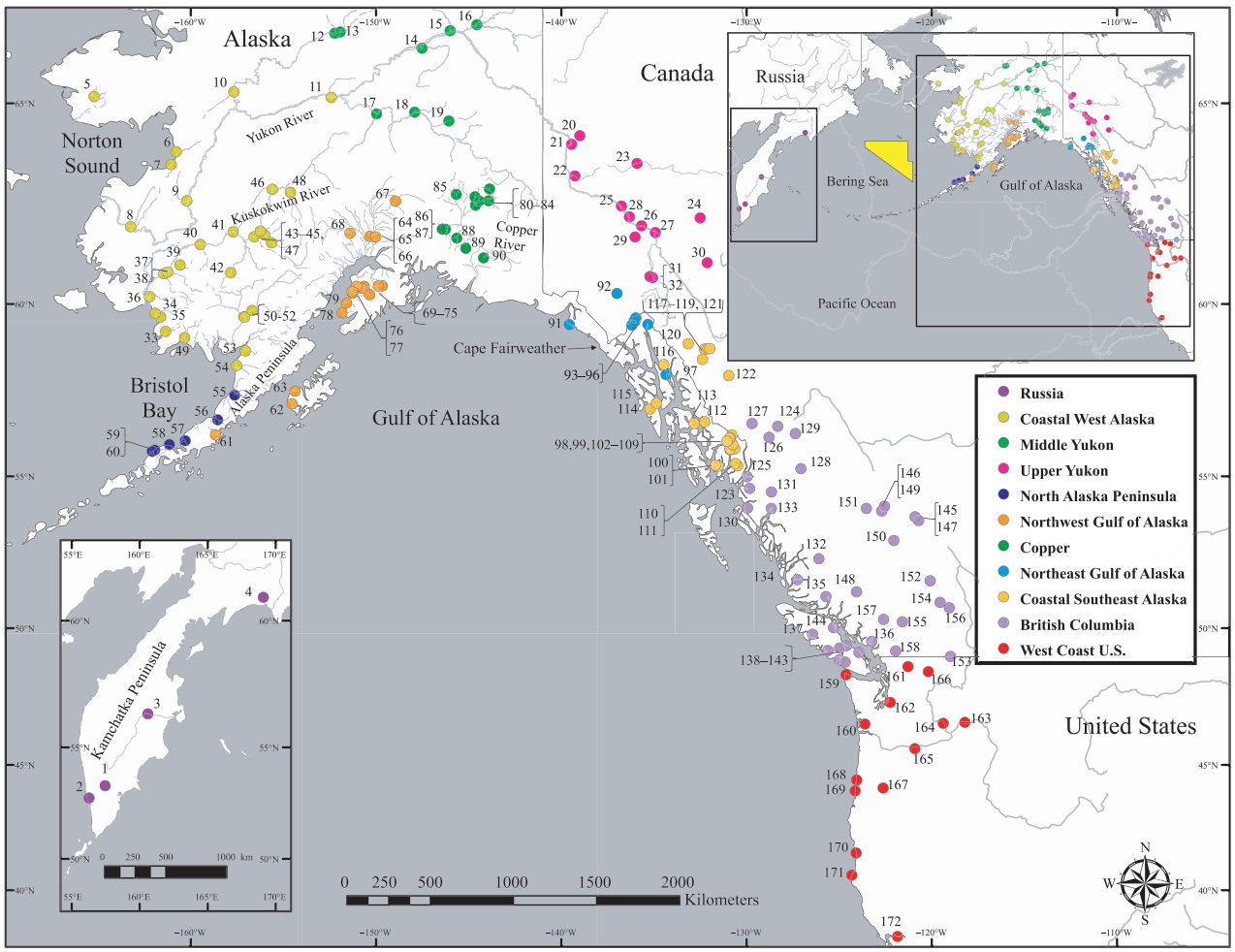

Fig. 2 Collection locations for populations of Chinook salmon represented in the rangewide baseline. Numbers on the map are identical to the population numbers listed in Appendix I. The location of the bycatch samples from the Bering Sea pollock fishery is indicated by the yellow polygon in the inset.

estimates (Allendorf & Phelps 1981; Waples 1990). Tissue samples collected prior to 2003 were obtained for allozyme analysis and contained heart, muscle, liver and eye. These samples were maintained at −80 °C in the Gene Conservation Laboratory archive at the Alaska Department of Fish and Game. Tissue samples collected from 2003 onward were generally axillary processes or fins preserved in ethanol. Samples were also available from fishery harvests. Samples from Chinook salmon harvested as bycatch in the Bering Sea pollock fishery were dried scales.

Laboratory analysis

Genomic DNA was extracted using a DNeasy® 96 Tissue kit by QIAGEN® (Valencia, CA, USA). Genetic data were collected from the samples as individual multilocus genotypes for the 45 loci that were assayed (one mitochondrial and 44 nuclear; Table 1).

Chinook salmon samples were genotyped using Taqman assays (Applied Biosystems, Foster City, CA, USA) in one of two processes following the methods described in Smith *et al.* (2005a) and Seeb *et al.* (2009a). The first process was performed as uniplex reactions in 384-well reaction plates. The plates were read on an Applied Biosystems (AB) Prism 7900HT Sequence Detection System after amplification and genotypes were determined (scored) using AB Sequence Detection software 2.2. The second process involved multiple parallel reactions using BioMark 48.48 Dynamic Arrays (Fluidigm http://www.fluidigm.com/biomark_genotyping.htm). The Dynamic Arrays were read on a BioMark Real-Time PCR System after amplification and scored using BioMark Genotyping Analysis software (Fluidigm).

Variation within populations

Genotype distributions were tested for deviation from Hardy–Weinberg (H–W) expectation using exact tests in GDA (Lewis & Zaykin 2001). Critical values were adjusted for multiple tests across markers within populations ($\alpha = 0.05$/number of loci) and multiple tests across populations within markers ($\alpha = 0.05$/number of populations) using the sequential Bonferroni adjusted values (Rice 1989).

All pairs of markers were tested for gametic disequilibrium within each population using exact tests in GDA. We defined a pair of markers to be significantly out of gametic equilibrium if tests for gametic disequilibrium were significant ($P < 0.01$) for greater than half of all collections. In this case, the locus of the pair with the most complete genotypes was retained and the other was dropped from the analysis.

Collections taken at the same spawning locations in different years were pooled following the recommendations of Waples (1990). The variation because of temporal sampling relative to the variation between populations was measured and tested for significance using the hierarchical ANOVA method implemented in the program GDA, where the variance component, σ_S, is associated with differences among collections within populations and the variance component, σ_P, is associated with differences among populations. This analysis only included the populations for which multiple samples of sufficient size ($N \geq 20$) were available.

Observed and expected heterozygosities and allelic richness were calculated for each population and each nuclear locus using FSTAT v2.9.3.2 (Goudet 1995, 2001). Genetic diversity as measured by F_{ST} (Cockerham & Weir 1993) was calculated for every locus and over all loci using the program GDA which allows the inclusion of mtDNA SNPs. Multilocus estimates were calculated following the method of Roussett (2007) where additional weight is given to loci with larger sample sizes.

Variation among populations

To infer genetic relationships between sample locations, we used two separate methods. First, genetic differentiation between each pair of populations was measured using F_{ST} (Cockerham & Weir 1993) calculated across all loci using the HIERFSTAT package (Goudet 1995) in the R statistical software environment (R Foundation for Statistical Computing, Vienna, Austria, http://www.R-project.org). The mtDNA SNP, *Ots_C3N3*, was included as haploid data in this analysis. F_{ST} values were used to construct a neighbour-joining tree, and support for each node was determined from 1000 bootstrap replicates sampled over loci. The second method used the spatial clustering of populations method in the software BAPS (http://www.rni.helsinki.fi/~mjs, Corander *et al.* 2008) to find the optimum partitioning of the data set. Latitude and longitude for each population were included as prior information. Populations were maintained as the unit of analysis for the spatial clustering, and the entire analysis was repeated 20 times to confirm the results. Nei's unbiased distances (Nei 1972) were calculated between clusters and a neighbour-joining tree was drawn.

Populations were organized hierarchically into both fine- and broad-scale regions based on genetic clustering from the previous analyses, geography and management needs. When grouping populations for management and research, genetic population structure is only one of several factors to be considered. Populations are also grouped by geographic features (e.g. peninsulas, embayments, river systems and/or sections of coastline), behaviour (e.g. time of migration or spawning), management structure and stakeholder interests. Fine-scale regions had a minimum of two populations. Because of lack of

Table 1 Single nucleotide polymorphisms surveyed in populations from across the range of Chinook salmon and used in the coastwide genetic baseline. The locus-specific ranges of frequencies of the most common allele, mean expected (H_E) and observed (H_O) heterozygosities, allelic richness and genetic diversity (F_{ST}) values are given. *Ots_C3N3* is a SNP in the mitochondrial DNA

Assay name	Source*	Range of common allele	Heterozygosity		Allelic richness	F_{ST}
			Observed (H_o)	Expected (H_s)		
Ots_GTH2B-550	a	0.000–0.916	0.399	0.393	1.985	0.172
Ots_NOD1	a	0.170–1.000	0.377	0.375	1.978	0.208
Ots_E2-275	b	0.005–0.997	0.385	0.385	1.991	0.152
Ots_arf-188	b	0.845–1.000	0.012	0.013	1.141	0.082
Ots_AsnRS-60	b	0.260–0.979	0.406	0.407	1.999	0.065
Ots_C3N3	e	0.000–1.000	–	–	–	0.564
Ots_ETIF1A	c	0.005–0.894	0.399	0.413	1.995	0.142
Ots_FARSLA-220	d	0.000–1.000	0.243	0.243	1.812	0.389
Ots_FGF6A	a	0.000–0.995	0.375	0.376	1.981	0.231
Ots_FGF6B†	a	0.293–1.000	0.329	0.327	1.984	0.068
Ots_GH2	e	0.220–1.000	0.262	0.265	1.861	0.193
Ots_GPDH-338	b	0.381–1.000	0.166	0.165	1.793	0.198
Ots_GPH-318	d	0.569–1.000	0.211	0.217	1.938	0.067
Ots_GST-207	d	0.117–1.000	0.179	0.178	1.839	0.284
Ots_GST-375	d	0.261–1.000	0.036	0.037	1.252	0.167
Ots_HGFA-446	b	0.661–1.000	0.010	0.010	1.119	0.133
Ots_hnRNPL-533	d	0.010–1.000	0.352	0.360	1.990	0.227
Ots_HSP90B-100	d	0.008–1.000	0.319	0.323	1.964	0.295
Ots_HSP90B-385†	d	0.373–1.000	0.192	0.192	1.795	0.159
Ots_IGF-I.1-76	b	0.235–1.000	0.350	0.346	1.865	0.176
Ots_Ikaros-250	b	0.750–1.000	0.092	0.092	1.526	0.083
Ots_il-1racp-166	b	0.014–1.000	0.422	0.388	1.990	0.079
Ots_LEI-292	d	0.817–1.000	0.044	0.045	1.475	0.039
Ots_MHC1	e	0.055–0.979	0.443	0.436	1.999	0.100
Ots_MHC2	e	0.000–1.000	0.188	0.191	1.802	0.417
Ots_ZNF330-181	b	0.849–1.000	0.020	0.019	1.269	0.044
Ots_LWSop-638	b	0.598–1.000	0.086	0.088	1.696	0.081
Ots_SWS1op-182	b	0.156–1.000	0.427	0.420	1.985	0.102
Ots_P450	e	0.004–0.995	0.349	0.348	1.980	0.249
Ots_Prl2	e	0.091–0.961	0.435	0.440	2.000	0.107
Ots_ins-115	b	0.831–1.000	0.036	0.036	1.435	0.048
Ots_RFC2-558	b	0.121–1.000	0.156	0.159	1.462	0.370
Ots_SClkF2R2-135	b	0.070–0.899	0.441	0.445	2.000	0.108
Ots_SERPC1-209	d	0.681–1.000	0.098	0.104	1.677	0.076
Ots_SL	e	0.000–0.984	0.385	0.381	1.977	0.170
Ots_TAPBP	c	0.206–1.000	0.194	0.196	1.859	0.128
Ots_Tnsf	e	0.000–1.000	0.310	0.314	1.966	0.240
Ots_u202-161	b	0.000–1.000	0.225	0.227	1.786	0.333
Ots_u211-85	b	0.000–1.000	0.175	0.177	1.704	0.434
Ots_U212-158	b	0.468–1.000	0.124	0.121	1.823	0.054
Ots_u4-92	b	0.275–1.000	0.137	0.138	1.772	0.131
Ots_u6-75	b	0.540–1.000	0.227	0.229	1.930	0.086
Ots_Zp3b-215	b	0.694–1.000	0.075	0.076	1.410	0.127
Ots_RAG3	a	0.069–1.000	0.235	0.240	1.809	0.380
Ots_S71	a	0.134–0.976	0.361	0.366	1.997	0.197
Overall			0.242	0.242		0.204

*Marker sources: a) Northwest Fisheries Science Center-NOAA (Unpublished); b) Smith *et al*. 2005a; c) Washington State University Vancouver (Unpublished); d) Smith *et al*. 2007; e) Smith *et al*. 2005b.

†These loci were removed from the analysis because they were in linkage disequilibrium with another locus.

adequate coverage, no fine-scale regions were constructed for the West Coast U.S. populations.

To measure how well the hierarchical structure fit the rangewide population structure of Chinook salmon, the genetic variation within and among these broad- and fine-scale regional groups was calculated using the hierarchical ANOVA method implemented in the program GDA. The ANOVA method in GDA was used to allow the joint analysis of nuclear and mitochondrial SNPs. Regional measures of allelic richness (A_r) were calculated using FSTAT and regional F_{ST} estimates were calculated with GDA to provide region-specific information. As a result of the potential biases in these measures owing to under-representation, the West Coast U.S. populations were excluded from these analyses.

Mixed stock analysis

The usefulness of the baseline and the regional structure for mixed stock analysis applications was examined with a series of proof tests in which individual Chinook salmon genotypes were sampled without replacement from the baseline to create mixtures of known composition. The first proof tests involved analysing mixtures comprised entirely of individual genotypes sampled without replacement from a single region using the reduced baseline (100% proof tests). Sample sizes were 200 individuals for broad-scale regions and 100 individuals for fine-scale regions. Proof tests were not performed on fine-scale regions if fewer than 200 individual genotypes would remain in the baseline after sampling. For broad-scale regions with fewer than 350 individuals, the sample size drawn for the proof test mixture was reduced to 100. A region was considered identifiable if 90% or more of the simulated mixture was correctly identified to region of origin.

The second set of proof tests involved estimating the composition of three mixtures of 200 genotypes sampled without replacement from different regions in the baseline. The relative proportions of the mixtures were set to reflect potential regional proportions that might be observed in samples of migrating fish taken from the Bering Sea and the Gulf of Alaska.

These tests provide a conservative evaluation of the accuracy and precision of the mixed stock analysis because a reduced baseline is used and individuals of known origin form the mixture. Proof tests were run using the Bayesian mixed stock analysis method implemented in BAYES (Pella & Masuda 2001) using three chains of 15 000 iterations beginning with different starting conditions. The posterior distribution was formed by combining the last 7500 steps of each chain, the mean was reported as the best estimate and the central 90% of the distribution was reported as the credibility interval. An uninformative prior was used based on the Dirichlet distribution in which stock proportions for regions were equal, and then the proportions were divided by the number of populations in each region to define the population parameters.

As an additional test, stock compositions were estimated for three sets of Chinook salmon captured in areas where the composition could be assumed to come from specific reporting regions. Genotype data were available for individuals captured in test fisheries in the Yukon and Kuskokwim rivers in western Alaska, and at fish wheels in the Copper River in southcentral Alaska (Seeb *et al.* 2009b). Stock compositions for each fishery sample were estimated with BAYES using the conditions previously described. Capture locations were well within the rivers, so all fish captured in the sample were expected to have originated within the particular drainage. This was the most challenging test of the method because error can be introduced by fish in the mixture originating from unrepresented populations in the baseline.

The utility of this baseline for mixed stock analysis in the Bering Sea was demonstrated by estimating the stock composition of a sample of 272 Chinook salmon harvested as bycatch in the 2005 pollock fishery in the Bering Sea. These samples were scales collected from a portion of the bycatch in North Pacific Fishery Management Council management area 521 (Fig. 2) as part of age, sex and length sampling by onboard observers between June and September, 2005. While these samples represent a potential mixture of populations in the Bering Sea, they were not collected under a designed sampling plan and thus may not represent the true proportions of the bycatch in this area.

Results

Tissue collections

A total of 23 269 fish from 288 collections representing 172 populations were analysed for the baseline. Samples available from throughout the species range were collected over a period of 21 years (Table 2; Appendix I; Fig. 2). While most populations were sampled in a single year, 84 populations were sampled in multiple years, and most were collected relatively recently (21 in the 1980s, 99 in the 1990s and 168 after 2000). The number of individual samples available from each population was generally quite large with only four populations represented by 50 or fewer individuals and more than 100 populations had more than 100 individuals.

Variation within populations

Of the 45 SNPs assayed across the range of Chinook salmon, 34 had a range of alternate allele frequencies >0.5,

Table 2 Summary statistics for the 11 broad-scale regions (bold type) and the 44 fine-scale regions identified in the Chinook salmon baseline. Map numbers refer to populations in Fig. 2 and Appendix I. Measures of genetic diversity within each region are mean allelic richness (A_r) and F_{ST}. The mean correct allocation to region (Est) and 90% credibility index from the proof tests are provided

Reporting region		Number of populations	Map numbers	Mean sample size (Range)	A_r	F_{ST}	Proof test	
Broad	Fine						Est	90% CI
Russia		**4**			**1.789**	**0.110**	**0.99**	**(0.97–1.00)**
	Okhotsk Sea Coast	2	1–2	86 (77–94)	1.778	0.005	–	–
	Bering Sea Coast	2	3–4	85 (50–119)	1.710	0.230	–	–
Coastal West Alaska		**27**			**1.788**	**0.013**	**0.99**	**(0.97–1.00)**
	Norton Sound	3	5–7	89 (72–112)	1.867	0.023	0.14	(0.00–0.39)
	Lower Yukon	4	8–11	202 (95–290)	1.796	0.017	0.94	(0.71–1.00)
	Kuskokwim Bay	3	33–35	253 (147–368)	1.848	0.003	0.90	(0.61–0.99)
	Lower Kuskokwim	11	36–46	166 (93–252)	1.833	0.004	0.64	(0.34–0.99)
	Upper Kuskokwim	2	47–48	143 (96–191)	1.806	0.047	0.80	(0.68–0.91)
	West Bristol Bay	4	49–52	100 (57–159)	1.852	0.003	0.13	(0.00–0.45)
	East Bristol Bay	2	53–54	88 (66–110)	1.819	0.002*	–	–
Middle Yukon		**8**			**1.750**	**0.026**	**0.98**	**(0.92–1.00)**
	Upper U.S. Yukon	5	12–16	106 (51–175)	1.728	0.028	0.98	(0.94–1.00)
	Tanana	3	17–19	189 (187–193)	1.716	0.015	0.99	(0.96–1.00)
Upper Yukon		**13**			**1.806**	**0.043**	**0.99**	**(0.98–1.00)**
	Canada Border	2	20–21	164 (79–249)	1.710	0.001*	0.97	(0.92–1.00)
	Pelly River	4	22–25	142 (99–197)	1.761	0.006	0.95	(0.88–1.00)
	Carmacks	5	26–30	99 (55–169)	1.717	0.019	0.99	(0.95–1.00)
	Takhini	2	31–32	202 (161–242)	1.751	0.040	0.99	(0.96–1.00)
North Alaska Peninsula		**6**			**1.761**	**0.026**	**0.99**	**(0.97–1.00)**
	Port Heiden	2	55–56	87 (42–131)	1.798	0.021	–	–
	Port Moller	4	57–60	77 (51–95)	1.767	0.027	0.71	(0.60–0.82)
Northwest Gulf of Alaska		**19**			**1.787**	**0.051**	**0.99**	**(0.96–1.00)**
	Chignik/Kodiak	3	61–63	117 (75–140)	1.741	0.079	0.98	(0.95–1.00)
	Susitna River	5	64–68	100 (52–251)	1.783	0.028	0.97	(0.89–1.00)
	Kenai Early	5	69–73	190 (95–266)	1.792	0.026	0.94	(0.76 –1.00)
	Kenai Late	2	74–75	211 (119–302)	1.826	0.031	0.67	(0.52 –0.83)
	Kasilof River†	2	76–77	314 (306–321)	1.813	0.030	0.97	(0.91 –1.00)
	Lower Kenai Peninsula	2	78–79	181 (162–200)	1.790	0.004	0.98	(0.94 –1.00)
Copper		**11**			**1.677**	**0.069**	**0.99**	**(0.98 –1.00)**
	Upper Copper River	5	80–84	109 (50–157)	1.604	0.026	0.98	(0.94 –1.00)
	Middle Copper	2	85–86	178 (144–211)	1.710	0.023	0.98	(0.95 –1.00)
	Lower Copper	4	87–90	70 (62–75)	1.752	0.020	0.99	(0.96 –1.00)
Northeast Gulf of Alaska		**7**			**1.797**	**0.111**	**0.99**	**(0.96–1.00)**
	Cape Fairweather	2	91–92	159 (143–174)	1.776	0.034	0.97	(0.92 –1.00)
	Northern Southeast Alaska†	5	93–97	134 (83–178)	1.806	0.096	0.99	(0.96 –1.00)
Coastal Southeast Alaska		**25**			**1.866**	**0.036**	**0.97**	**(0.92–1.00)**
	Chickamin River†	6	98–103	141 (56–331)	1.841	0.027	0.97	(0.87 –1.00)
	Unuk River†	6	104–109	142 (94–397)	1.887	0.009	0.95	(0.88 –0.99)
	Behm Canal	2	110–111	120 (95–144)	1.874	0.000*	0.98	(0.94 –1.00)
	Andrew Creek†	5	112–116	214 (94–397)	1.885	0.002	0.98	(0.92 –1.00)
	Transboundary Rivers	6	117–122	122 (86–143)	1.851	0.005	0.98	(0.95 –1.00)
British Columbia		**36**			**1.777**	**0.188**	**0.95**	**(0.87–1.00)**
	North Coast BC	5	123–127	86 (65–115)	1.798	0.091	0.98	(0.94 –1.00)
	Skeena	4	128–131	112 (86–142)	1.786	0.124	0.98	(0.95 –1.00)
	Central BC Coast	3	132–134	143 (141–144)	1.784	0.077	0.98	(0.93 –1.00)
	South BC Mainland	2	135–136	119 (83–154)	1.778	0.117	0.99	(0.96 –1.00)
	West Vancouver Island	5	137–141	125 (104–160)	1.748	0.128	0.99	(0.97 –1.00)
	East Vancouver Island	3	142–144	121 (93–144)	1.737	0.075	0.99	(0.96 –1.00)
	Upper Fraser	3	145–147	118 (94–154)	1.808	0.078	0.90	(0.81 –0.99)
	Middle Fraser	4	148–151	168 (120–246)	1.835	0.034	0.99	(0.96 –1.00)

Table 2 (Continued)

Reporting region		Number of populations	Map numbers	Mean sample size (Range)	A_r	F_{ST}	Proof test	
Broad	Fine						Est	90% CI
	North Thompson	2	152–153	166 (153–179)	1.785	0.144	0.99	(0.97 –1.00)
	South Thompson	3	154–156	97 (46–144)	1.783	0.087	0.98	(0.94 –1.00)
	Lower Fraser	2	157–158	95 (93–96)	1.666	0.200	–	–
West Coast U.S.		**14**	**159–172**	**111 (52–191)**	**1.681**	**0.227**	**1.00**	**(0.99 –1.00)**

*These F_{ST} estimates were not significantly different from 0.0.
†Some of these populations are broodstocks in remote hatcheries.

and six loci had ranges of 1.0, which means that alternate alleles were fixed in at least one population (Table 1; Table S1, Supporting Information). Mean allelic richness across populations ranged from near 1.0 indicating very low levels of variation (1.119 at *Ots_HGFA-446*) to 2.0 (*Ots_Prl2* and *Ots_SClkF2R2-135*) indicating that both alleles were present in all populations. Observed heterozygosities among SNP loci ranged widely from 0.010 (*Ots_HGFA-446*) to 0.443 (*Ots_MHC1*). Observed heterozygosity was similar to expected heterozygosity at nuclear markers with both averaging 0.243 (Table 1). The estimated F_{ST} over all loci was 0.204 across the range, but a few loci had considerably higher values. Three loci had F_{ST} estimates >0.400 (*Ots_C3N3*, *Ots_MHC2* and *Ots_u211-85*) and three others were >0.300 (*Ots_FARSLA-220*, *Ots_RFC2-558* and *Ots_u202-161*). Only three loci had F_{ST} values <0.050: *Ots_ins-115* (0.048), *Ots_ZNF330-181* (0.044) and *Ots_LEI-292* (0.039).

After adjusting for the number of tests across loci, most populations showed no significant departures from H–W equilibrium; only Middle Shuswap summer run (no. 156; three loci) showed more than two loci out of equilibrium. When checking H–W equilibrium across populations within nuclear loci, only one locus showed more than two populations out of equilibrium: *Ots_il-1racp*-166 (six populations). Significant gametic disequilibrium was found within two pairs of nuclear SNP markers in more than half of the 167 populations: *Ots_FGF6A* and *Ots_FGF6B* (126 populations) and *Ots_HSP90B-100* and *Ots_HSP90B-385* (108 populations). From these pairs, *Ots_FGF6B* and *Ots_HSP90B-385* were removed leaving a total of 42 nuclear SNPs for the remaining analyses.

There were 165 collections from 72 populations available for testing temporal variation within populations after excluding collections of fewer than 20 individuals (Appendix I). The variance component among collections within populations, σ_S, was 0.028 (95% CI: 0.021, 0.035), and the variance component for differences between populations, σ_P, was 2.110 (95% CI: 1.623, 2.562).

Variation among populations

Genetic relationships between populations as measured by pairwise F_{ST} showed a strong geographic component to the population structure visible in the neighbour-joining tree (Fig. 3). At the largest scale, populations were organized into two groups on the tree: a western group with populations from Russia to Cape Fairweather and an eastern group with populations from Northern Southeast Alaska south to California. The node that separates these groups appeared in 57% of the bootstrap trees based on F_{ST}. Branch length in the western group is generally shorter than in the eastern group indicating that differences between populations are smaller in this part of the range. The western group is further split into two main branches, populations in the Middle and Upper Yukon River (populations no. 12–32) and populations from the Alaska Peninsula to Cape Fairweather (populations no. 55–92). These groups are separated by populations from the West Coast of Alaska (populations no. 5–11, 33–54) where only low levels of structure are present. In general, populations group with geographically proximate populations by watersheds and sections of coastline.

The spatial clustering in BAPS partitioned the baseline into 87 population clusters, including 55 single-population clusters (Fig. 4). The general pattern of population structure produced by this method was similar to that produced by the F_{ST} method. This method did not support complete partitioning of some groups of populations into local spawning populations (e.g. populations no. 8–10 from the Lower Yukon River), even when populations were separated by large geographic distances (e.g. populations no. 5, 33 and 49 from Norton Sound, Kuskokwim Bay and West Bristol Bay, respectively). The largest cluster included 19 populations from the West Coast of Alaska (Norton Sound no. 6, Kuskokwim River no. 34–46 and Bristol Bay no. 50–54).

Populations were organized into 11 broad-scale and 44 fine-scale regions (Table 2; Appendix I) based on the

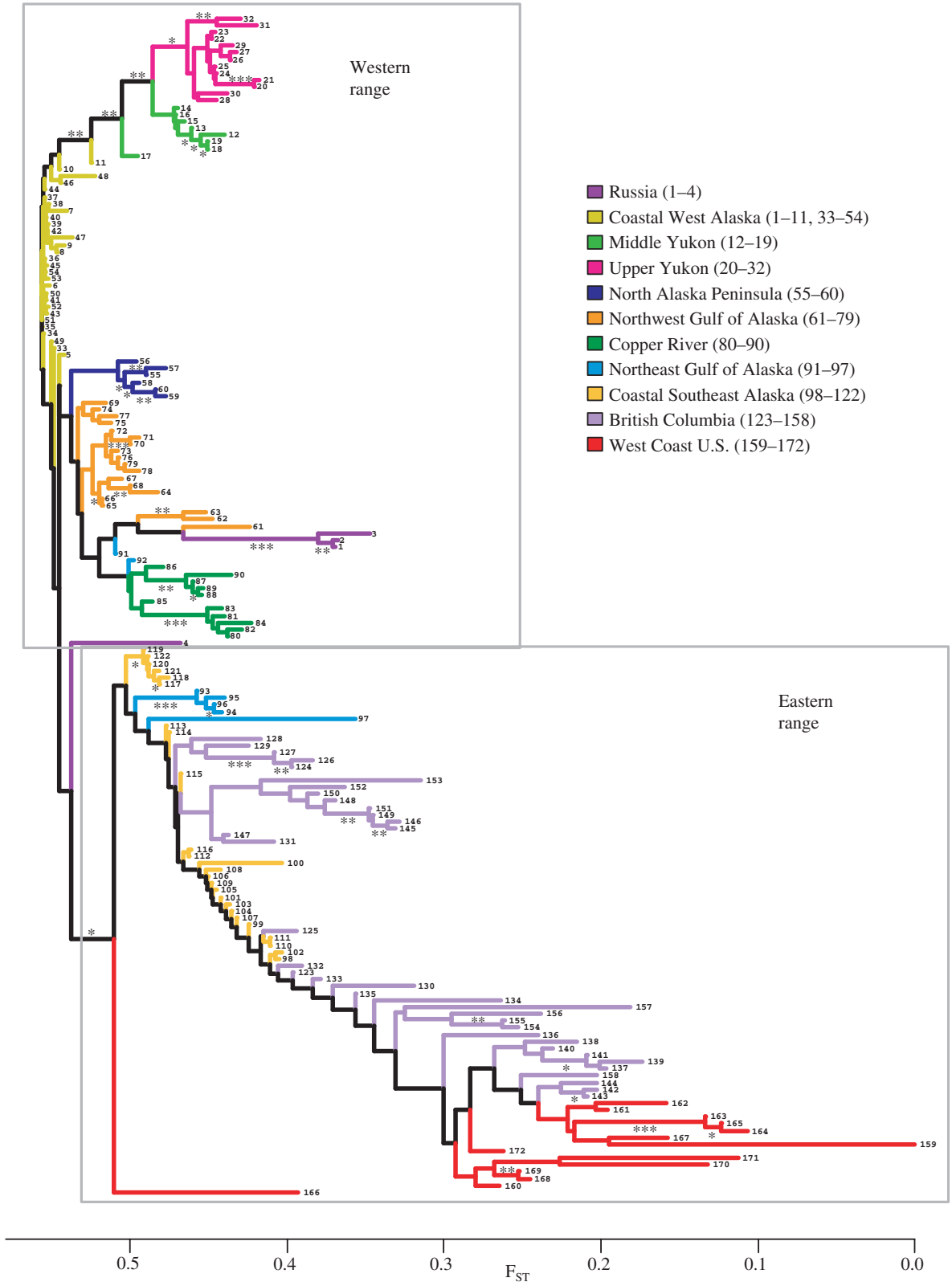

Fig. 3 Neighbour-joining tree based on pairwise F_{ST} between populations of Chinook salmon in the rangewide baseline. Three levels of bootstrap support for a node are indicated 50–70% (*), 70–95% (**) and over 95% (***). Colours indicate the broad-scale regional groups presented in Fig. 2 and numbers indicate populations in Appendix I.

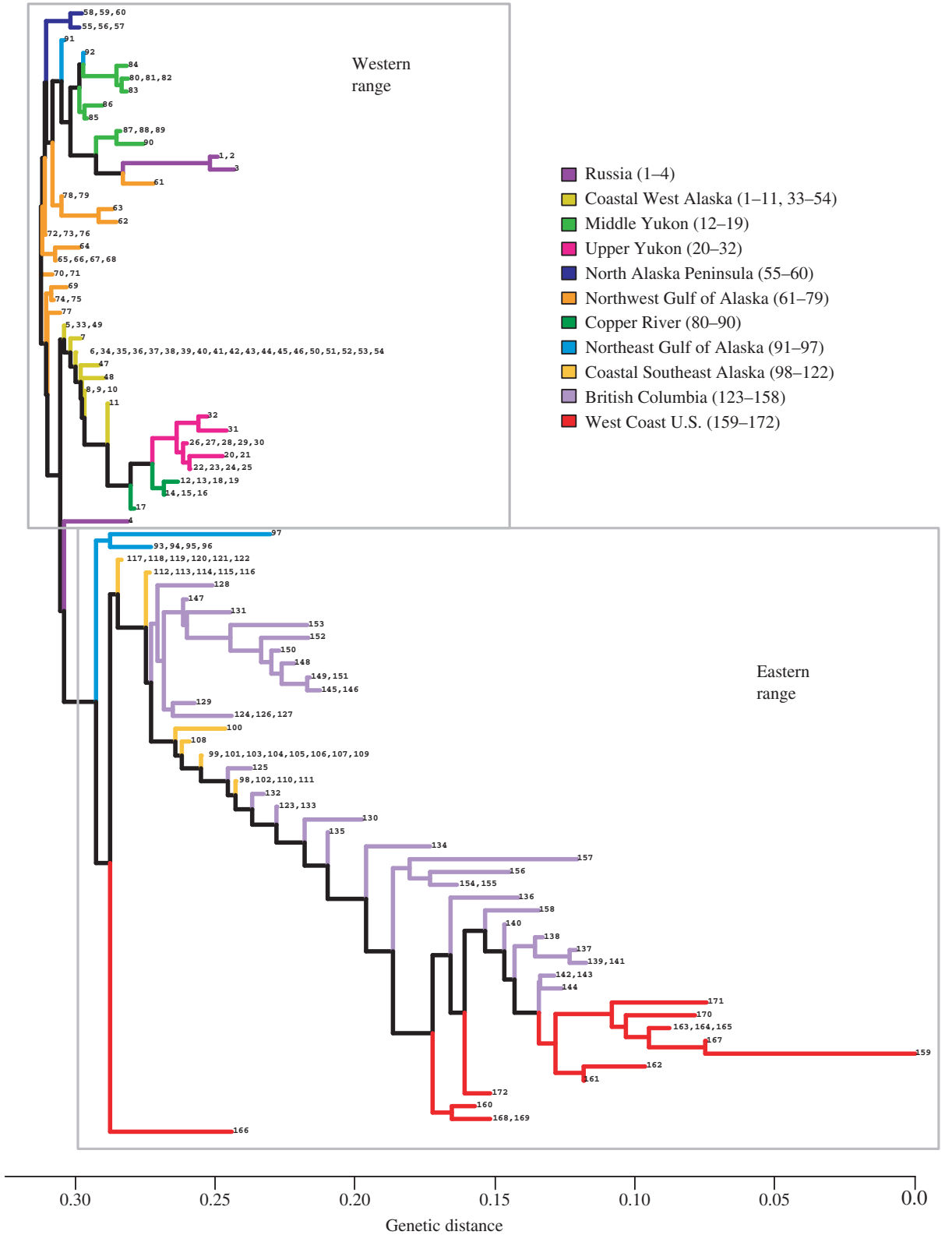

Fig. 4 Neighbour-joining tree based on pairwise Nei's distances between clusters of Chinook salmon populations defined by BAPS in the rangewide baseline. Colours indicate the broad-scale regional groups presented in Fig. 2 and numbers indicate populations in Appendix I.

genetic structure demonstrated in previous analyses, as well as geography and management needs. Too few populations were available from the West Coast U.S. broad-scale region to define meaningful fine-scale regions, and these populations were represented as a single broad-scale region for all analyses. The mean pairwise F_{ST} estimates for all broad-scale regions were significant and ranged from 0.013 (Coastal West Alaska) to 0.227 (West Coast U.S.). All mean pairwise F_{ST} values for fine-scale regions were significant with the exception of East Bristol Bay, Canada Border and Behm Canal. Some regions were supported by the occurrence of nodes in more than 50% of bootstrapped F_{ST} trees (e.g. Takhini River, Susitna River and Upper Copper River), but other regions had no significant nodes and display little internal substructure (e.g. all of the fine-scale regions in Coastal West Alaska) (Fig. 2).

The geographically large Coastal West Alaska broad-scale region was divided into seven fine-scale regions (Norton Sound, Lower Yukon, Kuskokwim Bay, Lower Kuskokwim, Upper Kuskokwim, West Bristol Bay and East Bristol Bay) based on management units and stakeholder uses. Genetic differences were small among these populations, but fine-scale regions were analysed to evaluate the precision and accuracy possible for this area.

In general population structure was hierarchical, populations within fine-scale regions clustered more closely with each other than with populations outside the region and fine-scale regions clustered within broad-scale regions. A few notable exceptions were the Situk (no. 91) and Alsek (Klukshu River, no. 92) populations that were similar to Chignik/Kodiak populations (no. 61–63) and Copper River populations (no. 80–90), respectively. However, these populations were genetically distinct and were grouped with the Northern Southeast Alaska populations because they are managed as part of southeast Alaska. The Russian populations from Kamchatka Peninsula (no. 1–3) also grouped with the Chignik/Kodiak populations, but the Pakhatcha River (no. 4) did not group closely with any other populations. Carson Hatchery (no. 166) from the Columbia River also did not group with other populations in either tree. Broad-scale groups were generally more cohesive in the western portion of the range than in the east, where fine-scale groups from British Columbia intermixed with Coastal Southeast Alaska and West Coast U.S.

In the hierarchical ANOVA based on the data set of 158 populations and 43 loci (Table 3), all results were statistically significant. The large estimates of variation among regional groups (both fine-scale, θ_S, and broad-scale, θ_P) relative to the variation within regions, θ_{SS}, indicate that populations are hierarchically structured and that grouping populations into these defined regions is well supported.

Mixed stock analysis

All 11 of the broad-scale regions performed well in the 100% proof tests; the lowest performing region was British Columbia with 95% correct allocation (Table 2). Of the 100% proof tests on fine-scale regions, six had composite sample sizes below the threshold, and no proof test was performed. The performance of the fine-scale regions in Coastal West Alaska was generally poor. Most of the Norton Sound proof test mixture (mean correct allocation: 14%) was misallocated to Kuskokwim Bay (62%) and Lower Kuskokwim River (14%). Likewise, most of the West Bristol Bay mixture (mean correct allocation: 13%) was misallocated to Kuskokwim Bay (29%) and Lower Kuskokwim River (49%). The other fine-scale regions with mean correct allocations under 90% were Port Moller (71%) and Kenai Late (67%). In each case, the misallocation was to the populations in the same broad-scale region (data not shown).

The results of the known mixture proof tests show that the broad-scale regions are highly identifiable in mixtures that might be expected in the Bering Sea (Fig. 5a, b). The estimated composition of each mixture was similar to expectations; all broad-scale regional estimates were within 4% of the true values and all 90% credibility indices contained the true values.

Table 3 Hierarchical analysis of variance (ANOVA) of the genetic differentiation of Chinook salmon populations from across the species range using 43 SNP markers. Populations were grouped into 44 fine-scale regions and 10 broad-scale regions (West Coast U.S. was not included). Estimates are provided for the differences between regions (θ), variance components (σ) and 90% confidence intervals

Source of variation	σ	90% CI	% of total	θ	90% CI
Among broad-scale	1.516	1.094, 1.980	11.7	0.117	0.089, 0.150
Within broad-scale among fine-scale	0.571	0.415, 0.745	4.4		
Among fine-scale	2.087	1.561, 2.644	16.2	0.162	0.130, 0.199
Within fine-scale among populations	0.326	0.131, 0.501	2.5		
Among populations	2.413	1.873, 2.979	18.7	0.187	0.157, 0.219
Within populations	10.490	8.726, 12.430	81.3		
Total	12.903	10.790, 15.110	100.0		

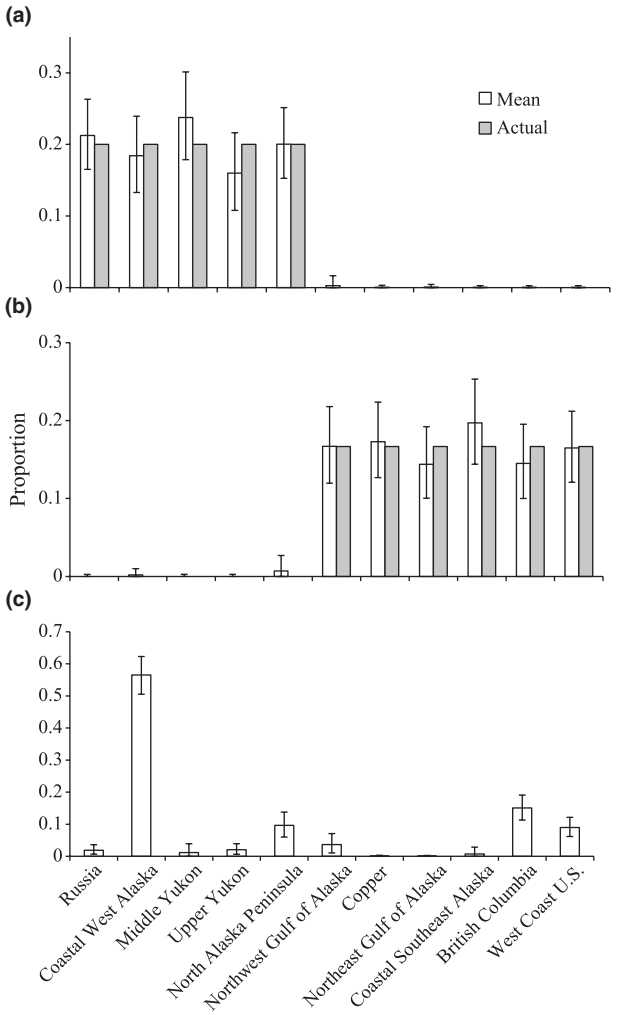

Fig. 5 Estimated composition and 90% credibility intervals for two known mixture proof tests and samples from the bycatch in the Bering Sea pollock fishery in 2005. Proportional compositions of 11 broad-scale regional groups are shown. The two proof tests consisted of (a) only Bering Sea populations (20% each) and (b) non-Bering Sea populations (17% each). The bycatch samples (c) were scales collected opportunistically by observers during the pollock fishery.

When the regional stock composition was estimated for mixtures taken from within three different rivers, each mixture was correctly identified to the broad-scale region(s) from which the mixture came: Yukon River 2008 (Coastal West Alaska 27%, Middle Yukon 27% and Upper Yukon 46%), Kuskokwim River 2005 (Coastal West Alaska 100%) and Copper River 2005 (97%). These estimates are at or above the threshold of 90% correct allocation used to classify regions as highly identifiable (e.g. Seeb *et al.* 2000). Within the Yukon River fishery sample, the Lower Yukon fine-scale region accounted for 19% of the Coastal West Alaska portion, and the remaining portion was misclassified as Lower Kuskokwim. For the Kuskokwim River fishery sample, contributions were assigned to Lower Yukon (1%) and West Bristol Bay (5%). The 3% estimated contribution of the Northeast Gulf of Alaska broad-scale region to the Copper River sample was attributed to the Klukshu River.

Analysis of the bycatch samples indicated that Chinook salmon from throughout the species range were present in the Bering Sea during the summer of 2005 (Fig. 5c). While the largest component of the sample was from Coastal West Alaska (57%), Chinook salmon from Russia (4%), British Columbia (15%) and West Coast U.S. (10%) were present.

Discussion

Population variability

We present a baseline for Chinook salmon based on 45 SNPs which contains representative populations from throughout the range of Chinook salmon, from Russia to California, with heavy representation from throughout Alaska and British Columbia. This is the first rangewide analysis of Chinook salmon using SNPs as genetic markers and the most comprehensive representation available for Chinook salmon in Alaska (99 populations). Two other baselines with rangewide coverage have been used for mixed stock analysis of Chinook salmon. The first is based on allozymes and includes only 44 populations from Alaska and the Yukon River (Teel *et al.* 1999). Twenty-one of these populations are in southeast Alaska and the remainder of Alaska is more sparsely characterized with three or fewer populations from most Chinook salmon-producing regions (Norton Sound, Yukon River, Kuskokwim River, North Alaska Peninsula, Kenai River and Copper River). For this reason, this baseline was generally limited to applications from the Situk River south to California, where western Alaska and Russia populations were not expected to contribute to the harvest. The second rangewide baseline is based on microsatellite markers (Beacham *et al.* 2006) and includes only 18 populations from Alaska (the U.S. portion of the Yukon River and southeast Alaska). There are no populations in the baseline from Norton Sound or from Kuskokwim River to the Copper River.

Gharrett *et al.* (1987) surveyed allozymes in samples from 13 drainages across the state including eight west of southeast Alaska. These included collections of juveniles in the Tanana and Susitna rivers and fishery samples from the Unalakleet, Yukon, Kuskokwim and Copper rivers. While this analysis provides a broad sense of genetic variation in Alaska, the samples generally do not represent the large number of spawning populations in these drainages and are not useful for mixed stock analysis.

Other genetic analyses of Chinook salmon within Alaska have limited range: Yukon River (Smith *et al.* 2005b; Templin *et al.* 2005; Beacham *et al.* 2008), Copper River (Seeb *et al.* 2009b) and southeast Alaska (Guthrie & Wilmot 2004). The baseline presented here provides more complete information for some of these areas and presents data for previously underrepresented areas (e.g. Alaska Peninsula, Kodiak Island and Cook Inlet) to form the most complete representation of Chinook salmon in Alaska.

The 43 populations from British Columbia almost completely overlap with the 44 populations in the baseline described in Seeb *et al.* (2007) representing 15 of the 16 reporting groups (missing the Lower Thompson River). That baseline was developed by a collaboration of laboratories and has been considered adequate for estimating the composition of population groups from British Columbia in fishery samples along the West Coast of North America.

This baseline also represents lineages from the western (Russia) and eastern (California) limits of their range. Russia was represented by four populations, including the two systems in Kamchatka that account for 90% of the Asian harvest of Chinook salmon, the Kamchatka and Bolshaya rivers (Bugaev & Myers 2009). Fourteen populations are included from the West Coast of the coterminous U.S. This can be compared to 56 populations in Seeb *et al.* (2007). This broad-scale region is identifiable in fishery mixtures, but in the absence of comprehensive representation from all fine-scale groups from this region, estimation of stock composition should continue to be limited to the broad-scale level.

Variability across the range

The tree produced from pairwise F_{ST} estimates between all populations (Fig. 3) is remarkably similar to the tree produced from Nei's distances between population clusters defined by Bayesian partitioning in BAPS (Fig. 4). With few exceptions, both methods produced very similar structure. The greatest difference is in the positions of Klamath (no. 170) and Eel (no. 171) rivers, where the F_{ST} tree places them with populations on the Oregon coast (Alsea no. 168 and Siuslaw no. 169), but the BAPS tree places them with populations from the Columbia River (Lyons Ferry no. 163, Hanford Reach no. 164 and Lower Deschutes River no. 165). In addition, Chignik (no. 61) does not cluster with the Kodiak Island populations (no. 62–63) in the BAPS tree as it does in the F_{ST} tree. The overall similarity is interesting given the differences between the algorithms in the two methods. In the first method, F_{ST} was estimated between all population pairs, while in BAPS populations were partitioned into composite ''populations'' and then Nei's distances were estimated using the group allele frequencies. This result supports the conclusion from the ANOVA that the hierarchical structure of Chinook salmon is strong relative to differences between individual populations.

This study confirms patterns of genetic variability proposed in past analyses involving large-scale surveys of Chinook salmon that included portions of Alaska (allozymes: Gharrett *et al.* 1987; microsatellites: Beacham *et al.* 2006). Temporal variation within populations was much less than the variation between populations. In general, the western portion of the species range (west of, and including, Klukshu River no. 92) displays a reduced level of genetic divergence in comparison with the eastern portion (Figs 3 and 4). The populations in Norton Sound, Lower Yukon River, Lower Kuskokwim River and Bristol Bay are genetically very similar. Although the populations in this region are spread along approximately 1800 km of coastline and include populations spawning hundreds of kilometres up three major river systems, the mean F_{ST} among populations in this composite region was only 0.013 (Table 2). Partitioning methods provided little support for segregating these populations, leaving 19 populations from Norton Sound, Kuskokwim River and Bristol Bay grouped in the best fit clustering. This pattern is not limited to Chinook salmon; Seeb *et al.* (2011b) show that chum salmon in this same large coastal area (from Norton Sound to Bristol Bay) also display a low level of genetic similarity (32 populations, F_{ST} = 0.004) and must be treated as a single group in some analyses.

We detected a sharp discontinuity in allele frequencies between fine-scale reporting groups within the Northeast Gulf of Alaska broad-scale region (Supplementary Table S1). This broad-scale region was constructed based on geographic proximity and management needs. The observed discontinuity is located between the Cape Fairweather fine-scale region (no. 91 and 92) and the Northern Southeast Alaska fine-scale region (no. 93–97). The Cape Fairweather region falls within the western cluster, while the Northern Southeast Alaska region falls within the eastern cluster on both the F_{ST} and BAPS trees (Figs 3 and 4). The placement of the two fine-scale regions in a single broad-scale region should not obscure the fact that the discontinuity likely reflects a secondary contact of two groups that were isolated in the Pleistocene (McPhail & Lindsey 1970; Gharrett *et al.* 1987; Martin *et al.* 2010).

Within previously reported portions of the range, population structure was similar to published results for the Yukon River (Smith *et al.* 2005b; Templin *et al.* 2005; Beacham *et al.* 2008) and Copper River (Seeb *et al.* 2009b). Significant isolation by distance is reported in both the Yukon and Copper rivers indicating that geography and population structure correspond closely in these drainages. This correspondence can be seen

throughout Alaska. For example, fine-scale regional structure in Northwest Gulf of Alaska is closely identified with river drainage (Kenai and Susitna rivers) and geographic proximity (Kodiak Island and Lower Kenai Peninsula). Nearby fine-scale regions cluster together within the broad-scale group (e.g. Susitna, Kenai and Kasilof rivers). Northern Alaska Peninsula populations (no. 55–60) form a single cluster that is genetically distinct from their nearest neighbours, including the Chignik River population (no. 61). Chignik River is geographically very close to the Meshik River (no. 56, <70 km), but is located on the south side of the peninsula and separated from the Meshik River by a range of mountains.

Mixed stock analysis

The hierarchical genetic structure revealed by SNP markers can be used to estimate the origins of Chinook salmon contributing to aggregates of migrating salmon encountered in freshwater or on the high seas. Tests of the accuracy and precision of stock composition of potential mixtures indicate that compositions can confidently be estimated to each of the 11 broad-scale regions and many of the fine-scale regions. This was true whether the mixture was comprised entirely of individuals from a single region (Table 2) or from several regions (Fig. 5a, b).

The poorest performance of fine-scale regions for mixed stock analysis was within Coastal West Alaska. This was not unexpected given the low genetic differentiation among these populations. This broad-scale region covers an extensive geographic area that includes tributaries to three large bays and three major river systems (Fig. 2). We assessed the precision and accuracy possible by segregating this broad-scale region into fine-scale regions that more closely match management units, fishery types (commercial and subsistence) and community groups. The Lower Yukon and Kuskokwim Bay fine-scale regions were sufficiently identifiable in mixtures. However, the other five fine-scale regions did not meet the threshold value of 90% correct allocation. In samples where Chinook salmon from throughout the Coastal West Alaska region might be present (e.g. Bering Sea bycatch), mixed stock analysis should be limited to providing results for the larger composite group. However, for samples from within the Yukon and Kuskokwim rivers, the appropriate fine-scale regions can provide reasonable estimates as demonstrated by the analysis of the test fishery samples.

When we applied the baseline to estimate the composition of a sample of unknown individuals from the pollock fishery bycatch, we found that individuals from throughout the range of Chinook salmon could be present in the Bering Sea (Fig. 5c). In our sample from the summer of 2005, more than half were estimated to have originated from Coastal West Alaska and an additional 13% from the Middle Yukon, Upper Yukon and northern Alaska Peninsula. While populations from British Columbia and West Coast U.S. were estimated to contribute almost a quarter of the sample, populations from the Gulf of Alaska coast were present in very small amounts. Given the variability in distribution and abundances among Chinook salmon populations and the lack of a sampling design when this sample was taken, these results should not be generalized to the entire bycatch, but they do emphasize the need for a comprehensive, rangewide, standardized baseline for studies in the Bering Sea and Gulf of Alaska.

The 11 broad-scale regional groups are conservative, but perform well. These reporting regions provide sufficient resolution for most fishery and research applications in the Bering Sea, where sample sizes are relatively small and the number of reporting groups should be held to low numbers (e.g. Habicht *et al.* 2010). However, estimating contributions at finer scales will remain a goal. Additional SNP markers are under development that may provide additional resolution of regions into smaller sets, some by adding more informative markers (e.g. Coastal West Alaska) and some by adding more populations to the baseline (West Coast U.S.).

The combining of the highly heterogeneous populations from the West Coast of the coterminous U.S. should not be interpreted as a statement that these populations cannot be separated by these SNP markers. Rather, it is because this region contains so much variability that 14 populations are not sufficient to reliably represent the structure of entire region. The microsatellite baseline developed for mixed stock analysis in this area with high genetic variation among populations (Northern Southeast Alaska to California) is approximately the same size as the baseline presented here (165 populations), and 44 identifiable reporting regions have been established for use with this baseline (Seeb *et al.* 2007). Narum *et al.* (2008) compared these 13 microsatellites to a set of 37 SNPs surveyed in 29 populations (16 of which are included in our analysis) and found very similar results between marker types. Currently, analyses are surveying SNPs in populations from the southern portion of the range and more complete baseline information on variation at SNP loci will be available in the near future.

Ascertainment bias

Ascertainment bias can occur when loci are chosen from an unrepresentative sample of individuals which are then used to infer aspects of population structure for a much larger set of individuals. This has the potential to intro-

duce a systematic bias, particularly if estimates of variation within and among populations are used in comparative analyses or when loci under putative-selection are included. The SNPs used in this study were ascertained primarily from western and southeastern Alaska (see Table 1), so we hypothesize that any effect of ascertainment bias would be outside our primary area of interest.

Evidence in support of this hypothesis is provided by the study of Smith *et al.* (2007) who performed a comprehensive examination of marker class bias on a subset of 16 of the populations from this study using a nearly overlapping panel of 41 SNPs. They compared results from these SNPs to those from 22 allozymes and nine microsatellite loci. They found that overall divergence (F_{ST}) was higher for SNPs than for allozymes; however, they attribute this to the choice of F_{ST} estimator which is influenced by relative heterozygosity. They did not observe any impact of ascertainment bias on branching order, overall divergence, variance partitioning or estimation of divergence among panel collections. However, effects of ascertainment bias were detected in measures of within-population diversity when based on SNPs developed from ascertainment panels originating from outside the geographic range of the tested populations.

In this study, we generally observed shorter branch length in the western group than in the eastern group indicating that differences between populations are smaller in that part of the range. Given the results of Smith *et al.* (2007) and previous results from other marker types, this is likely a reflection of inherent lower diversity levels and demographic history rather than a function of ascertainment bias.

Applications across the Pacific RIM

SNPs are rapidly becoming the marker of choice for large-scale analyses of Pacific salmon (e.g. Smith *et al.* 2007; Narum *et al.* 2008; Habicht *et al.* 2010) and are becoming increasingly used in many types of studies of nonmodel organisms including individual parentage analyses (Anderson & Garza 2006; Hauser *et al.* in press) as well as genetic monitoring (Karlsson *et al.* 2011), conservation management (McGlauflin *et al.* in press) and forensic applications (Morin *et al.* 2010; Ogden 2011). The many advantages of SNP markers (see reviews Morin *et al.* 2004; Smith *et al.* 2005b; Garvin *et al.* 2010) include the increased accuracy, ease of automation and transferability of data sets across national and international laboratories. SNPs also allow interrogation of both neutral and non-neutral variation, and non-neutral SNPs can be particularly informative for mixed stock analysis (Ackerman *et al.* in press). Two large-scale collaborations, both the *FishPopTrace* group, an international project funded by the European Union to generate panels of SNP markers for geographic assignment of four commercially important marine species (Martinsohn & Ogden 2009), and the *PACSNP* group (Seeb *et al.* 2011b) support the vision of shared, openly accessible international databases that can be applied to widely ranging questions of both a theoretical and applied nature. These same factors have now moved researchers working on Chinook salmon and funded by the Pacific Salmon Commission (http://www.psc.org/) beyond the existing 13-locus microsatellite panel (Seeb *et al.* 2007) to actively develop and expand the existing SNP databases (Smith *et al.* 2007; Narum *et al.* 2008; Seeb *et al.* 2009b). Here, we provide baseline data for Bering Sea bycatch and other fisheries applications in the eastern North Pacific Ocean. New SNP discovery approaches such as Seeb *et al.* (2011a) and Clemento *et al.* (2011) are rapidly adding more loci to increase population resolution. As with chum salmon in *PACSNP*, additional laboratories are adding data from additional loci and populations to expand and refine applications (e.g. Hess *et al.* 2011).

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Conflict of interest

The authors have no conflict of interest to declare and note that the sponsors of the issue had no role in the study design, data collection and analysis, decision to publish, or preparation of the manuscript.

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Data accessibility: SNP genotypes data deposited at Dryad: doi: 10.5061/dryad.8063.

Supporting Information

Additional supporting information may be found in the online version of this article.

Table S1 Observed allele frequencies for 45 SNP loci assayed in Chinook salmon populations from Kamchatka Peninsula in Russia to Sacramento River in California. Population numbers correspond to numbers in Table 1, Appendix I and Fig. 1.

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Appendix I Populations of Chinook salmon included in the coastwide baseline of SNP markers. For some populations, the run timing is indicated to specify the population which is represented: spring (Sp), summer (Su), fall (Fa) and winter (Wi). Sample size (N) is the total for all years sampled. Map numbers correspond to the numbers on Figs 2–4.

	Reporting region				
Map No.	Broad-scale	Fine-scale	Location	Sample year(s)	*N*
1	Russia	Okhotsk Sea Coast	Bistraya River	1998	94
2			Bolshaya River	1998, 2002	77
3		Bering Sea Coast	Kamchatka River Late	1997, 1998	119
4			Pakhatcha River	2002	50
5	Coastal West Alaska	Norton Sound	Pilgrim River	2005, 2006	72
6			Unalakleet River	2005	82
7			Golsovia River	2005, 2006	112
8		Lower Yukon	Andreafsky River	2002, 2003	236
9			Anvik River	2002	95
10			Gisasa River	2001	188
11			Tozitna River	2002, 2003	290
12	Middle Yukon	Upper U.S. Yukon	Henshaw Creek	2001	147
13			South Fork Koyukuk River	2003	56
14			Beaver Creek	1997	100
15			Chandalar River	2002, 2003, 2004	175
16			Sheenjek River	2002, 2004, 2006	51
17		Tanana	Kantishna River	2005	187
18			Chena River	2001	193
19			Salcha River	2005	188
20	Upper Yukon	Canada Border	Chandindu River	2000, 2001, 2003	249
21			Klondike River	1995, 2001, 2003	79
22		Pelly	Stewart River	1997	99
23			Mayo River	1992, 1997, 2003	197
24			Blind River	2003	134
25			Pelly River	1996, 1997	140
26		Carmacks	Little Salmon River	1987, 1997	100
27			Big Salmon River	1987, 1997	117
28			Tatchun Creek	1987, 1997, 2002, 2003	169
29			Nordenskiold River	2003	55
30			Nisutlin River	1987, 1997	56
31		Takhini	Takhini River	1997, 2002, 2003	161
32			Whitehorse Hatchery	1985, 1987, 1997	242
33	Coastal West Alaska	Kuskokwim Bay	Goodnews River	1993, 2005, 2006	368
34			Arolik River	2005	147
35			Kanektok River	1992, 1993, 2005	244
36		Lower Kuskokwim	Eek River	2002, 2005	173
37			Kwethluk River	2001	96
38			Kisaralik River	2001, 2005	191
39			Tuluksak River	1993, 1994, 2005	195
40			Aniak River	2002, 2006	252
41			George River	2002, 2005	191
42			Kogrukluk River	1992, 1993, 2005	149
43			Stony River	1994	93
44			Cheeneetnuk River	2002, 2006	117
45			Gagaryah River	2006	190
46			Takotna River	1994, 2005	176
47		Upper Kuskokwim	Tatlawiksuk River	2002, 2005	191
48			Salmon River – Pitka Fork	1995	96
49		West Bristol Bay	Togiak River	1993, 1994	159
50			Nushagak River	1992, 1993	57
51			Mulchatna River	1994	97
52			Stuyahok River	1993, 1994	87

Appendix I (Continued)

	Reporting region				
Map No.	Broad-scale	Fine-scale	Location	Sample year(s)	*N*
53		East Bristol Bay	Naknek River	1995, 2004	110
54			Big Creek	2004	66
55	North Alaska Peninsula	Port Heiden	King Salmon River	2006	131
56			Meshik River	2006	42
57		Port Moller	Milky River	2006	67
58			Nelson River	2006	95
59			Black Hills Creek	2006	51
60			Steelhead Creek	2006	93
61	Northwest Gulf of Alaska	Chignik/Kodiak	Chignik River	1995, 2006	75
62			Ayakulik River	1993, 2006	136
63			Karluk River	1993, 2006	140
64		Susitna	Deshka River	1995, 2005	251
65			Deception Creek	1991	67
66			Willow Creek	2005	73
67			Prairie Creek	1995	52
68			Talachulitna River	1995	58
69		Kenai Early	Crescent Creek	2006	164
70			Killey Creek	2005, 2006	266
71			Benjamin Creek	2005, 2006	205
72			Funny River	2005, 2006	220
73			Slikok Creek	2005	95
74		Kenai Late	Juneau Creek	2005, 2006	119
75			Kenai River mainstem	2003, 2004, 2006	302
76		Kasilof	Crooked Creek Hatchery	1992, 2005	306
77			Kasilof River mainstem	2005	321
78		Lower Kenai Peninsula	Anchor River	2006	200
79			Ninilchik River	2006	162
80	Copper	Upper Copper	Indian River	2004, 2005	50
81			Bone Creek	2004, 2005	78
82			E. Fork Chistochina River	2004	133
83			Otter Creek	2005	128
84			Sinona Creek	2004, 2005	157
85		Middle Copper	Gulkana River	2004	211
86			Mendeltna Creek	2004	144
87		Lower Copper	Kiana Creek	2004	75
88			Manker Creek	2004, 2005	62
89			Tonsina River	2004, 2006	75
90			Tebay River	2004, 2005, 2006	68
91	Northeast Gulf of Alaska	Cape Fairweather	Situk River	1988, 1990, 1991, 1992	143
92			Klukshu River	1989, 1990	174
93		Northern Southeast Alaska	Big Boulder Creek	1992, 1993, 1995, 2004	178
94			Tahini River	1992, 2004	169
95			Pullen Creek Hatchery	2005	83
96			Kelsall River	2004	96
97			King Salmon River	1989, 1990, 1993	144
98	Coastal Southeast Alaska	Chickamin	King Creek	2003	143
99			Chickamin River	1990, 2003	56
100			Little Port Walter Hatchery	1993, 2005	126
101			Whitman Lake Hatchery	1992, 1998, 2005	331
102			Humpy Creek	2003	94
103			Butler Creek	2004	95
104		Unuk	Clear Creek	1989, 2003, 2004	166
105			Cripple Creek	1988, 2003	143
106			Genes Creek	1989, 2003, 2004	95

Appendix I (Continued)

	Reporting region				
Map No.	Broad-scale	Fine-scale	Location	Sample year(s)	*N*
107			Kerr Creek	2003, 2004	151
108			Little Port Walter Hatchery	2005	150
109			Deer Mountain Hatchery	1992, 1994	147
110		Behm Canal	Keta River	1989, 2003	144
111			Blossom River	2004	95
112		Andrew	Andrew Creek	1989, 2004	152
113			Crystal Lake Hatchery	1992, 1994, 2005	397
114			Medvejie Hatchery	1998, 2005	273
115			Hidden Falls Hatchery	1994, 1998	155
116			Macaulay Hatchery	2005	94
117		Transboundary Rivers	Kowatua River	1989, 1990	138
118			Little Tatsemenie River	1989, 1990, 2005	143
119			Upper Nahlin River	1989, 1990	130
120			Nakina River	1989, 1990	140
121			Dudidontu River	2005	86
122			Tahltan River	1989	95
123	British Columbia	North Coast BC	Kateen River	2005	96
124			Damdochax Creek	1996	65
125			Kincolith Creek	1996	115
126			Kwinageese Creek	1996	73
127			Oweegee Creek	1996	81
128		Skeena	Bulkley River	1999	91
129			Sustut River	2001	130
130			Ecstall River	2001, 2002	86
131			Lower Kalum River	2001	142
132		Central BC Coast	Lower Atnarko River	1996	144
133			Kitimat River	1997	141
134			Wannock River	1996	144
135		South BC Mainland	Klinaklini River	1997	83
136			Porteau Cove	2003	154
137		West Vancouver Island	Conuma River	1997, 1998	110
138			Marble Creek	1996, 1999, 2000	144
139			Nitinat River	1996	104
140			Robertson Creek	1996, 2003	106
141			Sarita River	1997, 2001	160
142		East Vancouver Island	Big Qualicum River	1996	144
143			Nanaimo River	2002	93
144			Quinsam River	1996	127
145		Upper Fraser	Morkill River (Su)	2001	154
146			Salmon River (Su)	1997	94
147			Torpy River (Su)	2001	105
148		Middle Fraser	Chilko River (Su)	1995, 1996, 1999, 2002	246
149			Nechako River (Su)	1996	120
150			Quesnel River (Su)	1996	144
151			Stuart River (Su)	1996	161
152		North Thompson	Clearwater River (Su)	1997	153
153			Louis River (Sp)	2001	179
154		South Thompson	Lower Adams River (Fa)	1996	46
155			Lower Thompson River (Fa)	2001	100
156			Middle Shuswap River (Su)	1986, 1997	144
157		Lower Fraser	Birkenhead River (Sp)	1997, 1999, 2001, 2002, 2003	93
158			Harrison River	2002	96
159	West Coast U.S.		Makah National Fish Hatch. (Fa)	2001, 2003	94
160			Forks Creek (Fa)	2005	150

Appendix I (Continued)

Map No.	Reporting region		Location	Sample year(s)	*N*
	Broad-scale	Fine-scale			
161			Upper Skagit River (Su)	2006	93
162			Soos Creek Hatchery (Fa)	2004	119
163			Lyons Ferry Hatchery (Su/Fa)	2002, 2003	191
164			Hanford Reach	2000, 2004, 2006	191
165			Lower Deschutes River (Fa)	2002	96
166			Carson Hatchery (Sp)	2001	96
167			McKenzie River (Sp)	2004	95
168			Alsea River (Fa)	2004	93
169			Siuslaw River (Fa)	2001	95
170			Klamath River	1990, 2006	52
171			Eel River (Fa)	2000, 2001	88
172			Sacramento River (Wi)	2005	95

Appendix 3: Stock-structured distribution of Western Alaska and Yukon juvenile Chinook salmon (*Oncorhynchus tshawytscha*) from United States BASIS surveys, 2002-2007

Stock-Structured Distribution of Western Alaska and Yukon Juvenile Chinook Salmon (*Oncorhynchus tshawytscha*) from United States BASIS Surveys, 2002–2007

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Abstract: We describe migratory patterns of western Alaska and Yukon Chinook salmon (*Oncorhynchus tshawytscha*) using stock-structured distribution data from United States Bering-Aleutian Salmon International Surveys (BASIS), 2002–2007. Juvenile Chinook salmon were distributed within water depths less than 50 m and their highest densities were found close to river mouths of primary Chinook salmon-producing rivers in the eastern Bering Sea (Yukon, Kuskokwim, and Nushagak rivers) through their first summer at sea. This reflects a later marine dispersal from freshwater entry points than typically found in Gulf of Alaska stream-type Chinook salmon and resulted in the presence of juvenile Chinook salmon in shallow, non-trawlable habitats during the surveys. Juvenile Chinook salmon stock proportions in the northern shelf region (north of 60°N) were: 44% Upper Yukon, 24% Middle Yukon, 31% Coastal Western Alaska, and 1% other western Alaska stock groups. Juvenile Chinook salmon stock proportions present in the southern shelf region (south of 60°N) were: 95% Coastal Western Alaska, 1% Upper Yukon, and 4% other western Alaska stock groups. It is believed that these stock mixtures do not support significant northward migration of stocks from the southern shelf, and reflect limited mixing of salmon from the two production regions during their first summer at sea. Spatial distribution patterns and coded-wire tag recoveries provide evidence that the distribution of Yukon River Chinook salmon extends northward into the Chukchi Sea during their first summer at sea. Although the juveniles present in the Chukchi Sea represent a minor portion of the total Yukon River juvenile population, continued warming of the Arctic could increase the proportion of Yukon River Chinook salmon migrating north into the Chukchi Sea.

Keywords: Bering Sea, Chinook salmon, distribution, migration, stock structure

INTRODUCTION

Migratory corridors used by Chinook salmon (*Oncorhynchus tshawytscha*) and their distribution within the corridors provide key information on the early marine ecology and life-history strategies of juvenile salmon important to their growth and survival (Brodeur et al. 2000). Juvenile Chinook salmon from western Alaska and Yukon, Canada enter the marine waters of the eastern Bering Sea during the spring and summer and migrate along the coast of western Alaska during their first summer in the ocean (Healey 1991). An understanding of the underlying migratory patterns of salmon is also required to interpret and apply research survey data to population studies of Chinook salmon (Farley et al. 2005).

Although much of the historical work on salmon migration has relied on tagging and marking research (Hartt and Dell 1986; Orsi and Jaenicke 1996; Farley et al. 1997; Courtney et al. 2000), genetic methods have expanded the ability of research surveys to define migratory behavior of salmon in the ocean (Seeb et al. 2004; Templin et al. 2005). Recent developments in single nucleotide polymorphism (SNP) markers and genetic baselines provide efficient and accurate assignment of Chinook salmon to freshwater origin (Smith et al. 2005; Templin et al. 2005). SNP data can be collected and scored very rapidly compared to other genetic markers, thus increasing its power and efficiency to discriminate stock origins.

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Farley et al. (2005) initially described migratory pathways of juvenile Chinook salmon in the eastern Bering Sea using information on juvenile salmon size distribution. Reconstructing migration corridors from size data capitalizes on the fact that much of the variability in juvenile size reflects the time of ocean entry. Dispersal patterns of juvenile salmon from points of ocean entry are apparent in the spatial distribution of size, with the largest juvenile salmon (earliest out-migrants) distributed the greatest distance from their point of ocean entry. In the following analysis, migratory patterns of juvenile western Alaska and Yukon Chinook salmon are described using information on ocean distributions and freshwater origin from coded-wire tags and genetic stock identification methods.

METHODS

Juvenile Chinook salmon were collected with surface rope trawls during the U.S. Bering-Aleutian Salmon International Survey (BASIS) on the eastern Bering Sea shelf from 2002–2007 (Table 1). Start dates of the survey ranged from August 14 to August 21; end dates ranged from September 20 to October 8 (Table 1). Variation in start and end dates each year reflected changes in vessel availability and survey coverage and design. The initial survey design (2002 and 2003) used transect-based sampling along latitude and longitude lines (Farley et al. 2005). A grid-based sampling design with stations at each degree of longitude and 30 minutes of latitude was used from 2004 to 2007.

Juvenile Chinook salmon and other pelagic fish were collected with surface rope trawls built by Cantrawl Pacific Limited of Richmond, British Columbia (Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.). Trawls were 198 m long, had hexagonal mesh in wings and body, and included a 1.2-cm mesh liner in the codend (Murphy et al. 2003). Trawls were towed at the surface at an average speed of 4.3 knots, resulting in an average vertical mouth opening of 14 m and horizontal mouth opening of 58 m. Sampling depths were slightly deeper than the vertical opening as the center of the trawl often was just below the surface during the trawl deployment. Water depths shallower than 20 m were considered non-trawlable and were not sampled. Nor'eastern Trawl Systems 5-m alloy doors with 60-m bridle lengths were deployed typically 360 m astern of the boat. Buoys were secured to the wing-tips and center of the headrope to help keep the trawl at the surface and wingtip buoy wakes were monitored to ensure the headrope was maintained at the surface during the tow. Trawl speeds were adjusted to keep the trawl at the surface and trawl doors in the water. A Simrad FS900 net sounder was used to monitor the fishing dimensions and trawl geometry during each tow. All trawls were towed astern of the vessel for 30 min at each station. Catch per unit of fishing effort, CPUE, was used to describe salmon spatial distributions and the standardized unit of fishing effort was effort during a 30-min trawl set. Average area swept by the trawl at each station was 0.25 km^2.

Stations were sampled between 07:30–21:00 hours (Alaska Standard Time), and typically four stations were sampled each day. Stations were sampled during daylight with the exception of the first station of each day. The first station of the day was sampled just after sunrise, and occasionally sampling would occur during sunrise depending on the schedule set for vessel operations by the chief scientist. Salmon catch rates from the crepuscular time-period were not significantly different from other daylight samples (Farley et al. in press). Sample dates differed by location due to the order in which stations were sampled during the survey. Average sample dates were estimated with a weighted average date with weights provided by the catch at each station.

Standard research trawl protocols were used to process the trawl catch. All salmon were sorted and counted by spe-

Table 1. Number of surface trawl stations sampled during U.S. BASIS surveys on the eastern Bering Sea shelf by year and vessel, 2002–2007.

Year	Vessel	Start Date	End Date	Number of Trawl Stations
2002	F/V *Sea Storm*	20-Aug-02	07-Oct-02	152
	F/V *Northwest Explorer*	08-Sep-02	06-Oct-02	44
2003	F/V *Sea Storm*	21-Aug-03	08-Oct-03	151
2004	F/V *Sea Storm*	14-Aug-04	30-Sep-04	143
2005	F/V *Sea Storm*	14-Aug-05	06-Oct-05	127
2006	F/V *Sea Storm*	14-Aug-06	20-Sep-06	105
	F/V *Northwest Explorer*	21-Aug-06	04-Sep-06	53
2007	F/V *Sea Storm*	15-Aug-07	08-Oct-07	136
	NOAA Ship *Oscar Dyson*	05-Sep-07	26-Sep-07	50

cies and life-history stage; all juvenile Chinook salmon were examined for a missing adipose fin. Snouts were removed from juvenile Chinook salmon with a missing adipose fin and examined for the presence of a coded wire tag at the Auke Bay Laboratories in Juneau, Alaska. Individual lengths and weights were collected from a subsample of up to 50 Chinook salmon and genetic samples were collected from these fish.

Kriging models implemented in ArcGIS software package (ESRI 2006) were used to construct the spatial distribution map of juvenile Chinook salmon on the eastern Bering Sea shelf. The spatial mean was removed with a local polynomial regression model prior to fitting the Kriging model and the spatial covariance of juvenile Chinook salmon was modeled with a spherical variogram (Cressie 1991). The spatial model was used to estimate the distribution of juvenile Chinook salmon in non-trawlable habitats with the addition of boundary conditions. Boundary conditions were created by adding with zero catch points on land at spatial scales matching the survey sampling grid.

Freshwater stock origins of juvenile Chinook salmon were determined from coded-wire tag (Jefferts et al. 1963) recoveries and from genetic stock identification analysis. Coded-wire tags were assigned to freshwater origin using the coast-wide mark database maintained by the Pacific States Marine Fisheries Commission (http://www.rmpc.org/) and by coded-wire tag release information provided by the Whitehorse Rapids Fish Hatchery (YRJTC 2009).

A coast-wide baseline of 42 SNP genetic markers for Chinook salmon (updated from Templin et al. 2005) was used to assign freshwater origin of juvenile Chinook salmon. SNP data were obtained from 1,356 juvenile Chinook salmon collected during 2002–2006 following the methods of Seeb at al. (2009), and stock mixtures were estimated for three locations on the eastern Bering Sea shelf. Mixed stock proportions at each location were estimated using conditional maximum likelihood models implemented in the SPAM 3.7 mixed-stock software program (Debevec et al. 2000). Accuracy of mixed stock assignment to freshwater origins considered in this analysis was greater than 90% using the 42-SNP baseline (Templin et al. 2005).

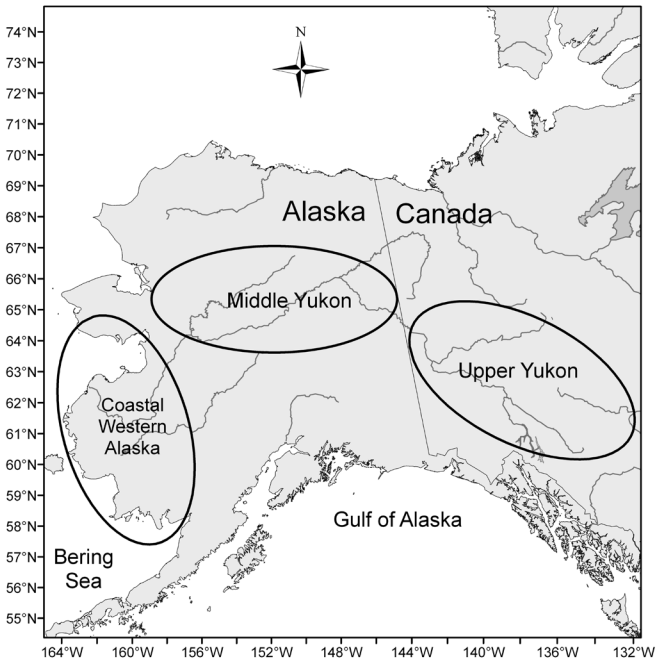

Fig. 1. Approximate locations of regional genetic stock groups of juvenile Chinook salmon (Coastal Western Alaska, Middle Yukon, and Upper Yukon) captured during U.S. BASIS surface trawl surveys on the eastern Bering Sea shelf.

Chinook salmon outside of the eastern Bering Sea were not assumed to be present in the area sampled by the U.S. BASIS survey during their first summer at sea (juvenile life-history stage); therefore, only Chinook salmon stocks from eastern Bering Sea river systems were considered in the mixed stock analysis. Stock groups included in the analysis were: the Upper Yukon River stock group, the Middle Yukon River stock group, the Coastal Western Alaska stock group, and an 'Other' stock group (Fig. 1). The Coastal Western Alaska stock group included the Lower Yukon Chinook salmon stocks and all other western Alaska stock groups outside of the Yukon River except the Upper Kuskokwim River and North Alaska Peninsula stock groups. For simplicity, these two stock groups were combined into a single 'Other' stock group. The Lower Yukon stock group included Alaskan tributary streams draining the Andreafsky Hills and Kaltag Mountains; the Middle Yukon stock group included Alaskan tributary streams in the upper Koyukuk River and Tanana River basins; the Upper Yukon stock group included Canadian tributary streams draining the Pelly and Big Salmon mountains (Lingnau and Bromaghin 1999).

Juvenile mixtures in the northern shelf region (north of 60°N) were compared with expected adult stock mixtures in the Yukon River. Expected adult stock mixtures were estimated by the average mixtures present in historical and recent commercial and subsistence harvests in the Yukon River (DuBois and DeCovich 2008; Bue and Hayes 2009). These estimates were not corrected for potential stock selective harvest.

RESULTS

Juvenile Chinook salmon were primarily distributed within water depths less than 50 m through their first summer at sea (middle of August through the middle of October). The highest densities of juvenile Chinook salmon were found close to river mouths of primary Chinook salmon-producing rivers in the eastern Bering Sea (Yukon, Kuskokwim, and Nushagak rivers) (Fig. 2). Juvenile Chinook salmon were distributed as far north as the Chukchi Sea and the southern extent of their distribution was along the north shore of Bristol Bay. The migratory corridor of juvenile Chinook salmon was broader in the northern shelf (north of 60°N) than in the

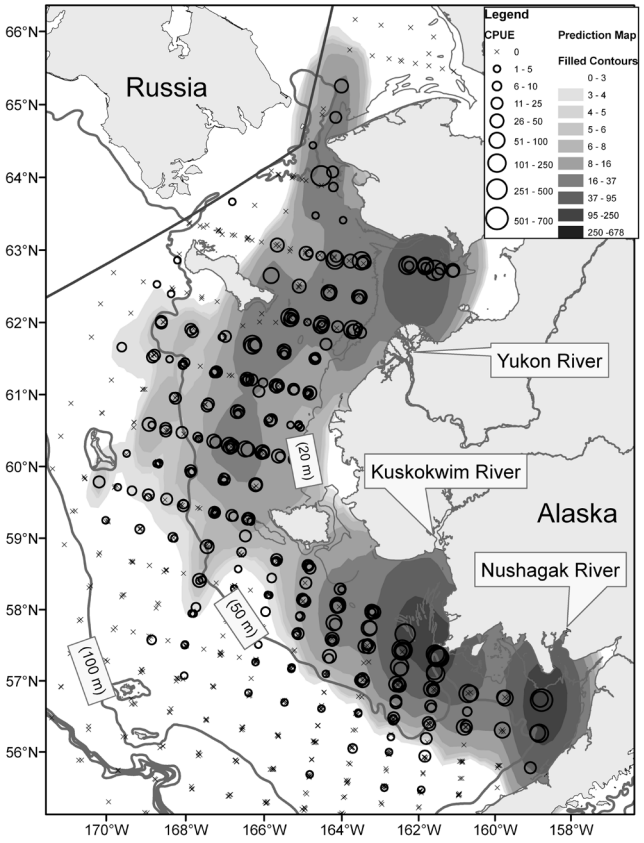

Fig. 2. Distribution of juvenile Chinook salmon during U.S. BASIS surface trawl surveys on the eastern Bering Sea shelf (mid August to early October), 2002–2007. Distribution is based on catch per unit of effort (CPUE) with a 30-min trawl haul used as the standard unit of effort. Individual trawl catches are overlaid on the CPUE prediction surface from a Kriging spatial model. Contours are shaded at geometric intervals of the prediction surface.

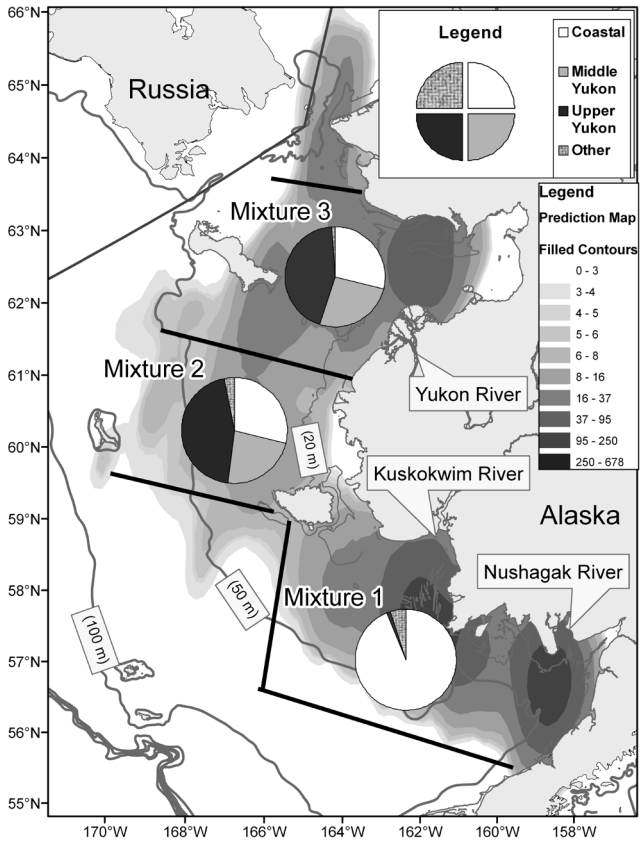

Fig. 3. Genetic stock mixtures of juvenile Chinook salmon (Coastal Western Alaska, Middle Yukon, Upper Yukon, and 'other' stock groups) captured during U.S. BASIS surface trawl surveys on the eastern Bering Sea shelf (mid August to early October), 2002–2006. Mixtures are overlaid on a map of juvenile Chinook salmon distribution and black bars identify the spatial extent of samples used for each mixture. Genetic mixtures are overlaid on the CPUE prediction surface from a Kriging spatial model. Contours are shaded at geometric intervals of the prediction surface.

Table 2. Estimated stock mixtures of juvenile Chinook salmon (with 95% confidence intervals) collected during U.S. BASIS surface trawl surveys on the eastern Bering Sea shelf by region and location, 2002–2006. Average sample dates and DNA sample sizes are included.

Stock Mixture	Region	Location	Average Sample Date	Sample Size	Stock Group			
					Coastal Western Alaska	Middle Yukon	Upper Yukon	Other
1	Southern Bering Shelf	< 167°W	24-Aug	819	0.95 (0.89–0.98)	0.00 (0.00–0.00)	0.01 (0.00–0.01)	0.04 (0.02–0.11)
2	Northern Bering Shelf	60°N<>62°N	24-Sep	238	0.31 (0.23–0.37)	0.23 (0.15–0.30)	0.44 (0.37–0.52)	0.02 (0.00–0.08)
3	Northern Bering Shelf	62°N<>64.5°N	10-Sep	299	0.30 (0.25–0.35)	0.26 (0.20–0.32)	0.43 (0.37–0.50)	0.01 (0.00–0.03)
2 & 3	Northern Bering Shelf	60°N<>64.5°N	14-Sep	537	0.31 (0.26–0.35)	0.24 (0.20–0.29)	0.44 (0.40–0.49)	0.01 (0.00–0.03)

southern shelf region. Peak densities of juvenile Chinook salmon occurred in the shallowest water depths sampled during the survey. Significant numbers of juvenile Chinook salmon were estimated to be present in water depths shallower than could be sampled by the trawl gear (20 m).

Average sample dates of the genetic mixtures differed due to the order in which stations were sampled during the survey (Table 2). The average sample date of mixtures 1, 2, and 3 were: August 24, September 24, and September 10, respectively. The average sample date of mixtures 2 and 3 combined was September 16.

Stock mixtures differed by region and location (Table 2, Fig. 3). In the southern Bering Sea shelf (mixture 1), stock proportions were: 95% Coastal Western Alaska, 1% Upper Yukon, and 4% other western Alaska stock groups. In the northern Bering Shelf, mixture 2 contained 44% Upper Yukon, 23% Middle Yukon, and 31% Coastal Western Alaska stocks, and 2% other western Alaska stock groups. Mixture 3 was similar to mixture 2 with 43% Upper Yukon, 26% Middle Yukon, 30% Coastal Western Alaska, and 1% other western Alaska stock groups. Stock proportions from mixtures 2 and 3 combined, were 44% upper Yukon, 24% Middle Yukon, 31% Coastal Western Alaska stocks, and 1% other Western Alaska stock groups.

Stock proportions between juvenile populations and adult harvests were similar enough to discount significant bias due to incomplete sampling of the juvenile population within the northern shelf region. The proportion of the Coastal Western Alaska stock group in the juveniles from the northern shelf region (mixtures 2 and 3 combined, 31%, SD = 3%) was slightly higher than the proportion in the harvest (21%, SD = 8%), but within the range expected for Yukon River harvests (DuBois and DeCovich 2008). The proportion of the Middle Yukon River stock group in the juvenile population (24%, SD = 3%) was similar to the proportion observed in historic harvests (23%, SD = 10%). The proportion of the Upper Yukon stock group in the juvenile population (44%, SD = 3%) was lower than the average proportion in historic harvests (56%, SD = 8%), but higher than the proportion in recent harvests. The Upper Yukon stock group comprised 37% and 36% of the total harvest in 2007 and 2008, respectively (Bue and Hayes 2009).

Coded-wire tags all matched tag codes from the Whitehorse Rapids Fish Hatchery located near Whitehorse, Yukon. Coded-wire tag codes from juvenile Chinook salmon released by the Whitehorse Rapids Fish Hatchery in 2002 included release location codes (Table 3). Tag codes from 2007 only included information on agency and year of release. However, as no other tagged Canadian juvenile Chinook entered the ocean in the Bering Sea in 2007, it was possible to assign origin to the Whitehorse Rapids Fish Hatchery.

Coded-wire tags were recovered at the mouth of the Yukon River and just south of the Bering Strait (Fig. 4). Coded-wire tags from 2002 were recovered near the mouth of the Yukon River at 63°N and at 64.1°N. Coded-wire tags recovered from 2007 were all recovered just south of the Bering Strait at 65.2°N, confirming the presence of a northward migration corridor for juvenile Yukon Chinook salmon.

All coded-wire tagged juveniles were age-0 (or fall-type Chinook salmon), a known life-history feature of Chinook

Table 3. Coded-wire tag recoveries from juvenile Chinook salmon captured during U.S. BASIS surface trawl surveys on the eastern Bering Sea shelf, 2002–2007. Release information provided by the Whitehorse Rapids Fish Hatchery (YRJTC, 2009).

Freshwater Origin	Tag Code	Release Data		Recovery Data				
		Date	Weight (g)	Date	Latitude	Longitude	Length (mm)	Weight (g)
Whitehorse Rapids Hatchery: Michie Creek	185061	2-Jun-02	3.2	4-Oct-02	63.0°N	166.0°W	155	49
Whitehorse Rapids Hatchery: Michie Creek	185106	10-Jun-02	3.2	3-Oct-02	64.1°N	164.5°W	193	79
Whitehorse Rapids Hatchery: Wolf Creek	185102	2-Jun-02	3.1	3-Oct-02	64.1°N	164.5°W	153	43
Whitehorse Rapids Hatchery	18	2007	--	13-Sep-07	65.2°N	168.1°W	176	58
Whitehorse Rapids Hatchery	18	2007	--	13-Sep-07	65.2°N	168.1°W	125	18
Whitehorse Rapids Hatchery	18	2007	--	13-Sep-07	65.2°N	168.1°W	179	58

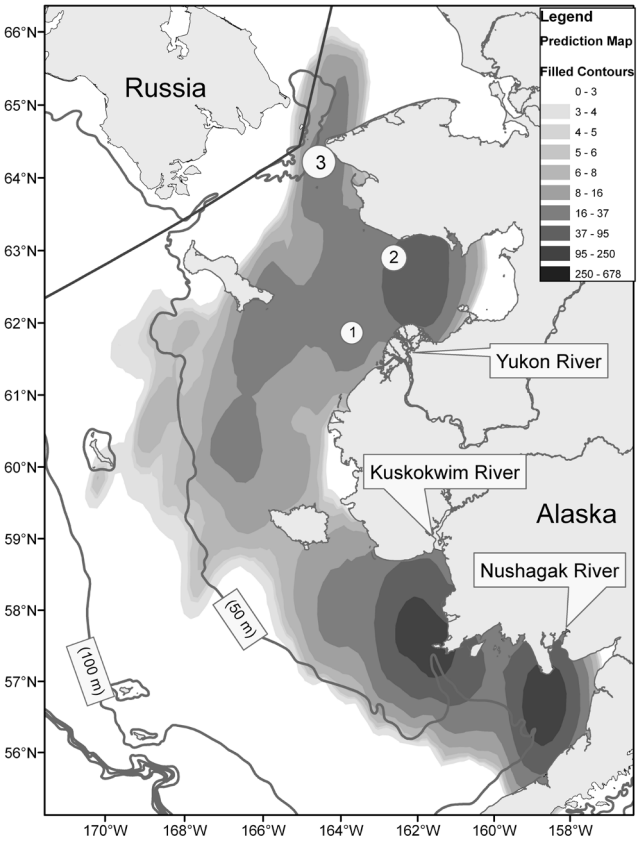

Fig. 4. Locations of coded-wire tag recoveries of Whitehorse Rapids Fish Hatchery Chinook salmon from the Yukon River during U.S. BASIS surface trawl surveys on the eastern Bering Sea shelf (mid August to early October), 2002–2007. Circles indicate coded-wire tag recovery locations and are overlaid on a map of juvenile Chinook salmon distribution. Numbers in each circle indicates the number of coded-wire tags recovered at each location and are overlaid on the CPUE prediction surface from a Kriging spatial model. Contours are shaded at geometric intervals of the prediction surface.

salmon produced from the Whitehorse Rapids Fish Hatchery. The size of hatchery juveniles (125–193 mm; 18–79 g) were significantly smaller than the average size of juvenile Chinook salmon captured during the survey (213 mm, 127 g), and hatchery juveniles still had visible parr marks at the time of capture (average date of September 10). The presence of parr marks on hatchery juveniles indicates an ocean entry date much later than most wild juvenile Chinook salmon on the eastern Bering Sea shelf and is consistent with their classification as ocean-type Chinook salmon.

DISCUSSION

The estuarine and early ocean habitats of juvenile salmon in the Bering Sea differ from juvenile salmon habitats in the Gulf of Alaska. Juvenile salmon occupy a broad shallow shelf with relatively stable waters in the Bering Sea. In the Gulf of Alaska, juvenile salmon occupy habitats ranging from a network of narrow corridors associated with fjords in southeast Alaska, to the narrow shelf and highly dynamic waters of northern California (Brodeur et al. 2000; Orsi et al. 2000). Migratory corridors of juvenile salmon in summer are largely thought to be constrained to epipelagic waters over the continental shelf once they reach the open ocean in the Gulf of Alaska (Brodeur et al. 2000; Orsi et al. 2000; Fisher et al. 2007). Juvenile salmon migratory corridors in all open ocean regions are most likely defined by oceanographic, not bathymetric features; however, the close association of these features in the Gulf of Alaska (Mundy 2005) often results in the use of the continental shelf to describe juvenile salmon migratory corridors. The broad continental shelf of the Bering Sea provides the opportunity to investigate biological and physical features such as water mass types and frontal regions that structure migratory pathways of juvenile salmon.

Juvenile Chinook salmon were primarily distributed within water depths < 50 m throughout their first summer at sea (middle of August through the middle of October) and the highest densities of juvenile Chinook salmon were found close to river mouths of primary Chinook salmon-producing rivers in the eastern Bering Sea (Yukon, Kuskokwim, and Nushagak rivers). This reflects a later dispersal from freshwater entry points than typically found in Gulf of Alaska stream-type Chinook salmon (Fisher et al. 2007). This is likely the effect of later ocean entry dates and slower marine dispersal rates of juvenile Chinook salmon on the eastern Bering Sea shelf.

Foraging behavior of salmon within the Coastal Domain may play a key role in defining juvenile Chinook salmon habitat and dispersal rates during their first summer at sea. The Coastal Domain is typically found in water depths < 50 m on the eastern Bering Sea Shelf (Schumacher and Stabeno 1998) and is associated with reduced water column stability, tight pelagic-benthic coupling, and high benthic productivity (Grebmeier et al. 2006). These structural components of the Coastal Domain favor forage fish species such as capelin and Pacific sand lance, which are the principal prey of juvenile Chinook salmon (Farley et al. in press). It is possible that feeding behavior of Chinook salmon on these forage fish species may be contributing to a delayed dispersal from the Coastal Domain. An apparent preference for the Coastal Domain is also seen in coho salmon (Farley et al. 2005) which also preferentially feed on the forage fish species in the Coastal Domain (Farley et al. in press).

The adequacy of the U.S. BASIS survey design for juvenile Chinook salmon populations differed by region. The broad migratory corridor of juvenile Chinook salmon and later survey sampling dates in the northern Bering Shelf region resulted in most juvenile Chinook salmon from this region present within trawlable habitats (> 20 m). The narrow migratory corridor and earlier sampling dates in the southern shelf region resulted in a higher proportion of the juvenile salmon population present in non-trawlable habitats. The inability to distinguish between primary stock groups contrib-

uting to the southern shelf index area also limits our ability to evaluate how well the survey reflects juvenile Chinook salmon stocks in this region.

Stock mixtures of juvenile salmon did not support significant northward migration of stocks from the southern shelf, reflecting limited mixing of salmon from different production regions during their first summer at sea. Juvenile Chinook salmon in the southern region were primarily from the Coastal Western Alaska stock group (95%). Therefore, the presence of juveniles from the southern region would increase the proportion of juvenile Chinook salmon assigned to the Coastal Western Alaska stock group. Similarity in juvenile salmon stock mixtures from both spatial strata in the northern region indicates that if juveniles from the southern shelf region were migrating north, they would need to be equally present in both northern spatial strata. This is unlikely, given the apparent dispersal rates of juvenile Chinook salmon from the southern region. Comparisons between stock proportions of the juvenile population in the northern shelf region and Yukon River harvests also did not support significant northward migration of southern stocks. If significant numbers of juvenile Chinook salmon from southern shelf were migrating north, the estimated proportions of the Coastal Western Alaska stock group would be significantly higher in the northern shelf region than expected for Yukon River Chinook salmon. The proportion of Coastal Western Alaska stocks in the northern shelf region was within the range expected for Yukon River Chinook salmon. Stock differences between the juveniles and historic harvests are most likely the result of reduced production of the Upper Yukon stock group relative to historic returns to the Yukon River (Bue and Hayes 2009). Limited northward migration of juvenile Chinook salmon from the southern shelf region is consistent with the interpretation of size and distribution data summarized by Farley et al. (2005).

Coded-wire tag recoveries of Yukon River Chinook salmon near the Bering Strait provide evidence that Yukon River Chinook salmon distributions can extend northward into the Bering Strait. The combined pattern of juvenile Chinook salmon distribution and coded-wire tag recoveries (Fig. 4) suggests that Yukon River Chinook salmon distributions can also extend into the Chukchi Sea. Although the proportion of Yukon River Chinook salmon that are believed to migrate into the Chukchi Sea is small relative to their total marine distribution, anticipated changes in Arctic climate and sea-ice levels could alter the proportion of Yukon River salmon migrating into the Chukchi Sea (Moss et al. 2009). The northward extension of juvenile Chinook salmon distribution into the Chukchi Sea was primarily due to catches in 2007—a year with record loss of Arctic sea ice and an exceptionally warm summer (Moss et al. 2009). Northward advection or migration of Yukon River Chinook salmon is in contrast to the lack of significant northward advection or migration observed in juvenile Chinook salmon from the southern shelf region. This may reflect differences in marine habitats (water depths, freshwater discharge levels, seasonal currents, surface temperatures, prey fields, e.g.) or simply differences in the behavior or life-history of juvenile Chinook salmon from the two regions.

Life-history differences between wild and hatchery fish can result in different marine distributions; therefore it is not appropriate to characterize the distribution of Yukon River stocks with hatchery coded-wire tag recoveries alone. Stock identification data are needed to adequately describe marine distributions. Wild Yukon River Chinook are characterized as stream-type Chinook salmon (also known as spring-type as they generally enter the marine habitat in the spring) (Gilbert 1922). Hatchery Yukon River Chinook salmon are characterized as ocean-type Chinook salmon (also known as fall-type as they enter the marine habitat in the fall), which have a freshwater age of zero (age-0) (YRJTC 2009). However, life histories of wild and hatchery Yukon River Chinook salmon are not completely unique. Several unmarked or wild juvenile Chinook salmon were similar in size to or smaller than hatchery Chinook salmon and had visible parr marks during September. This suggests that ocean-type or age-0 juveniles are present in wild populations; although, they are believed to represent only a minor portion of the total juvenile population. Size and timing of ocean entry of Yukon River Chinook salmon summarized by Martin et al. (1987) also suggests the presence of age-0, -1, and older Chinook salmon in wild Yukon River stocks. The presence of freshwater age-0 Yukon River Chinook salmon in wild populations emphasizes the importance of freshwater age plasticity in stream-type Chinook salmon as part of their natural life-history variation and not simply an artifact of hatchery rearing (Beckman and Dickhoff 1998).

The following conclusions can be made concerning the U.S. BASIS survey data as it applies to juvenile Chinook salmon populations on the eastern Bering Sea shelf. Juvenile Chinook salmon are present in non-trawlable habitats; therefore, the effect of non-trawlable habitats needs to be considered when applying survey data to juvenile Chinook salmon populations, particularly in the southern shelf region. Limited mixing of juvenile Chinook salmon from different production regions (northern and southern shelf regions) is thought to occur during their first summer at sea. However, stock mixtures of juvenile Chinook salmon within each region will be needed to evaluate the status of managed stock groups. Although Yukon River Chinook salmon stocks can extend northward into the Chukchi Sea, the proportion of Yukon River Chinook salmon present in the Chukchi Sea is small relative to the total marine distribution of juvenile Yukon River salmon. However, it is also important to recognize that changes in Arctic climate and the loss of sea ice could increase the proportion of Yukon River Chinook salmon present in the Chukchi Sea during their first summer at sea.

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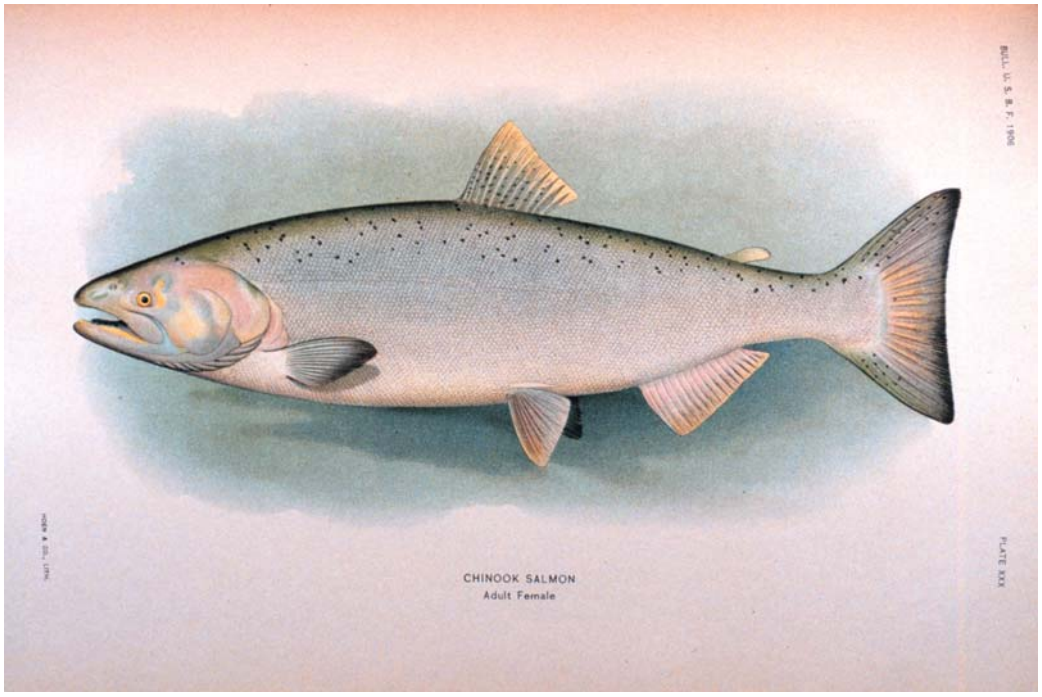
Appendix 4: Excerpts from the "Bering Sea Chinook Salmon Bycatch Management. Volume I Final Environmental Impact Statement"

Bering Sea Chinook Salmon Bycatch Management

Volume I
Final Environmental Impact Statement



North Pacific Fishery Management Council

United States Department of Commerce
National Oceanic and Atmospheric Administration
National Marine Fisheries Service, Alaska Region

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Bering Sea Chinook Salmon Bycatch Management

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FINAL ENVIRONMENTAL IMPACT STATEMENT

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Abstract: The Environmental Impact Statement (EIS) provides decision-makers and the public with an evaluation of the environmental effects of alternative measures to minimize Chinook salmon bycatch in the Bering Sea pollock fishery. The alternatives analyzed in this EIS generally involve limits or "caps" on the number of Chinook salmon that may be caught in the Bering Sea pollock fishery and closure of all or a part of the Bering Sea to pollock fishing once the cap is reached. These closures would occur when a Chinook salmon bycatch cap is reached, even if the entire pollock total allowable catch has not yet been harvested. This document addresses the requirements of the National Environmental Policy Act and other applicable federal law. The Regulatory Impact Review, in Volume II, provides decision-makers and the public with an evaluation of the social and economic effects of these alternatives to address the requirements of Executive Order 12866, Executive Order 12898, and other applicable federal law.

Table 3-6 Estimates of coefficients of variation of Chinook salmon bycatch estimates by season and calendar age based on the mean of 100 bootstrap samples of available length and age data.

A season	Age 3	Age 4	Age 5	Age 6	Age 7
1991	14%	6%	6%	10%	31%
1992	20%	9%	4%	9%	27%
1993	22%	9%	5%	10%	37%
1994	27%	12%	3%	10%	30%
1995	25%	12%	5%	6%	22%
1996	19%	6%	2%	9%	21%
1997	35%	12%	6%	7%	28%
1998	16%	9%	3%	10%	23%
1999	19%	10%	5%	11%	91%
2000	25%	9%	6%	9%	27%
2001	10%	6%	3%	7%	22%
2002	15%	6%	3%	4%	16%
2003	14%	6%	3%	8%	21%
2004	15%	6%	2%	5%	20%
2005	18%	6%	3%	7%	23%
2006	17%	5%	3%	7%	22%
2007	22%	5%	4%	8%	25%
B season	**Age 3**	**Age 4**	**Age 5**	**Age 6**	**Age 7**
1991	23%	8%	12%	27%	67%
1992	9%	9%	25%	69%	87%
1993	19%	4%	9%	20%	65%
1994	17%	6%	6%	14%	27%
1995	21%	5%	12%	23%	48%
1996	6%	3%	7%	11%	29%
1997	12%	3%	10%	12%	39%
1998	5%	6%	9%	23%	36%
1999	16%	3%	8%	22%	149%
2000	9%	5%	8%	25%	49%
2001	7%	3%	8%	20%	52%
2002	6%	2%	8%	17%	43%
2003	8%	3%	5%	15%	32%
2004	6%	2%	5%	12%	30%
2005	5%	2%	5%	10%	23%
2006	4%	3%	8%	15%	33%
2007	6%	2%	7%	13%	28%

3.3.2 Estimating genetic composition of Chinook salmon bycatch

This section provides an overview the best available information used to determine the region or river of origin of the Chinook salmon caught as bycatch in the Bering Sea pollock fishery. The AEQ model uses genetic estimates of Chinook salmon taken as bycatch in the Bering Sea pollock fishery to determine where the AEQ Chinook salmon would have returned. To determine the stock composition mixtures of Chinook salmon in the Bering Sea, the model uses best available genetics analysis from ADF&G scientists (Templin et al. 2008). Genetic stock identification estimated the relative composition of 15 regional groups in the bycatch samples. For this analysis, estimates are provided for the 8 largest contributing groups and the remaining components were combined into the 'other' category, resulting in 9 stock groups (Table 3-7).

A scale pattern analysis completed in 2003 estimated age and stock composition of Chinook salmon in the 1997-1999 BSAI groundfish fishery bycatch samples from the NMFS Groundfish Observer Program database (Myers et al. 2003). Results indicated that bycatch samples were dominated by younger (age 1.2) fish in summer and older (age 1.3 and 1.4) fish in winter (Myers et al. 2003). The stock structure was dominated by western Alaskan stocks, with the estimated overall stock composition of 56% western Alaska, 31% Cook Inlet, 8% Southeast Alaska-British Columbia and 5% Russia. Here "western Alaska" included the Yukon River, Kuskokwim River, and Bristol Bay (Nushagak and Togiak) rivers. Within this aggregate grouping, the proportion of the sub-regional stock composition estimates averaged 40% Yukon River, 34% Bristol Bay and 26% Kuskokwim Chinook salmon Table 3-8Myers et al. 2003).

For comparison against previous estimates, results from Myers and Rogers (1988) scale pattern analysis of bycatch samples from 1979-1982 (collected by U.S. foreign fishery observes on foreign or joint venture vessels in the Bering Sea EEZ) indicated that stock structure was dominated by western Alaskan stocks with estimated overall stock composition of 60% western Alaska, 17% South Central, 13% Asia (Russia) and 9% Southeast Alaska-British Columbia. Within the aggregated western Alaskan group, 17% were of Yukon River salmon, with 29% Bristol Bay and 24% Kuskokwim salmon.

As indicated in Myers et al. (2003), the origin of salmon also differs by season. In the winter, age-1.4 western Alaskan Chinook were primarily from the subregions of the Yukon and Kuskokwim. In the fall, results indicated that age-1.2 western Alaskan Chinook were from subregions of the Kuskokwim and Bristol Bay with a large component of Cook Inlet Chinook salmon stocks as well.

The proportions of western Alaskan subregional stocks (Yukon, Kuskokwim, and Bristol Bay) appear to vary considerably with factors such as brood year, time and area (Myers et al. 2003). Yukon River Chinook are often the dominant stock in winter while Bristol Bay, Cook Inlet, and other Gulf of Alaska stocks are often the dominant stocks in the eastern BSAI in the fall (Myers et al. 2003). Additional studies from high seas tagging results as well as scale pattern analyses from Japanese driftnet fishery in the Bering Sea indicate that in the summer immature western Alaskan Chinook are distributed further west in the Bering Sea than other North American stocks. For the scale-pattern analyses, freshwater-type (age 0.1, 0.2, etc) Chinook were omitted. Although the proportion of these samples were relatively small, the extent that Chinook bycatch could be attributed to southern stocks where this type is more common (e.g., from the Columbia River) may be underestimated in the Myers et al. (2003) analysis.

More recent analyses of bycatch samples are underway (Templin et al. 2008). For purposes of evaluation of impacts of alternatives on individual river systems, the most recent estimates (Seeb et al. 2008) are the main reference for evaluating the impact of bycatch on the 9 sets of river systems. These more recent estimates were chosen since they are most representative of the timeframe analyzed. Earlier work presented in Myers et al. (2003) had a different resolution to stock composition and was from samples covering an earlier period.

To illustrate the influence of bycatch temporal and spatial variability regarding bycatch stock composition, retrospective analyses were performed using the available genetics data collected from 2005-2007. We acknowledge that this assumption (i.e., constant stock composition within season-area strata) may be poor, especially for years beyond this period. For the main impact analysis the time period was selected to be from 2003-2007 which overlaps with the sample collection period and may reduce concerns about mis-matches between the sampling period for genetics work and the application period for impact analysis.

Scientists at ADF&G developed a DNA baseline to resolve the stock composition mixtures of Chinook salmon in the Bering Sea (Templin et al. 2008). This baseline includes 24,100 individuals sampled from

over 175 rivers from the Kamchatka Peninsula, Russia, to the central Valley in California (see Table 3-7 for list of rivers).

The Templin et al. (2008) genetic stock identification (GSI) study used classification criteria whereby the accuracy of resolution to region-of-origin must be greater than or equal to 90%. This analysis identified 15 regional groups for reporting results and for purposes of this analysis these were combined into nine stock units. The nine stock units are: Pacific Northwest (PNW, comprised of baseline stocks across BC, OR, WA and CA); Coastal western Alaska (Coast WAK comprised of the lower Yukon, the Kuskokwim River and Bristol Bay (Nushagak) river systems); Cook Inlet; Middle Yukon; Northern Alaska Peninsula (NAK Penin); Russia; Southeast and Transboundary River Systems (TBR); and Upper Yukon, while minor components in the bycatch are combined into the "other" category for clarity. Consistent with previous observations regarding the seasonal and regional differences in stock origin of bycatch samples (Myers et al. 2003), bycatch samples were stratified by year, season and region (Table 3-9).

The Seeb et al. (2008) study analyzed samples taken from the bycatch during the 2005 B season, both A and B seasons during 2006, and a sample from an excluder test fishery during the 2007 A season. Where possible, the genetics samples from the bycatch were segregated by major groundfish bycatch regions. Effectively, this entailed a single region for the entire fishery during winter (which is typically concentrated in space to the region east of 170°W) and two regions during the summer, a NW region (west of 170°W) and a southeast region (east of 170°W). The genetic sampling distribution varies considerably by season and region compared to the level of bycatch (as reported by the NMFS Alaska Region, Table 3-3).

The samples used in the Seeb et al. (2008) analysis were obtained opportunistically for a study to evaluate using scales and other tissues as collected by the NMFS observer program for genetic sampling. Unfortunately, during this study, the collected samples failed to cover the bycatch in groundfish fisheries in a comprehensive manner. For example, in 2005 most sampling was completed prior to the month (October) when most of the bycatch occurred (Fig. 3-5). To account for these sampling issues we computed a weighted average of the samples over years within regions and seasons. The 2005 B-season stock composition results were given one third of the weight since sampling effort was low during October of that year (relative to the bycatch) while the 2006 B-season stock composition data was given two-thirds of the weight in simulating stock apportionments. For the A season, the 2007 data (collected from a limited number of tows) were given one fifth the weight while the 2006 was weighted 4 times that value.

Once these mean stock composition estimates (and associated uncertainties) were obtained, it was necessary to apply the stratum-specific stock composition levels (Table 3-11) to the stratum specific bycatch totals to arrive at an annual stock-specific bycatch level for application in the model (Fig. 3-6). An important feature of this analysis is that the bycatch amounts by location and season were used explicitly for the estimates of the relative contribution of bycatch from different salmon regions (e.g. Fig. 3-8). This is also an important distinction from previous studies (e.g. Myers et al, 2003) which assumed that the stock identification samples were proportional to the season and area specific bycatch over all years.

For the purposes of assigning the bycatch to region of origin, the level of uncertainty is important to characterize. While there are many approaches to implement assignment uncertainty, the method chosen here assumes that the stratified stock composition estimates are unbiased and that the assignment uncertainty based on a classification algorithm (Seeb et al. 2008; Table 3-9) adequately represents the uncertainty (i.e., the estimates and their standard errors are used to propagate this component of uncertainty). Inter-annual variability is introduced two ways: (1) by accounting for inter-annual variability in bycatch among strata; and (2) by using the point estimates (and errors) from the data (Table

3-11) over the different years (2005-2007) while weighting appropriately for the sampling intensity. The procedure for introducing variability in regional stock assignments of bycatch followed a Monte Carlo procedure with the point estimates and their variances used to simulate beta distributed random variables (which have the desirable property of being bounded by 0.0 and 1.0) and applied to the catch weightings (for the summer/fall (B) season) where areas are disaggregated. Areas were combined for the winter fishery since the period of bycatch by the fishery is shorter and from a more restricted area.

Application of GSI to estimate the composition of the bycatch by reporting region suggests that, if the goal is to provide estimates on the stock composition of the bycatch, there is a need to adjust for the magnitude of bycatch occurring within substrata (e.g., east and west of 170°W during the B season, top panels of Fig. 3-6). Applying the stock composition results presented in Table 3-11 over different years and weighted by catch gives stratified proportions that have similar characteristics to the raw genetics data (Table 3-9). Importantly, these stratified stock composition estimates can be applied to bycatch levels in other years which will result in overall annual differences in bycatch proportions by salmon stock region. These simulations can be characterized graphically in a way that shows the covariance structure among regional stock composition estimates. This application extrapolates beyond the current analysis of these genetic data however and additional investigation of the temporal variation in stock composition is recommended.

The preliminary stock composition estimates for this more recent study based on the genetics are shown broken out by regions, year and season for the 9 stock units identified (Table 3-9). Accounting for sampling variability, the mean stock compositions by strata, and mean apportionments of the bycatch to stock (region) of origins by area and season of the pollock fishery are shown in Table 3-11.

While stock units differ from previous studies in levels of aggregation, results for western Alaskan aggregate river systems (e.g., AYK region) are similar to the scale-pattern study presented by Myers and Rogers (1988) and Myers et al. (2003; Table 3-12). The three studies indicate similarities in overall estimates of stock composition by river system even though aggregation levels, years of samples, and methodologies differ (Table 3-12). However, comparisons of stock composition estimates from other areas are more variable. For example the contribution from Cook Inlet stocks ranges from 4%-31% amongst studies while Russian stocks vary from 2%-14% (Table 3-12). There is particular variation amongst the two scale patterns studies (Myers and Rogers 1988 and Myers et al. 2003) for these other stocks. Due to this apparent variability the impact analysis focused mainly on the AYK stocks, in particular the Yukon, Kuskokwim and Bristol Bay river systems. Impacts are characterized in aggregate for these stocks, in aggregate for Coastal western Alaska grouping (which includes the lower Yukon, Kuskokwim and other minor stocks) as well as by individual river system. Impacts are reported in general for stocks such as Cook Inlet, aggregate Pacific Northwest, and Russia but discussions of these are limited due to the uncertainty.

For this impact analysis, it was desirable to provide some estimates of AEQ specific to the following western Alaska river systems individually: Yukon, Kuskokwim, Bristol Bay. The recent genetics study treated these stocks as a group. Thus, for purposes of discussion in this analysis, the AEQ results for the Coastal western Alaska stock grouping were combined with results for the middle and upper Yukon and the resulting aggregate broken out to individual river systems using the proportions estimated by Myers et al. (2003). Doing so provides a way to make rough comparisons of bycatch impacts (AEQ) and river system specific measures of run size, harvest, and escapement. However, impacts presented in this analysis are characterized to the extent possible within the limitations of the data. AEQ estimation was employed to provide some information on the relative impacts by genetic groupings and in conjunction with scale pattern estimates by western Alaskan river systems. As noted previously, these data are limited by their uncertainty thus extensions of these results beyond the scope of the data was carefully avoided.

Use of total run-size estimates for impact analysis by river system or in aggregate is problematic. As described in sections 5.2 assessment of total run size and escapement by river system is highly variable between systems. Some river systems in the WAK region lack total run or escapement estimates. As such, combining available estimates to determine an "aggregate total run" for WAK is inappropriate due to magnification of errors as well as masking the uncertainties and data limitations associated with individual river system estimates. Use of individual run estimates to compare with bycatch AEQ is also complicated by the caveats associated with the stock composition estimates. AEQ estimation to river of origin is used to estimate the relative changes under various cap scenarios. These estimates are also uncertain and that uncertainty increases with further extrapolations historically and to finer resolutions. Therefore, judgments with respect to detailed impacts were avoided, especially in cases where it would require interpretations beyond the extent of the data. Finally, impact rates by river system (i.e., explicit comparison of AEQ with run size for runs) would presume analyses on productivity thresholds about river systems that are beyond the scope of this analysis.

Additional funding and research focus is being directed towards both collection of samples from the EBS trawl fishery for Chinook salmon species as well as the related genetic analyses to estimate stock composition of the bycatch. Additional information on the status of these data collections and analysis programs will be forthcoming.

Table 3-7 Chinook baseline collections used in analysis of bycatch mixtures for genetics studies (from Templin et al. 2008).

No.	Region	Location	Years	N
1	Russia	Bistraya River	1998	94
2		Bolshaya River	1998, 2002	77
3		Kamchatka River (Late)	1997, 1998	119
4		Pakhatcha River	2002	50
5	Coast W AK (Norton Sound)	Pilgrim River	2005, 2006	82
6		Unalakleet River	2005	82
7		Golsovia River	2005, 2006	111
8	Coast W AK (Lower Yukon)	Andreafsky River	2002, 2003	236
9		Anvik River	2002	95
10		Gisasa River	2001	188
11		Tozitna River	2002, 2003	290
12	Middle Yukon	Henshaw Creek	2001	147
13		S. Fork Koyuk	2003	56
14		Kantishna River	2005	187
15		Chena River	2001	193
16		Salcha River	2005	188
17		Beaver Creek	1997	100
18		Chandalar River	2002, 2003, 2004	175
19		Sheenjek River	2002, 2004, 2006	51
20	Upper Yukon	Chandindu River	2000, 2001, 2003	247
21		Klondike River	1995, 2001, 2003	79
22		Stewart River	1997	99
23		Mayo River	1992, 1997, 2003	197
24		Blind River	2003	134
25		Pelly River	1996, 1997	140
26		Little Salmon River	1987, 1997	100
27		Big Salmon River	1987, 1997	117
28		Tatchun Creek	1987, 1996, 1997, 2002, 2003	369
29		Nordenskiold River	2003	55
30		Nisutlin River	19,871,997	56
31		Takhini River	1997, 2002, 2003	162
32		Whitehorse Hatchery	1985, 1987, 1997	242
33	Coast W AK (Kuskokwim)	Goodnews River	1993, 2005, 2006	368
34		Arolik River	2005	147
35		Kanektok River	1992, 1993, 2005	244
36		Eek River	2002, 2005	173
37		Kwethluk River	2001	96
38		Kisaralik River	2001, 2005	191
39		Tuluksak River	1993, 1994, 2005	195
40		Aniak River	2002, 2005, 2006	336
41		George River	2002, 2005	191
42		Kogrukluk River	1992, 1993, 2005	149
43		Stony River	1994	93
44		Cheeneetnuk River	2002, 2006	117
45		Gagaryah River	2006	190
46		Takotna River	1994, 2005	176
47	Upper Kuskokwim	Tatlawiksuk River	2002, 2005	191
48		Salmon River (Pitka Fork)	1995	96
49	Coast W AK (Bristol Bay)	Togiak River	1993, 1994	159
50		Nushagak River	1992, 1993	57
51		Mulchatna River	1994	97
52		Stuyahok River	1993, 1994	87
53		Naknek River	1995, 2004	110
54		Big Creek	2004	66
55		King Salmon River	2006	131
56	N. AK Peninsula	Meshik River	2006	42
57		Milky River	2006	67
58		Nelson River	2006	95
59		Black Hills Creek	2006	51
60		Steelhead Creek	2006	93
61	S. AK Peninsula	Chignik River	1995, 2006	75
62		Ayakulik River	1993, 2006	136
63		Karluk River	1993, 2006	140

Table 3-7 (continued) Chinook baseline collections used in analysis of bycatch mixtures for genetics studies (from Templin et al. 2008).

No.	Region	Location	Years	N
64	Cook Inlet	Deshka River	1995, 2005	251
65		Deception Creek	1991	67
66		Willow Creek	2005	73
67		Prairie Creek	1995	52
68		Talachulitna River	1995	58
69		Crescent Creek	2006	164
70		Juneau Creek	2005, 2006	119
71		Killey Creek	2005, 2006	266
72		Benjamin Creek	2005, 2006	205
73		Funny River	2005, 2006	220
74		Slikok Creek	2005	95
75		Kenai River (mainstem)	2003, 2004, 2006	302
76		Crooked Creek	1992, 2005	306
77		Kasilof River	2005	321
78		Anchor River	2006	200
79		Ninilchik River	2006	162
80	Upper Copper River	Indian River	2004, 2005	50
81		Bone Creek	2004, 2005	78
82		E. Fork Chistochina River	2004	145
83		Otter Creek	2005	128
84		Sinona Creek	2004, 2005	157
85	Lower Copper River	Gulkana River	2004	211
86		Mendeltna Creek	2004	144
87		Kiana Creek	2004	75
88		Manker Creek	2004, 2005	62
89		Tonsina River	2004, 2005	75
90		Tebay River	2004, 2005, 2006	68
91	Northern SE AK	Situk River	1988, 1990, 1991, 1992	143
92		Big Boulder Creek	1992, 1993, 1995, 2004	178
93		Tahini River	1992, 2004	169
94		Tahini River (LMH) Pullen Creek Hatchery	2005	83
95		Kelsall River	2004	96
96		King Salmon River	1989, 1990, 1993	144
97	Coast SE AK	King Creek	2003	143
98		Chickamin River	1990, 2003	56
99		Chickamin River - Little Port Walter	1993, 2005	126
100		Chickamin River - Whitman Lake Hatchery	1992, 1998, 2005	331
101		Humpy Creek	2003	94
102		Butler Creek	2004	95
103		Clear Creek	1989, 2003, 2004	166
104		Cripple Creek	1988, 2003	143
105		Genes Creek	1989, 2003, 2004	95
106		Kerr Creek	2003, 2004	151
107		Unuk River - Little Port Walter	2005	150
108		Unuk River - Deer Mountain Hatchery	1992, 1994	147
109		Keta River	1989, 2003	144
110		Blossom River	2004	95
111	Andrew Cr	Andrews Creek	1989, 2004	152
112		Crystal Lake Hatchery	1992, 1994, 2005	397
113		Medvejie Hatchery	1998, 2005	273
114		Hidden Falls Hatchery	1994, 1998	155
115		Macaulay Hatchery	2005	94
116	TBR Taku	Klukshu River	1989, 1990	174
117		Kowatua River	1989, 1990	144
118		Little Tatsemeanie River	1989, 1990, 2005	144
119		Upper Nahlin River	1989, 1990	130
120		Nakina River	1989, 1990	141
121		Dudidontu River	2005	86
122		Tahltan River	1989	95

Table 3-7 (continued) Chinook baseline collections used in analysis of bycatch mixtures for genetics studies (from Templin et al. 2008).

No.	Region	Location	Years	N
123	BC/WA/OR	Kateen River	2005	96
124		Damdochax Creek	1996	65
125		Kincolith Creek	1996	115
126		Kwinageese Creek	1996	73
127		Oweegee Creek	1996	81
128		Babine Creek	1996	167
129		Bulkley River	1999	91
130		Sustut	2001	130
131		Ecstall River	2001, 2002	86
132		Lower Kalum	2001	142
133		Lower Atnarko	1996	144
134		Kitimat	1997	141
135		Wannock	1996	144
136		Klinaklini	1997	83
137		Nanaimo	2002	95
138		Porteau Cove	2003	154
139		Conuma River	1997, 1998	110
140		Marble Creek	1996, 1999, 2000	144
141		Nitinat River	1996	104
142		Robertson Creek	1996, 2003	106
143		Sarita	1997, 2001	160
144		Big Qualicum River	1996	144
145		Quinsam River	1996	127
146		Morkill River	2001	154
147		Salmon River	1997	94
148		Swift	1996	163
149		Torpy River	2001	105
150		Chilko	1995, 1996, 1999, 2002	246
151		Nechako River	1996	121
152		Quesnel River	1996	144
153		Stuart	1997	161
154		Clearwater River	1997	153
155		Louis Creek	2001	179
156		Lower Adams	1996	46
157		Lower Thompson River	2001	100
158		Middle Shuswap	1986, 1997	144
159		Birkenhead Creek	1997, 1999, 2002, 2003	93
160		Harrison	2002	96
161		Makah National Fish Hatchery	2001, 2003	94
162		Forks	2005	150
163		Upper Skagit River	2006	93
164		Soos Creek Hatchery	2004	119
165		Lyons Ferry Hatchery	2002, 2003	191
166		Hanford Reach	2000, 2004, 2006	191
167		Lower Deschutes River	2002	96
168		Lower Kalama	2001	95
169		Carson Stock - Mid and Upper Columbia spring	2001	96
170		McKenzie - Willamette River	2004	95
171		Alsea	2004	93
172		Siuslaw	2001	95
173		Klamath	1990, 2006	52
174		Butte Creek	2003	96
175		Eel River	2000, 2001	88
176		Sacramento River - winter run	2005	95

Table 3-8 Maximum likelihood estimates (MLE) of the western Alaska subregional (Yukon, Kuskokwim, and Bristol Bay) stock composition of Chinook salmon in incidental catches by U.S. commercial groundfish fisheries in the eastern Bering Sea portion of the U.S. exclusive economic zone in 1997-1999 (from Myers et al. 2003). The estimates are summarized by (a) brood year (BY) 1991-1995 and (b) for the fishery area east of 170°W by fishery season, year, and age group. Fishery season: fall = July-December, winter = January-June. Numbers in parentheses are 95% confidence intervals (CI) derived from 1000 bootstrap runs (random sampling with replacement). An estimate of zero without a confidence interval indicates that the stock was not present and the data were re-analyzed without those baseline groups. Percentages represented by 0.0 are small numbers, less than 0.05 but greater than zero. Dashes indicate that no baseline data were available for that regional stock group.

Sample			Kamchatka		Yukon		Kuskokwim		Bristol Bay		Cook Inlet		SE Alaska		British Columbia	
Description	**Age(s)**	**N**	**MLE**	**(95% CI)**	**MLE**	**(95% CI)**	**MLE**	**(95% CI)**	**MLE**	**(95% CI)**	**MLE**	**(95% CI)**	**MLE**	**(95% CI)**	**MLE**	**(95% CI)**
(a) Summary by brood year:																
BY91	1.4-1.5	373	4.1	(0.0-10.0)	37.2	(17.2-56.1)	27.0	(4.4-47.4)	4.2	(0.0-12.1)	27.5	(18.3-37.5)	-	-	0	
BY92	1.3-1.5	530	6.0	(2.5-9.6)	29.7	(16.6-39.9)	5.5	(0.0-22.1)	21.0	(12.4-29.2)	33.4	(24.6-41.3)	-	-	4.4	(1.5-8.2)
BY93	1.2-1.4	1111	5.9	(3.0-9.5)	12.7	(4.0-23.2)	24.5	(11.4-37.3)	17.9	(11.1-25.3)	28.5	(21.8-34.1)	8.5	(5.7-11.2)	2.0	(0.0-4.1)
BY94	1.1-1.3	762	0		20.2	(12.3-30.4)	0		41.7	(33.9-49.7)	30.0	(20.5-37.5)	8.1	(5.1-11.8)	-	-
BY95	1.1-1.2	481	4.4	(0.1-10.2)	12.2	(4.2-20.7)	15.8	(6.7-24.1)	10.6	(0.0-28.1)	41.9	(28.4-52.4)	15.1	(9.2-22.0)	-	-
(b) Summary for the fishery area east of 170°W by fishery season, year, and age group:																
Fall 1998	1.1	134	0		6.1	(0-15.0)	3.9	(0-9.4)	0		57.7	(37.1-74.8)	32.3	(16.5-47.9)	-	-
Fall 1997	1.2	286	3.8	(0.0-8.7)	0.0	(0-13)	16.1	(1.7-25.4)	17.6	(9.5-28.5)	49.2	(37.1-58.5)	8.5	(3.7-14.5)	4.8	(0.2-10.5)
Fall 1998	1.2	249	0		10.2	(2.5-21.4)	0		41.4	(29.8-51.6)	38.7	(25.5-50.2)	9.7	(4.7-16.2)	-	-
Fall 1999	1.2	222	5.8	(0.0-12.9)	13.0	(2.0-25.3)	18.3	(5.6-33.3)	27.2	(4.5-50.2)	31.3	(16.3-44.7)	4.4	(0.0-9.8)	-	-
Winter 1997	1.3	240	5.7	(1.5-10.4)	24.6	(10.2-38.3)	5.9	(0.0-27.6)	28.0	(14.5-39.5)	30.0	(18.2-40.8)	-	-	5.8	(1.3-11.3)
Winter 1998	1.3	428	4.6	(0.8-9.7)	23.1	(11.2-36.9)	22.8	(6.7-38.8)	17.3	(8.8-27.3)	18.2	(9.9-26.4)	11.9	(7.5-16.3)	2.1	(0-6.3)
Winter 1999	1.3	279	0		34.7	(23.0-47.4)	0		37.6	(27.4-47.8)	18.5	(8.9-28.3)	9.2	(5.3-13.5)	-	-
Winter 1997	1.4	327	3.9	(0.0-9.7)	34.6	(14.8-53.7)	28.4	(6.8-48.9)	4.7	(0.0-13.4)	28.4	20.3-34.6)	-	-	0	
Winter 1998	1.4	178	10.9	(3.8-18.6)	35.0	(17.4-49.9)	12.8	(0.0-34.9)	10.1	(0.0-21.0)	31.2	(19.3-41.9)	-	-	0	
Winter 1999	1.4	122	22.0	(9.1-36.4)	9.9	(0.0-31.2)	32.2	(8.6-50)	2.9	(0-13.5)	28.2	(11.2-44.4)	4.8	(0-10.4)	0	

Table 3-9 ADF&G preliminary estimates of stock composition based on genetic samples stratified by year, season, and region (SE=east of 170°W, NW=west of 170°W). Standard errors of the estimates are shown in parentheses and were used to evaluate uncertainty of stock composition. Source: Seeb et al. 2008.

Year / Season / Area	PNW	Coast W AK	Cook Inlet	Middle Yukon	N AK Penin	Russia	TBR	Upper Yukon	Other
2005 B SE	45.3%	34.2%	5.3%	0.2%	8.8%	0.6%	3.3%	0.0%	2.4%
N = 313	(0.032)	(0.032)	(0.019)	(0.003)	(0.021)	(0.005)	(0.016)	(0.001)	(0.015)
2005 B NW	6.5%	70.9%	2.2%	4.7%	6.7%	2.0%	3.5%	2.8%	0.7%
N = 543	(0.012)	(0.047)	(0.011)	(0.013)	(0.042)	(0.007)	(0.012)	(0.009)	(0.008)
2006 B SE	38.4%	37.2%	7.5%	0.2%	7.0%	0.6%	4.3%	0.1%	4.7%
N = 309	(0.029)	(0.032)	(0.020)	(0.004)	(0.019)	(0.005)	(0.017)	(0.002)	(0.020)
2006 B NW	6.4%	67.3%	3.0%	8.0%	2.1%	3.3%	0.5%	8.0%	1.4%
N = 296	(0.016)	(0.035)	(0.020)	(0.020)	(0.016)	(0.013)	(0.007)	(0.019)	(0.014)
2006 A All	22.9%	38.2%	0.2%	1.1%	31.2%	1.1%	1.1%	2.3%	1.9%
N = 902	(0.015)	(0.038)	(0.004)	(0.005)	(0.039)	(0.004)	(0.007)	(0.006)	(0.011)
2007 A All	9.4%	75.2%	0.1%	0.5%	12.0%	0.2%	0.1%	0.1%	2.4%
N = 380	(0.016)	(0.031)	(0.004)	(0.005)	(0.025)	(0.003)	(0.002)	(0.003)	(0.014)

Table 3-10 NMFS regional office estimates of Chinook salmon bycatch in the pollock fishery compared to genetics sampling levels by season and region, 2005-2007 (SE=east of 170°W, NW=west of 170°W).

			Area			Area	
		Season	SE	NW	Total	SE	NW
Bycatch	2005	B	26,425	13,793	40,217	66%	34%
	2006	B	21,922	2,484	24,405	90%	10%
	2006	A			58,753		
	2007	A			69,261		
Genetic Samples	2005	B	489	282	771	63%	37%
	2006	B	286	304	590	48%	52%
	2006	A			801		
	2007	A			360		

Table 3-11 Mean values of catch-weighted stratified proportions of stock composition based on genetic sampling by season, and region (SE=east of 170°W, NW=west of 170°W). Standard errors of the estimates (in parentheses) were derived from 200 simulations based on the estimates from Table 3-9 and weighting annual results as explained in the text.

Season / Area	PNW	Coast W AK	Cook Inlet	Middle Yukon	N AK Penin	Russia	TBR	Upper Yukon	Other
B SE	45.0%	34.7%	5.1%	0.1%	8.6%	0.6%	3.4%	0.0%	2.4%
	(0.025)	(0.024)	(0.017)	(0.002)	(0.016)	(0.004)	(0.014)	(0.001)	(0.014)
B NW	6.4%	68.9%	2.6%	6.6%	4.4%	2.7%	1.8%	5.6%	1.0%
	(0.010)	(0.023)	(0.012)	(0.011)	(0.019)	(0.007)	(0.006)	(0.012)	(0.008)
A All	12.1%	67.7%	0.1%	0.6%	16.0%	0.4%	0.2%	0.6%	2.3%
	(0.012)	(0.021)	(0.003)	(0.004)	(0.019)	(0.002)	(0.002)	(0.003)	(0.010)

Table 3-12 Comparison of stock composition estimates for three different studies on Chinook bycatch samples taken from trawl fisheries in the eastern Bering Sea.

Study	Myers and Rogers (1988)				Myers et al (2003)			Seeb et al. 2008		
Years sampled	1979-1982				1997-1999			2005-2007[1]		
Stocks and estimated aggregate % composition in bycatch Smaller scale breakouts (where available) listed to the right (with associated % contrib. of aggregate below)	Western AK	60%			56%					
		Yukon	Bristol Bay	Kusko-kwim	Yukon	Bristol Bay	Kusko-kwim			
		17%	29%	24%	40%	34%	26%			
	Coastal WAK (also includes Norton Sound)							48%		
								Lower Yukon	Kusko-kwim	Bristol Bay
								Na	Na	Na
	Middle Yukon							3%		
	Upper Yukon							3%		
	NAK Penin							13%		
	Cook Inlet	17%			31%			4%		
	SEAK/Can	9%			8%					
	TBR							2%		
	PNW[2]							23%		
	Russia	14%			5%			2%		
	Other[3]							3%		

[1]note for purposes of comparison, only 2006 stock composition estimates *averaged annually and across regions* are shown here.

[2]PNW is an aggregate of 54 stocks from British Columbia, Washington, Oregon and California. For a full list of stocks included see Table 3-7

[3]'other' is comprised of minor components after aggregation to major river systems as described in Table 3-7.

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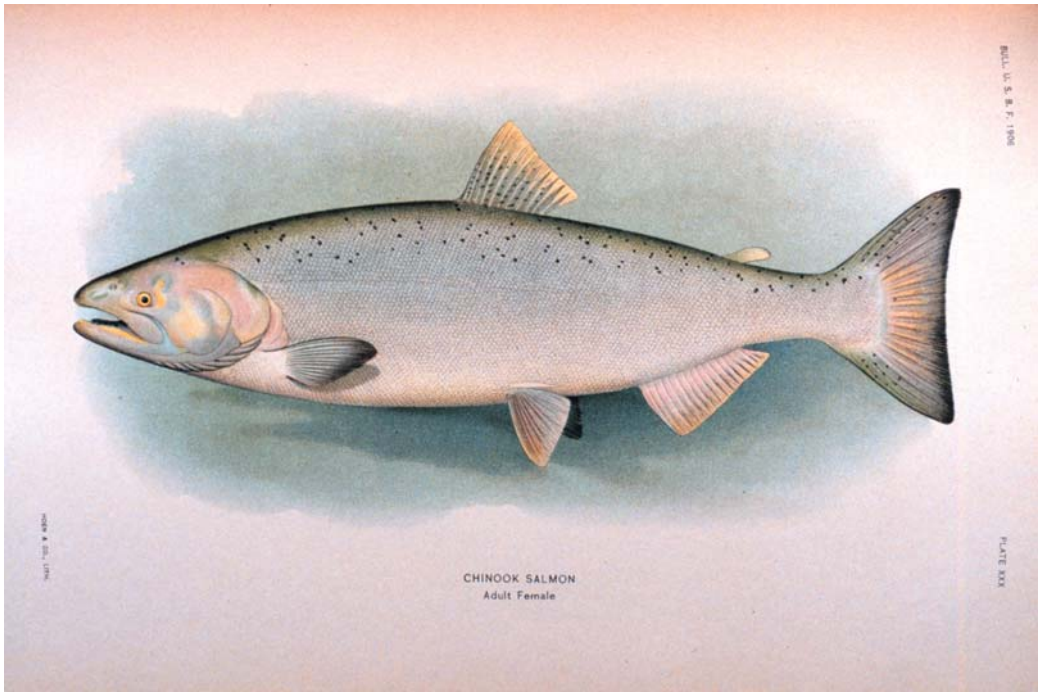

North Pacific Fishery Management Council

United States Department of Commerce
National Oceanic and Atmospheric Administration
National Marine Fisheries Service, Alaska Region

December 2009

Bering Sea Chinook Salmon Bycatch Management

Volume I
FINAL ENVIRONMENTAL IMPACT STATEMENT

December 2009

Lead Agency:	National Oceanic and Atmospheric Administration National Marine Fisheries Service Alaska Region Juneau, Alaska
Cooperating Agency:	State of Alaska Department of Fish and Game Juneau, Alaska
Responsible Official:	Robert D. Mecum Acting Administrator Alaska Region
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Abstract: The Environmental Impact Statement (EIS) provides decision-makers and the public with an evaluation of the environmental effects of alternative measures to minimize Chinook salmon bycatch in the Bering Sea pollock fishery. The alternatives analyzed in this EIS generally involve limits or "caps" on the number of Chinook salmon that may be caught in the Bering Sea pollock fishery and closure of all or a part of the Bering Sea to pollock fishing once the cap is reached. These closures would occur when a Chinook salmon bycatch cap is reached, even if the entire pollock total allowable catch has not yet been harvested. This document addresses the requirements of the National Environmental Policy Act and other applicable federal law. The Regulatory Impact Review, in Volume II, provides decision-makers and the public with an evaluation of the social and economic effects of these alternatives to address the requirements of Executive Order 12866, Executive Order 12898, and other applicable federal law.

Table 3-6 Estimates of coefficients of variation of Chinook salmon bycatch estimates by season and calendar age based on the mean of 100 bootstrap samples of available length and age data.

A season	Age 3	Age 4	Age 5	Age 6	Age 7
1991	14%	6%	6%	10%	31%
1992	20%	9%	4%	9%	27%
1993	22%	9%	5%	10%	37%
1994	27%	12%	3%	10%	30%
1995	25%	12%	5%	6%	22%
1996	19%	6%	2%	9%	21%
1997	35%	12%	6%	7%	28%
1998	16%	9%	3%	10%	23%
1999	19%	10%	5%	11%	91%
2000	25%	9%	6%	9%	27%
2001	10%	6%	3%	7%	22%
2002	15%	6%	3%	4%	16%
2003	14%	6%	3%	8%	21%
2004	15%	6%	2%	5%	20%
2005	18%	6%	3%	7%	23%
2006	17%	5%	3%	7%	22%
2007	22%	5%	4%	8%	25%
B season	**Age 3**	**Age 4**	**Age 5**	**Age 6**	**Age 7**
1991	23%	8%	12%	27%	67%
1992	9%	9%	25%	69%	87%
1993	19%	4%	9%	20%	65%
1994	17%	6%	6%	14%	27%
1995	21%	5%	12%	23%	48%
1996	6%	3%	7%	11%	29%
1997	12%	3%	10%	12%	39%
1998	5%	6%	9%	23%	36%
1999	16%	3%	8%	22%	149%
2000	9%	5%	8%	25%	49%
2001	7%	3%	8%	20%	52%
2002	6%	2%	8%	17%	43%
2003	8%	3%	5%	15%	32%
2004	6%	2%	5%	12%	30%
2005	5%	2%	5%	10%	23%
2006	4%	3%	8%	15%	33%
2007	6%	2%	7%	13%	28%

3.3.2 Estimating genetic composition of Chinook salmon bycatch

This section provides an overview the best available information used to determine the region or river of origin of the Chinook salmon caught as bycatch in the Bering Sea pollock fishery. The AEQ model uses genetic estimates of Chinook salmon taken as bycatch in the Bering Sea pollock fishery to determine where the AEQ Chinook salmon would have returned. To determine the stock composition mixtures of Chinook salmon in the Bering Sea, the model uses best available genetics analysis from ADF&G scientists (Templin et al. 2008). Genetic stock identification estimated the relative composition of 15 regional groups in the bycatch samples. For this analysis, estimates are provided for the 8 largest contributing groups and the remaining components were combined into the 'other' category, resulting in 9 stock groups (Table 3-7).

A scale pattern analysis completed in 2003 estimated age and stock composition of Chinook salmon in the 1997-1999 BSAI groundfish fishery bycatch samples from the NMFS Groundfish Observer Program database (Myers et al. 2003). Results indicated that bycatch samples were dominated by younger (age 1.2) fish in summer and older (age 1.3 and 1.4) fish in winter (Myers et al. 2003). The stock structure was dominated by western Alaskan stocks, with the estimated overall stock composition of 56% western Alaska, 31% Cook Inlet, 8% Southeast Alaska-British Columbia and 5% Russia. Here "western Alaska" included the Yukon River, Kuskokwim River, and Bristol Bay (Nushagak and Togiak) rivers. Within this aggregate grouping, the proportion of the sub-regional stock composition estimates averaged 40% Yukon River, 34% Bristol Bay and 26% Kuskokwim Chinook salmon Table 3-8Myers et al. 2003).

For comparison against previous estimates, results from Myers and Rogers (1988) scale pattern analysis of bycatch samples from 1979-1982 (collected by U.S. foreign fishery observes on foreign or joint venture vessels in the Bering Sea EEZ) indicated that stock structure was dominated by western Alaskan stocks with estimated overall stock composition of 60% western Alaska, 17% South Central, 13% Asia (Russia) and 9% Southeast Alaska-British Columbia. Within the aggregated western Alaskan group, 17% were of Yukon River salmon, with 29% Bristol Bay and 24% Kuskokwim salmon.

As indicated in Myers et al. (2003), the origin of salmon also differs by season. In the winter, age-1.4 western Alaskan Chinook were primarily from the subregions of the Yukon and Kuskokwim. In the fall, results indicated that age-1.2 western Alaskan Chinook were from subregions of the Kuskokwim and Bristol Bay with a large component of Cook Inlet Chinook salmon stocks as well.

The proportions of western Alaskan subregional stocks (Yukon, Kuskokwim, and Bristol Bay) appear to vary considerably with factors such as brood year, time and area (Myers et al. 2003). Yukon River Chinook are often the dominant stock in winter while Bristol Bay, Cook Inlet, and other Gulf of Alaska stocks are often the dominant stocks in the eastern BSAI in the fall (Myers et al. 2003). Additional studies from high seas tagging results as well as scale pattern analyses from Japanese driftnet fishery in the Bering Sea indicate that in the summer immature western Alaskan Chinook are distributed further west in the Bering Sea than other North American stocks. For the scale-pattern analyses, freshwater-type (age 0.1, 0.2, etc) Chinook were omitted. Although the proportion of these samples were relatively small, the extent that Chinook bycatch could be attributed to southern stocks where this type is more common (e.g., from the Columbia River) may be underestimated in the Myers et al. (2003) analysis.

More recent analyses of bycatch samples are underway (Templin et al. 2008). For purposes of evaluation of impacts of alternatives on individual river systems, the most recent estimates (Seeb et al. 2008) are the main reference for evaluating the impact of bycatch on the 9 sets of river systems. These more recent estimates were chosen since they are most representative of the timeframe analyzed. Earlier work presented in Myers et al. (2003) had a different resolution to stock composition and was from samples covering an earlier period.

To illustrate the influence of bycatch temporal and spatial variability regarding bycatch stock composition, retrospective analyses were performed using the available genetics data collected from 2005-2007. We acknowledge that this assumption (i.e., constant stock composition within season-area strata) may be poor, especially for years beyond this period. For the main impact analysis the time period was selected to be from 2003-2007 which overlaps with the sample collection period and may reduce concerns about mis-matches between the sampling period for genetics work and the application period for impact analysis.

Scientists at ADF&G developed a DNA baseline to resolve the stock composition mixtures of Chinook salmon in the Bering Sea (Templin et al. 2008). This baseline includes 24,100 individuals sampled from

over 175 rivers from the Kamchatka Peninsula, Russia, to the central Valley in California (see Table 3-7 for list of rivers).

The Templin et al. (2008) genetic stock identification (GSI) study used classification criteria whereby the accuracy of resolution to region-of-origin must be greater than or equal to 90%. This analysis identified 15 regional groups for reporting results and for purposes of this analysis these were combined into nine stock units. The nine stock units are: Pacific Northwest (PNW, comprised of baseline stocks across BC, OR, WA and CA); Coastal western Alaska (Coast WAK comprised of the lower Yukon, the Kuskokwim River and Bristol Bay (Nushagak) river systems); Cook Inlet; Middle Yukon; Northern Alaska Peninsula (NAK Penin); Russia; Southeast and Transboundary River Systems (TBR); and Upper Yukon, while minor components in the bycatch are combined into the "other" category for clarity. Consistent with previous observations regarding the seasonal and regional differences in stock origin of bycatch samples (Myers et al. 2003), bycatch samples were stratified by year, season and region (Table 3-9).

The Seeb et al. (2008) study analyzed samples taken from the bycatch during the 2005 B season, both A and B seasons during 2006, and a sample from an excluder test fishery during the 2007 A season. Where possible, the genetics samples from the bycatch were segregated by major groundfish bycatch regions. Effectively, this entailed a single region for the entire fishery during winter (which is typically concentrated in space to the region east of 170°W) and two regions during the summer, a NW region (west of 170°W) and a southeast region (east of 170°W). The genetic sampling distribution varies considerably by season and region compared to the level of bycatch (as reported by the NMFS Alaska Region, Table 3-3).

The samples used in the Seeb et al. (2008) analysis were obtained opportunistically for a study to evaluate using scales and other tissues as collected by the NMFS observer program for genetic sampling. Unfortunately, during this study, the collected samples failed to cover the bycatch in groundfish fisheries in a comprehensive manner. For example, in 2005 most sampling was completed prior to the month (October) when most of the bycatch occurred (Fig. 3-5). To account for these sampling issues we computed a weighted average of the samples over years within regions and seasons. The 2005 B-season stock composition results were given one third of the weight since sampling effort was low during October of that year (relative to the bycatch) while the 2006 B-season stock composition data was given two-thirds of the weight in simulating stock apportionments. For the A season, the 2007 data (collected from a limited number of tows) were given one fifth the weight while the 2006 was weighted 4 times that value.

Once these mean stock composition estimates (and associated uncertainties) were obtained, it was necessary to apply the stratum-specific stock composition levels (Table 3-11) to the stratum specific bycatch totals to arrive at an annual stock-specific bycatch level for application in the model (Fig. 3-6). An important feature of this analysis is that the bycatch amounts by location and season were used explicitly for the estimates of the relative contribution of bycatch from different salmon regions (e.g. Fig. 3-8). This is also an important distinction from previous studies (e.g. Myers et al, 2003) which assumed that the stock identification samples were proportional to the season and area specific bycatch over all years.

For the purposes of assigning the bycatch to region of origin, the level of uncertainty is important to characterize. While there are many approaches to implement assignment uncertainty, the method chosen here assumes that the stratified stock composition estimates are unbiased and that the assignment uncertainty based on a classification algorithm (Seeb et al. 2008; Table 3-9) adequately represents the uncertainty (i.e., the estimates and their standard errors are used to propagate this component of uncertainty). Inter-annual variability is introduced two ways: (1) by accounting for inter-annual variability in bycatch among strata; and (2) by using the point estimates (and errors) from the data (Table

3-11) over the different years (2005-2007) while weighting appropriately for the sampling intensity. The procedure for introducing variability in regional stock assignments of bycatch followed a Monte Carlo procedure with the point estimates and their variances used to simulate beta distributed random variables (which have the desirable property of being bounded by 0.0 and 1.0) and applied to the catch weightings (for the summer/fall (B) season) where areas are disaggregated. Areas were combined for the winter fishery since the period of bycatch by the fishery is shorter and from a more restricted area.

Application of GSI to estimate the composition of the bycatch by reporting region suggests that, if the goal is to provide estimates on the stock composition of the bycatch, there is a need to adjust for the magnitude of bycatch occurring within substrata (e.g., east and west of 170°W during the B season, top panels of Fig. 3-6). Applying the stock composition results presented in Table 3-11 over different years and weighted by catch gives stratified proportions that have similar characteristics to the raw genetics data (Table 3-9). Importantly, these stratified stock composition estimates can be applied to bycatch levels in other years which will result in overall annual differences in bycatch proportions by salmon stock region. These simulations can be characterized graphically in a way that shows the covariance structure among regional stock composition estimates. This application extrapolates beyond the current analysis of these genetic data however and additional investigation of the temporal variation in stock composition is recommended.

The preliminary stock composition estimates for this more recent study based on the genetics are shown broken out by regions, year and season for the 9 stock units identified (Table 3-9). Accounting for sampling variability, the mean stock compositions by strata, and mean apportionments of the bycatch to stock (region) of origins by area and season of the pollock fishery are shown in Table 3-11.

While stock units differ from previous studies in levels of aggregation, results for western Alaskan aggregate river systems (e.g., AYK region) are similar to the scale-pattern study presented by Myers and Rogers (1988) and Myers et al. (2003; Table 3-12). The three studies indicate similarities in overall estimates of stock composition by river system even though aggregation levels, years of samples, and methodologies differ (Table 3-12). However, comparisons of stock composition estimates from other areas are more variable. For example the contribution from Cook Inlet stocks ranges from 4%-31% amongst studies while Russian stocks vary from 2%-14% (Table 3-12). There is particular variation amongst the two scale patterns studies (Myers and Rogers 1988 and Myers et al. 2003) for these other stocks. Due to this apparent variability the impact analysis focused mainly on the AYK stocks, in particular the Yukon, Kuskokwim and Bristol Bay river systems. Impacts are characterized in aggregate for these stocks, in aggregate for Coastal western Alaska grouping (which includes the lower Yukon, Kuskokwim and other minor stocks) as well as by individual river system. Impacts are reported in general for stocks such as Cook Inlet, aggregate Pacific Northwest, and Russia but discussions of these are limited due to the uncertainty.

For this impact analysis, it was desirable to provide some estimates of AEQ specific to the following western Alaska river systems individually: Yukon, Kuskokwim, Bristol Bay. The recent genetics study treated these stocks as a group. Thus, for purposes of discussion in this analysis, the AEQ results for the Coastal western Alaska stock grouping were combined with results for the middle and upper Yukon and the resulting aggregate broken out to individual river systems using the proportions estimated by Myers et al. (2003). Doing so provides a way to make rough comparisons of bycatch impacts (AEQ) and river system specific measures of run size, harvest, and escapement. However, impacts presented in this analysis are characterized to the extent possible within the limitations of the data. AEQ estimation was employed to provide some information on the relative impacts by genetic groupings and in conjunction with scale pattern estimates by western Alaskan river systems. As noted previously, these data are limited by their uncertainty thus extensions of these results beyond the scope of the data was carefully avoided.

Use of total run-size estimates for impact analysis by river system or in aggregate is problematic. As described in sections 5.2 assessment of total run size and escapement by river system is highly variable between systems. Some river systems in the WAK region lack total run or escapement estimates. As such, combining available estimates to determine an "aggregate total run" for WAK is inappropriate due to magnification of errors as well as masking the uncertainties and data limitations associated with individual river system estimates. Use of individual run estimates to compare with bycatch AEQ is also complicated by the caveats associated with the stock composition estimates. AEQ estimation to river of origin is used to estimate the relative changes under various cap scenarios. These estimates are also uncertain and that uncertainty increases with further extrapolations historically and to finer resolutions. Therefore, judgments with respect to detailed impacts were avoided, especially in cases where it would require interpretations beyond the extent of the data. Finally, impact rates by river system (i.e., explicit comparison of AEQ with run size for runs) would presume analyses on productivity thresholds about river systems that are beyond the scope of this analysis.

Additional funding and research focus is being directed towards both collection of samples from the EBS trawl fishery for Chinook salmon species as well as the related genetic analyses to estimate stock composition of the bycatch. Additional information on the status of these data collections and analysis programs will be forthcoming.

Table 3-7 Chinook baseline collections used in analysis of bycatch mixtures for genetics studies (from Templin et al. 2008).

No.	Region	Location	Years	N
1	Russia	Bistraya River	1998	94
2		Bolshaya River	1998, 2002	77
3		Kamchatka River (Late)	1997, 1998	119
4		Pakhatcha River	2002	50
5	Coast W AK (Norton Sound)	Pilgrim River	2005, 2006	82
6		Unalakleet River	2005	82
7		Golsovia River	2005, 2006	111
8	Coast W AK (Lower Yukon)	Andreafsky River	2002, 2003	236
9		Anvik River	2002	95
10		Gisasa River	2001	188
11		Tozitna River	2002, 2003	290
12	Middle Yukon	Henshaw Creek	2001	147
13		S. Fork Koyuk	2003	56
14		Kantishna River	2005	187
15		Chena River	2001	193
16		Salcha River	2005	188
17		Beaver Creek	1997	100
18		Chandalar River	2002, 2003, 2004	175
19		Sheenjek River	2002, 2004, 2006	51
20	Upper Yukon	Chandindu River	2000, 2001, 2003	247
21		Klondike River	1995, 2001, 2003	79
22		Stewart River	1997	99
23		Mayo River	1992, 1997, 2003	197
24		Blind River	2003	134
25		Pelly River	1996, 1997	140
26		Little Salmon River	1987, 1997	100
27		Big Salmon River	1987, 1997	117
28		Tatchun Creek	1987, 1996, 1997, 2002, 2003	369
29		Nordenskiold River	2003	55
30		Nisutlin River	19,871,997	56
31		Takhini River	1997, 2002, 2003	162
32		Whitehorse Hatchery	1985, 1987, 1997	242
33	Coast W AK (Kuskokwim)	Goodnews River	1993, 2005, 2006	368
34		Arolik River	2005	147
35		Kanektok River	1992, 1993, 2005	244
36		Eek River	2002, 2005	173
37		Kwethluk River	2001	96
38		Kisaralik River	2001, 2005	191
39		Tuluksak River	1993, 1994, 2005	195
40		Aniak River	2002, 2005, 2006	336
41		George River	2002, 2005	191
42		Kogrukluk River	1992, 1993, 2005	149
43		Stony River	1994	93
44		Cheeneetnuk River	2002, 2006	117
45		Gagaryah River	2006	190
46		Takotna River	1994, 2005	176
47	Upper Kuskokwim	Tatlawiksuk River	2002, 2005	191
48		Salmon River (Pitka Fork)	1995	96
49	Coast W AK (Bristol Bay)	Togiak River	1993, 1994	159
50		Nushagak River	1992, 1993	57
51		Mulchatna River	1994	97
52		Stuyahok River	1993, 1994	87
53		Naknek River	1995, 2004	110
54		Big Creek	2004	66
55		King Salmon River	2006	131
56	N. AK Peninsula	Meshik River	2006	42
57		Milky River	2006	67
58		Nelson River	2006	95
59		Black Hills Creek	2006	51
60		Steelhead Creek	2006	93
61	S. AK Peninsula	Chignik River	1995, 2006	75
62		Ayakulik River	1993, 2006	136
63		Karluk River	1993, 2006	140

Table 3-7 (continued) Chinook baseline collections used in analysis of bycatch mixtures for genetics studies (from Templin et al. 2008).

No.	Region	Location	Years	N
64	Cook Inlet	Deshka River	1995, 2005	251
65		Deception Creek	1991	67
66		Willow Creek	2005	73
67		Prairie Creek	1995	52
68		Talachulitna River	1995	58
69		Crescent Creek	2006	164
70		Juneau Creek	2005, 2006	119
71		Killey Creek	2005, 2006	266
72		Benjamin Creek	2005, 2006	205
73		Funny River	2005, 2006	220
74		Slikok Creek	2005	95
75		Kenai River (mainstem)	2003, 2004, 2006	302
76		Crooked Creek	1992, 2005	306
77		Kasilof River	2005	321
78		Anchor River	2006	200
79		Ninilchik River	2006	162
80	Upper Copper River	Indian River	2004, 2005	50
81		Bone Creek	2004, 2005	78
82		E. Fork Chistochina River	2004	145
83		Otter Creek	2005	128
84		Sinona Creek	2004, 2005	157
85	Lower Copper River	Gulkana River	2004	211
86		Mendeltna Creek	2004	144
87		Kiana Creek	2004	75
88		Manker Creek	2004, 2005	62
89		Tonsina River	2004, 2005	75
90		Tebay River	2004, 2005, 2006	68
91	Northern SE AK	Situk River	1988, 1990, 1991, 1992	143
92		Big Boulder Creek	1992, 1993, 1995, 2004	178
93		Tahini River	1992, 2004	169
94		Tahini River (LMH) Pullen Creek Hatchery	2005	83
95		Kelsall River	2004	96
96		King Salmon River	1989, 1990, 1993	144
97	Coast SE AK	King Creek	2003	143
98		Chickamin River	1990, 2003	56
99		Chickamin River - Little Port Walter	1993, 2005	126
100		Chickamin River - Whitman Lake Hatchery	1992, 1998, 2005	331
101		Humpy Creek	2003	94
102		Butler Creek	2004	95
103		Clear Creek	1989, 2003, 2004	166
104		Cripple Creek	1988, 2003	143
105		Genes Creek	1989, 2003, 2004	95
106		Kerr Creek	2003, 2004	151
107		Unuk River - Little Port Walter	2005	150
108		Unuk River - Deer Mountain Hatchery	1992, 1994	147
109		Keta River	1989, 2003	144
110		Blossom River	2004	95
111	Andrew Cr	Andrews Creek	1989, 2004	152
112		Crystal Lake Hatchery	1992, 1994, 2005	397
113		Medvejie Hatchery	1998, 2005	273
114		Hidden Falls Hatchery	1994, 1998	155
115		Macaulay Hatchery	2005	94
116	TBR Taku	Klukshu River	1989, 1990	174
117		Kowatua River	1989, 1990	144
118		Little Tatsemeanie River	1989, 1990, 2005	144
119		Upper Nahlin River	1989, 1990	130
120		Nakina River	1989, 1990	141
121		Dudidontu River	2005	86
122		Tahltan River	1989	95

Table 3-7 (continued) Chinook baseline collections used in analysis of bycatch mixtures for genetics studies (from Templin et al. 2008).

No.	Region	Location	Years	N
123	BC/WA/OR	Kateen River	2005	96
124		Damdochax Creek	1996	65
125		Kincolith Creek	1996	115
126		Kwinageese Creek	1996	73
127		Oweegee Creek	1996	81
128		Babine Creek	1996	167
129		Bulkley River	1999	91
130		Sustut	2001	130
131		Ecstall River	2001, 2002	86
132		Lower Kalum	2001	142
133		Lower Atnarko	1996	144
134		Kitimat	1997	141
135		Wannock	1996	144
136		Klinaklini	1997	83
137		Nanaimo	2002	95
138		Porteau Cove	2003	154
139		Conuma River	1997, 1998	110
140		Marble Creek	1996, 1999, 2000	144
141		Nitinat River	1996	104
142		Robertson Creek	1996, 2003	106
143		Sarita	1997, 2001	160
144		Big Qualicum River	1996	144
145		Quinsam River	1996	127
146		Morkill River	2001	154
147		Salmon River	1997	94
148		Swift	1996	163
149		Torpy River	2001	105
150		Chilko	1995, 1996, 1999, 2002	246
151		Nechako River	1996	121
152		Quesnel River	1996	144
153		Stuart	1997	161
154		Clearwater River	1997	153
155		Louis Creek	2001	179
156		Lower Adams	1996	46
157		Lower Thompson River	2001	100
158		Middle Shuswap	1986, 1997	144
159		Birkenhead Creek	1997, 1999, 2002, 2003	93
160		Harrison	2002	96
161		Makah National Fish Hatchery	2001, 2003	94
162		Forks	2005	150
163		Upper Skagit River	2006	93
164		Soos Creek Hatchery	2004	119
165		Lyons Ferry Hatchery	2002, 2003	191
166		Hanford Reach	2000, 2004, 2006	191
167		Lower Deschutes River	2002	96
168		Lower Kalama	2001	95
169		Carson Stock - Mid and Upper Columbia spring	2001	96
170		McKenzie - Willamette River	2004	95
171		Alsea	2004	93
172		Siuslaw	2001	95
173		Klamath	1990, 2006	52
174		Butte Creek	2003	96
175		Eel River	2000, 2001	88
176		Sacramento River - winter run	2005	95

Table 3-8 Maximum likelihood estimates (MLE) of the western Alaska subregional (Yukon, Kuskokwim, and Bristol Bay) stock composition of Chinook salmon in incidental catches by U.S. commercial groundfish fisheries in the eastern Bering Sea portion of the U.S. exclusive economic zone in 1997-1999 (from Myers et al. 2003). The estimates are summarized by (a) brood year (BY) 1991-1995 and (b) for the fishery area east of 170°W by fishery season, year, and age group. Fishery season: fall = July-December, winter = January-June. Numbers in parentheses are 95% confidence intervals (CI) derived from 1000 bootstrap runs (random sampling with replacement). An estimate of zero without a confidence interval indicates that the stock was not present and the data were re-analyzed without those baseline groups. Percentages represented by 0.0 are small numbers, less than 0.05 but greater than zero. Dashes indicate that no baseline data were available for that regional stock group.

Sample			Kamchatka		Yukon		Kuskokwim		Bristol Bay		Cook Inlet		SE Alaska		British Columbia	
Description	**Age(s)**	**N**	**MLE**	**(95% CI)**	**MLE**	**(95% CI)**	**MLE**	**(95% CI)**	**MLE**	**(95% CI)**	**MLE**	**(95% CI)**	**MLE**	**(95% CI)**	**MLE**	**(95% CI)**
(a) Summary by brood year:																
BY91	1.4-1.5	373	4.1	(0.0-10.0)	37.2	(17.2-56.1)	27.0	(4.4-47.4)	4.2	(0.0-12.1)	27.5	(18.3-37.5)	-	-	0	
BY92	1.3-1.5	530	6.0	(2.5-9.6)	29.7	(16.6-39.9)	5.5	(0.0-22.1)	21.0	(12.4-29.2)	33.4	(24.6-41.3)	-	-	4.4	(1.5-8.2)
BY93	1.2-1.4	1111	5.9	(3.0-9.5)	12.7	(4.0-23.2)	24.5	(11.4-37.3)	17.9	(11.1-25.3)	28.5	(21.8-34.1)	8.5	(5.7-11.2)	2.0	(0.0-4.1)
BY94	1.1-1.3	762	0		20.2	(12.3-30.4)	0		41.7	(33.9-49.7)	30.0	(20.5-37.5)	8.1	(5.1-11.8)	-	-
BY95	1.1-1.2	481	4.4	(0.1-10.2)	12.2	(4.2-20.7)	15.8	(6.7-24.1)	10.6	(0.0-28.1)	41.9	(28.4-52.4)	15.1	(9.2-22.0)	-	-
(b) Summary for the fishery area east of 170°W by fishery season, year, and age group:																
Fall 1998	1.1	134	0		6.1	(0-15.0)	3.9	(0-9.4)	0		57.7	(37.1-74.8)	32.3	(16.5-47.9)	-	-
Fall 1997	1.2	286	3.8	(0.0-8.7)	0.0	(0-13)	16.1	(1.7-25.4)	17.6	(9.5-28.5)	49.2	(37.1-58.5)	8.5	(3.7-14.5)	4.8	(0.2-10.5)
Fall 1998	1.2	249	0		10.2	(2.5-21.4)	0		41.4	(29.8-51.6)	38.7	(25.5-50.2)	9.7	(4.7-16.2)	-	-
Fall 1999	1.2	222	5.8	(0.0-12.9)	13.0	(2.0-25.3)	18.3	(5.6-33.3)	27.2	(4.5-50.2)	31.3	(16.3-44.7)	4.4	(0.0-9.8)	-	-
Winter 1997	1.3	240	5.7	(1.5-10.4)	24.6	(10.2-38.3)	5.9	(0.0-27.6)	28.0	(14.5-39.5)	30.0	(18.2-40.8)	-	-	5.8	(1.3-11.3)
Winter 1998	1.3	428	4.6	(0.8-9.7)	23.1	(11.2-36.9)	22.8	(6.7-38.8)	17.3	(8.8-27.3)	18.2	(9.9-26.4)	11.9	(7.5-16.3)	2.1	(0-6.3)
Winter 1999	1.3	279	0		34.7	(23.0-47.4)	0		37.6	(27.4-47.8)	18.5	(8.9-28.3)	9.2	(5.3-13.5)	-	-
Winter 1997	1.4	327	3.9	(0.0-9.7)	34.6	(14.8-53.7)	28.4	(6.8-48.9)	4.7	(0.0-13.4)	28.4	20.3-34.6)	-	-	0	
Winter 1998	1.4	178	10.9	(3.8-18.6)	35.0	(17.4-49.9)	12.8	(0.0-34.9)	10.1	(0.0-21.0)	31.2	(19.3-41.9)	-	-	0	
Winter 1999	1.4	122	22.0	(9.1-36.4)	9.9	(0.0-31.2)	32.2	(8.6-50)	2.9	(0-13.5)	28.2	(11.2-44.4)	4.8	(0-10.4)	0	

Table 3-9 ADF&G preliminary estimates of stock composition based on genetic samples stratified by year, season, and region (SE=east of 170°W, NW=west of 170°W). Standard errors of the estimates are shown in parentheses and were used to evaluate uncertainty of stock composition. Source: Seeb et al. 2008.

Year / Season / Area	PNW	Coast W AK	Cook Inlet	Middle Yukon	N AK Penin	Russia	TBR	Upper Yukon	Other
2005 B SE	45.3%	34.2%	5.3%	0.2%	8.8%	0.6%	3.3%	0.0%	2.4%
N = 313	(0.032)	(0.032)	(0.019)	(0.003)	(0.021)	(0.005)	(0.016)	(0.001)	(0.015)
2005 B NW	6.5%	70.9%	2.2%	4.7%	6.7%	2.0%	3.5%	2.8%	0.7%
N = 543	(0.012)	(0.047)	(0.011)	(0.013)	(0.042)	(0.007)	(0.012)	(0.009)	(0.008)
2006 B SE	38.4%	37.2%	7.5%	0.2%	7.0%	0.6%	4.3%	0.1%	4.7%
N = 309	(0.029)	(0.032)	(0.020)	(0.004)	(0.019)	(0.005)	(0.017)	(0.002)	(0.020)
2006 B NW	6.4%	67.3%	3.0%	8.0%	2.1%	3.3%	0.5%	8.0%	1.4%
N = 296	(0.016)	(0.035)	(0.020)	(0.020)	(0.016)	(0.013)	(0.007)	(0.019)	(0.014)
2006 A All	22.9%	38.2%	0.2%	1.1%	31.2%	1.1%	1.1%	2.3%	1.9%
N = 902	(0.015)	(0.038)	(0.004)	(0.005)	(0.039)	(0.004)	(0.007)	(0.006)	(0.011)
2007 A All	9.4%	75.2%	0.1%	0.5%	12.0%	0.2%	0.1%	0.1%	2.4%
N = 380	(0.016)	(0.031)	(0.004)	(0.005)	(0.025)	(0.003)	(0.002)	(0.003)	(0.014)

Table 3-10 NMFS regional office estimates of Chinook salmon bycatch in the pollock fishery compared to genetics sampling levels by season and region, 2005-2007 (SE=east of 170°W, NW=west of 170°W).

			Area			Area	
		Season	SE	NW	Total	SE	NW
Bycatch	2005	B	26,425	13,793	40,217	66%	34%
	2006	B	21,922	2,484	24,405	90%	10%
	2006	A			58,753		
	2007	A			69,261		
Genetic Samples	2005	B	489	282	771	63%	37%
	2006	B	286	304	590	48%	52%
	2006	A			801		
	2007	A			360		

Table 3-11 Mean values of catch-weighted stratified proportions of stock composition based on genetic sampling by season, and region (SE=east of 170°W, NW=west of 170°W). Standard errors of the estimates (in parentheses) were derived from 200 simulations based on the estimates from Table 3-9 and weighting annual results as explained in the text.

Season / Area	PNW	Coast W AK	Cook Inlet	Middle Yukon	N AK Penin	Russia	TBR	Upper Yukon	Other
B SE	45.0%	34.7%	5.1%	0.1%	8.6%	0.6%	3.4%	0.0%	2.4%
	(0.025)	(0.024)	(0.017)	(0.002)	(0.016)	(0.004)	(0.014)	(0.001)	(0.014)
B NW	6.4%	68.9%	2.6%	6.6%	4.4%	2.7%	1.8%	5.6%	1.0%
	(0.010)	(0.023)	(0.012)	(0.011)	(0.019)	(0.007)	(0.006)	(0.012)	(0.008)
A All	12.1%	67.7%	0.1%	0.6%	16.0%	0.4%	0.2%	0.6%	2.3%
	(0.012)	(0.021)	(0.003)	(0.004)	(0.019)	(0.002)	(0.002)	(0.003)	(0.010)

Table 3-12 Comparison of stock composition estimates for three different studies on Chinook bycatch samples taken from trawl fisheries in the eastern Bering Sea.

Study	Myers and Rogers (1988)				Myers et al (2003)			Seeb et al. 2008		
Years sampled	1979-1982				1997-1999			2005-2007[1]		
Stocks and estimated aggregate % composition in bycatch Smaller scale breakouts (where available) listed to the right (with associated % contrib. of aggregate below)	Western AK	60%			56%					
		Yukon	Bristol Bay	Kusko-kwim	Yukon	Bristol Bay	Kusko-kwim			
		17%	29%	24%	40%	34%	26%			
	Coastal WAK (also includes Norton Sound)							48%		
								Lower Yukon	Kusko-kwim	Bristol Bay
								Na	Na	Na
	Middle Yukon							3%		
	Upper Yukon							3%		
	NAK Penin							13%		
	Cook Inlet	17%			31%			4%		
	SEAK/Can	9%			8%					
	TBR							2%		
	PNW[2]							23%		
	Russia	14%			5%			2%		
	Other[3]							3%		

[1]note for purposes of comparison, only 2006 stock composition estimates *averaged annually and across regions* are shown here.

[2]PNW is an aggregate of 54 stocks from British Columbia, Washington, Oregon and California. For a full list of stocks included see Table 3-7

[3]'other' is comprised of minor components after aggregation to major river systems as described in Table 3-7.

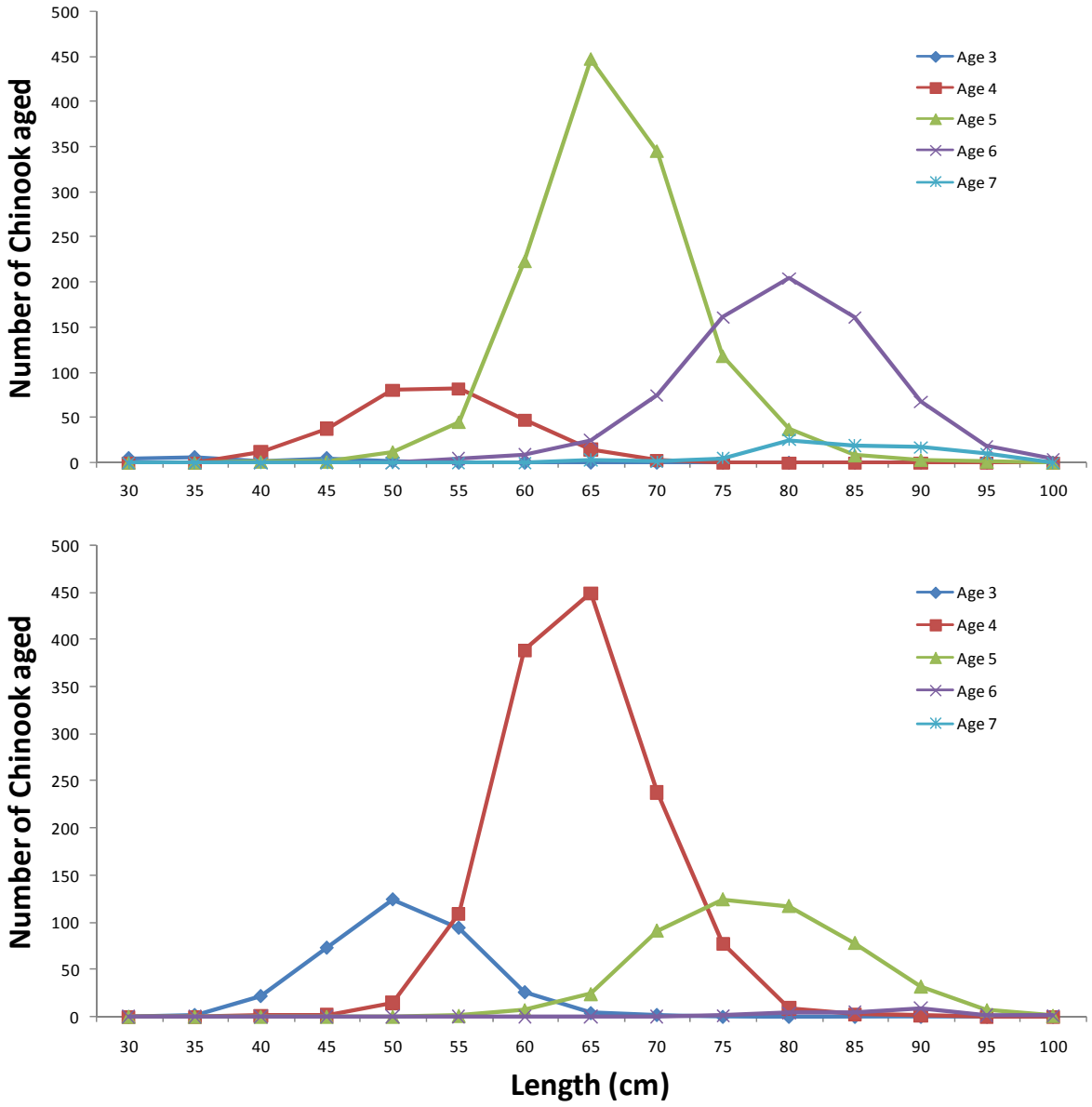

Fig. 3-1 Summary distribution of age samples by length collected by the NMFS groundfish observer program during 1997-1999 and analyzed by University of Washington scientists (Myers et al. (2003) for the A-season (top panel) and B season (bottom panel).

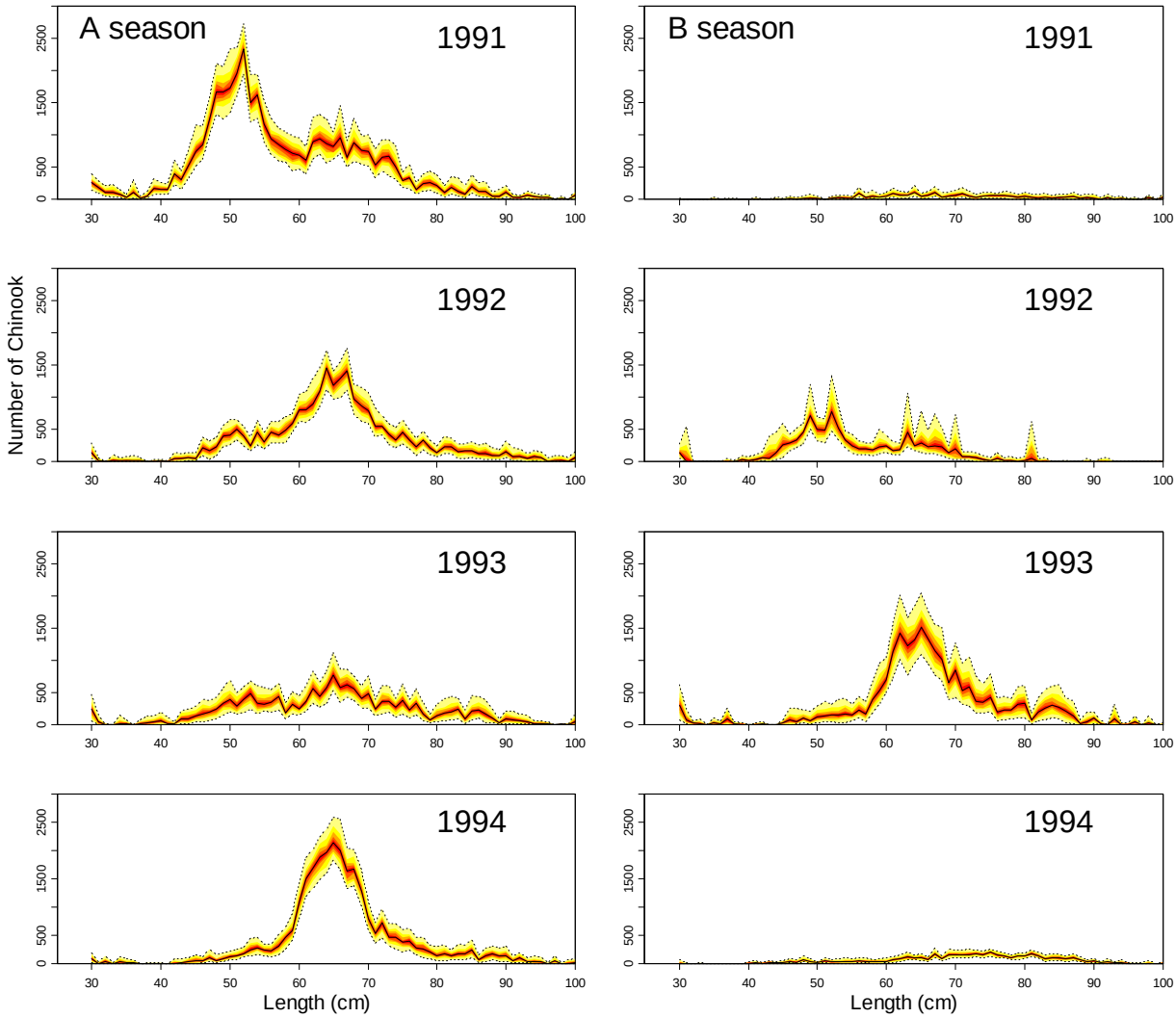

Fig. 3-2 Length frequency by season and year of Chinook salmon occurring as bycatch in the pollock fishery. Error distributions based on two-stage bootstrap re-sampling procedure.

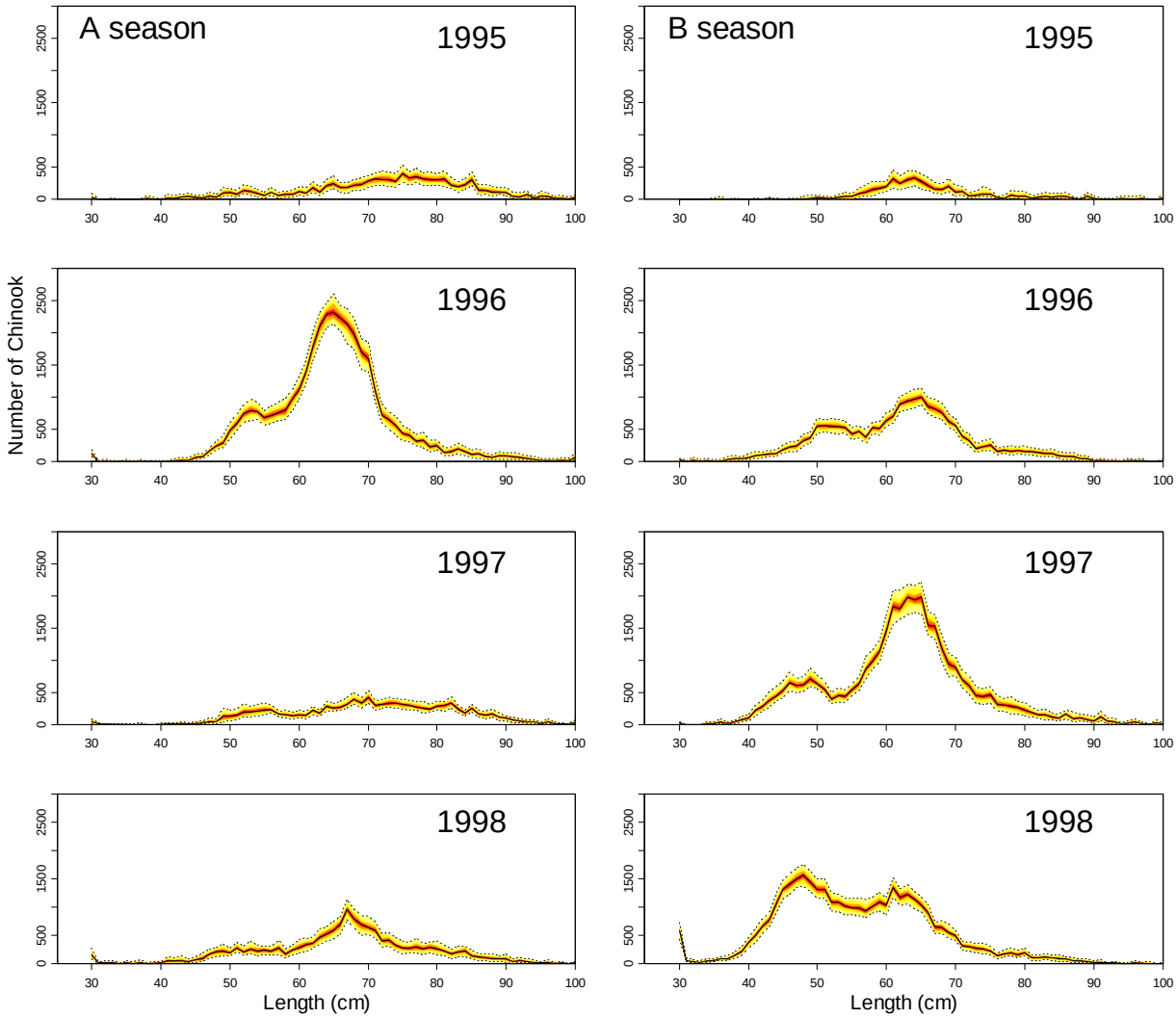

Fig. 3-2 (continued) Length frequency by season and year of Chinook salmon occurring as bycatch in the pollock fishery. Error distributions based on two-stage bootstrap re-sampling procedure.

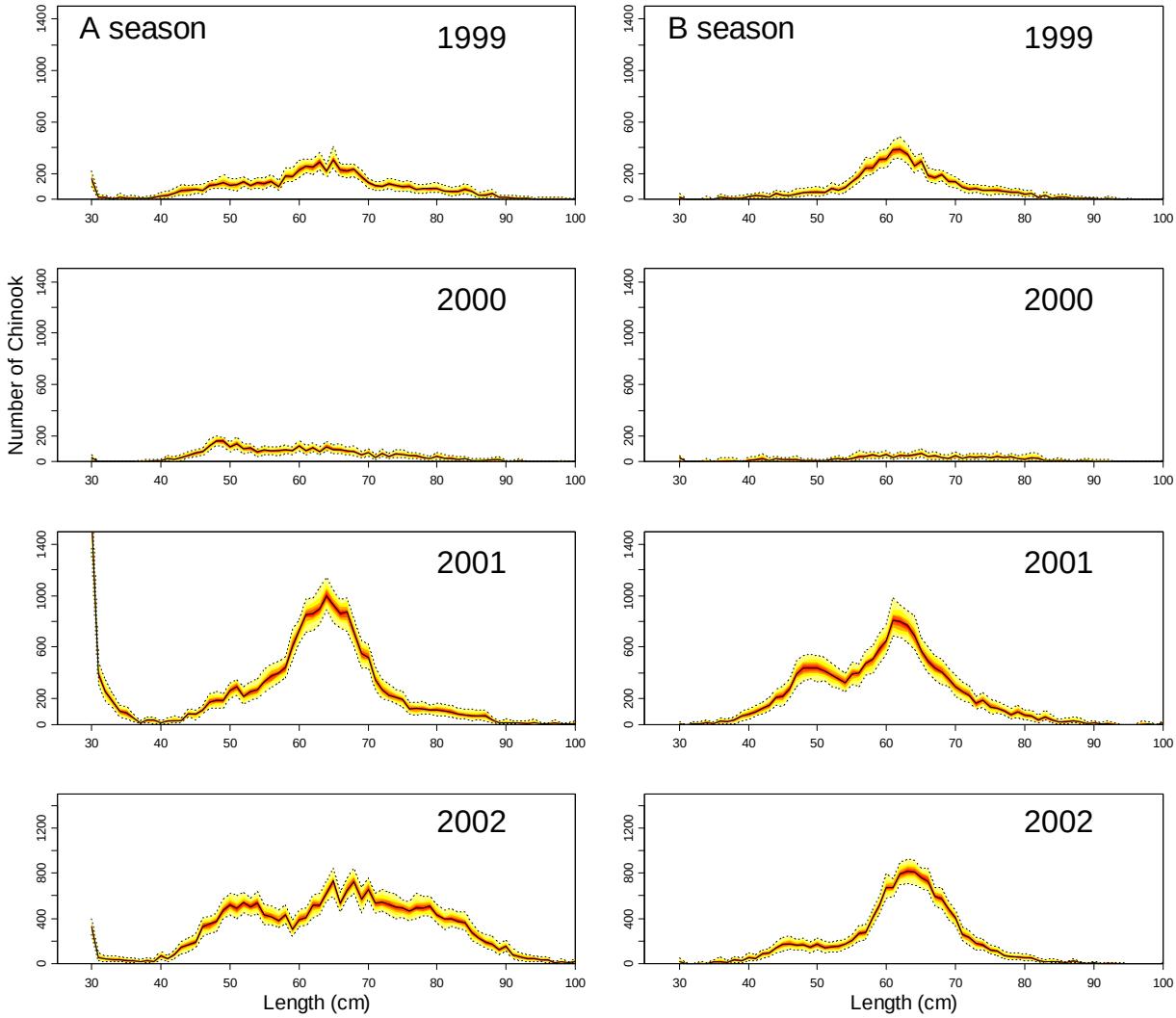

Fig. 3-2 (continued) Length frequency by season and year of Chinook salmon occurring as bycatch in the pollock fishery. Error distributions based on two-stage bootstrap re-sampling procedure.

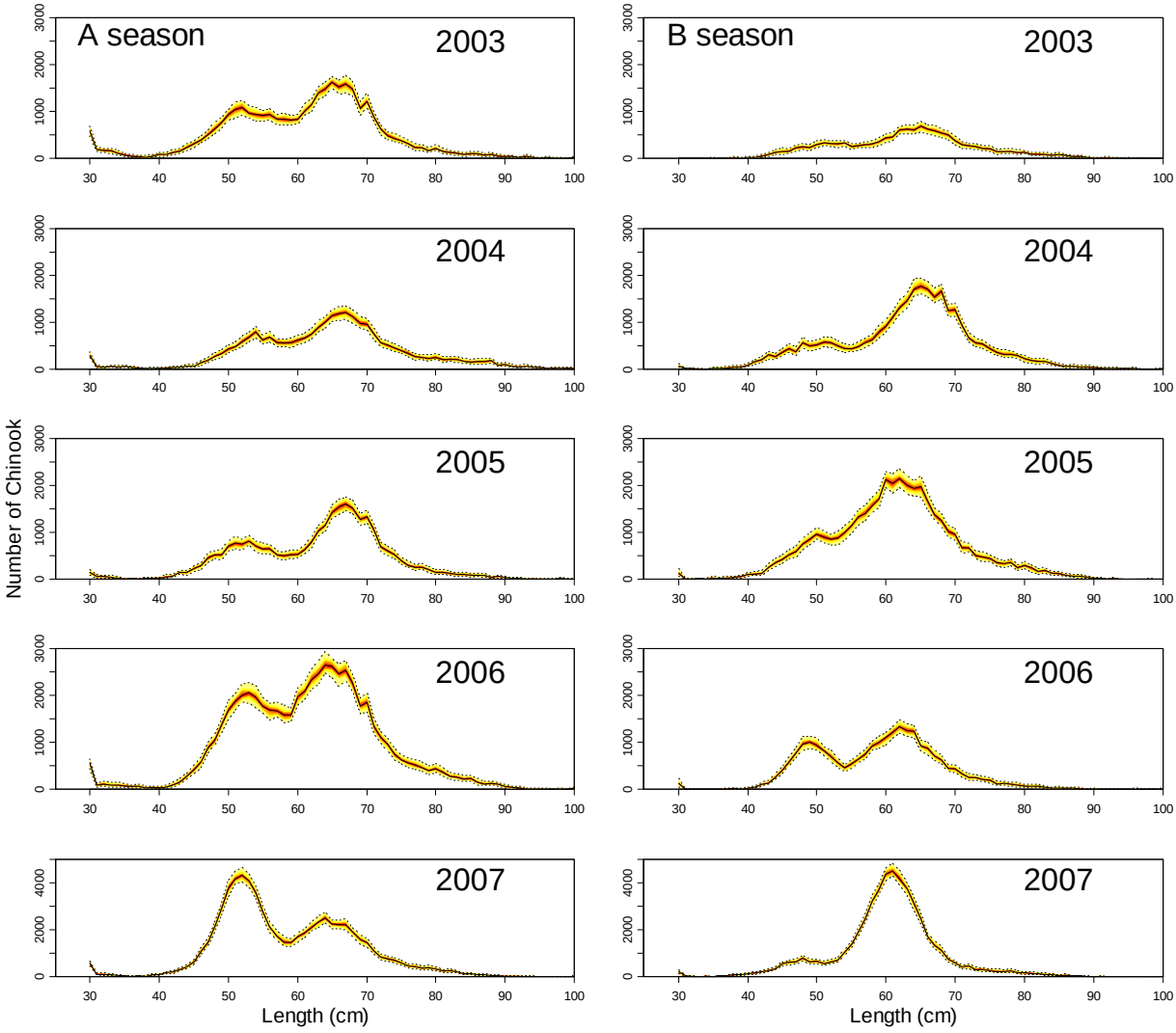

Fig. 3-2 (continued) Length frequency by season and year of Chinook salmon occurring as bycatch in the pollock fishery. Error distributions based on two-stage bootstrap re-sampling procedure.

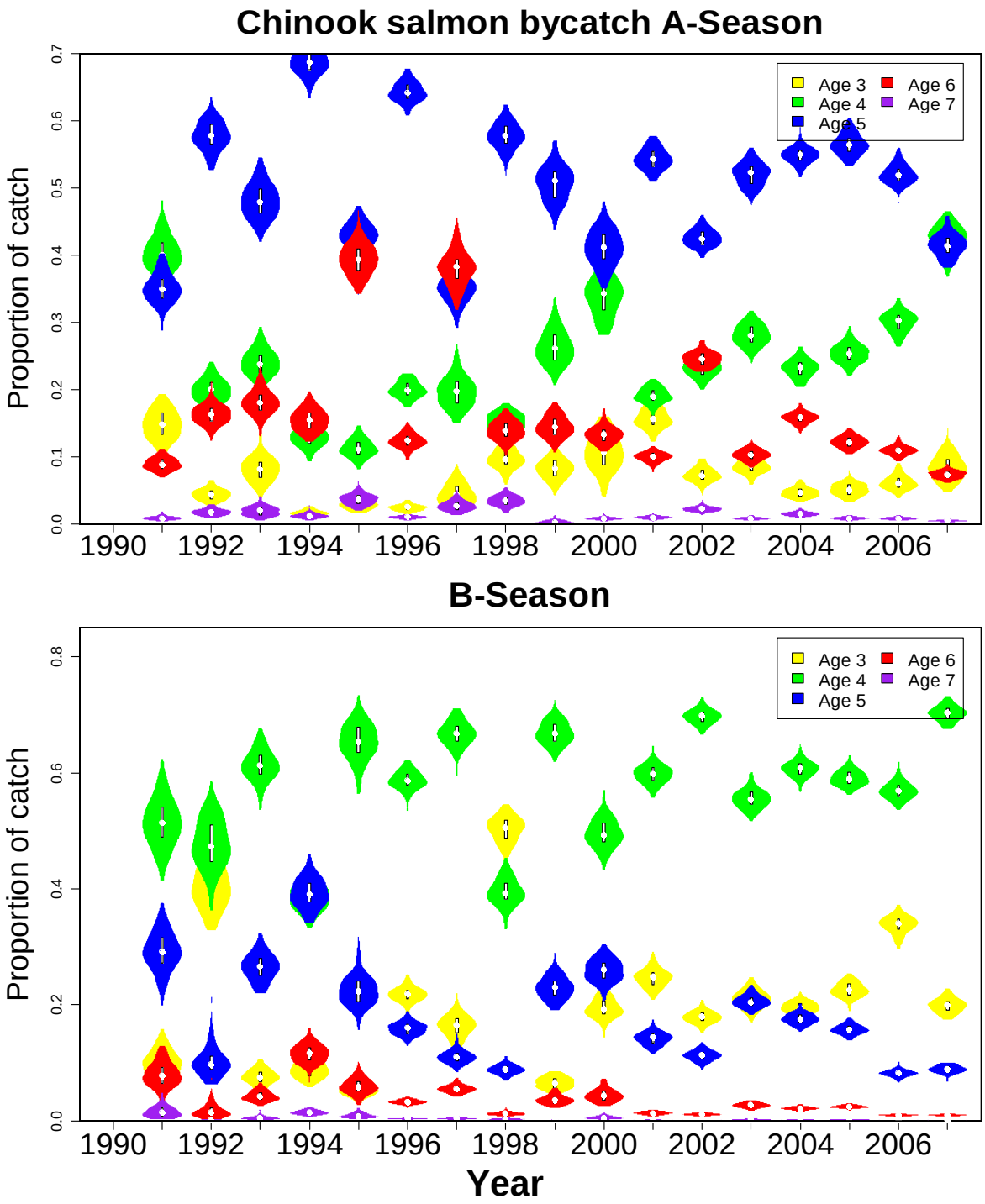

Fig. 3-3 Chinook salmon bycatch age composition by year and A-season (top) and B-season (bottom). Vertical spread of blobs represent uncertainty as estimated from the two-stage bootstrap re-sampling procedure.

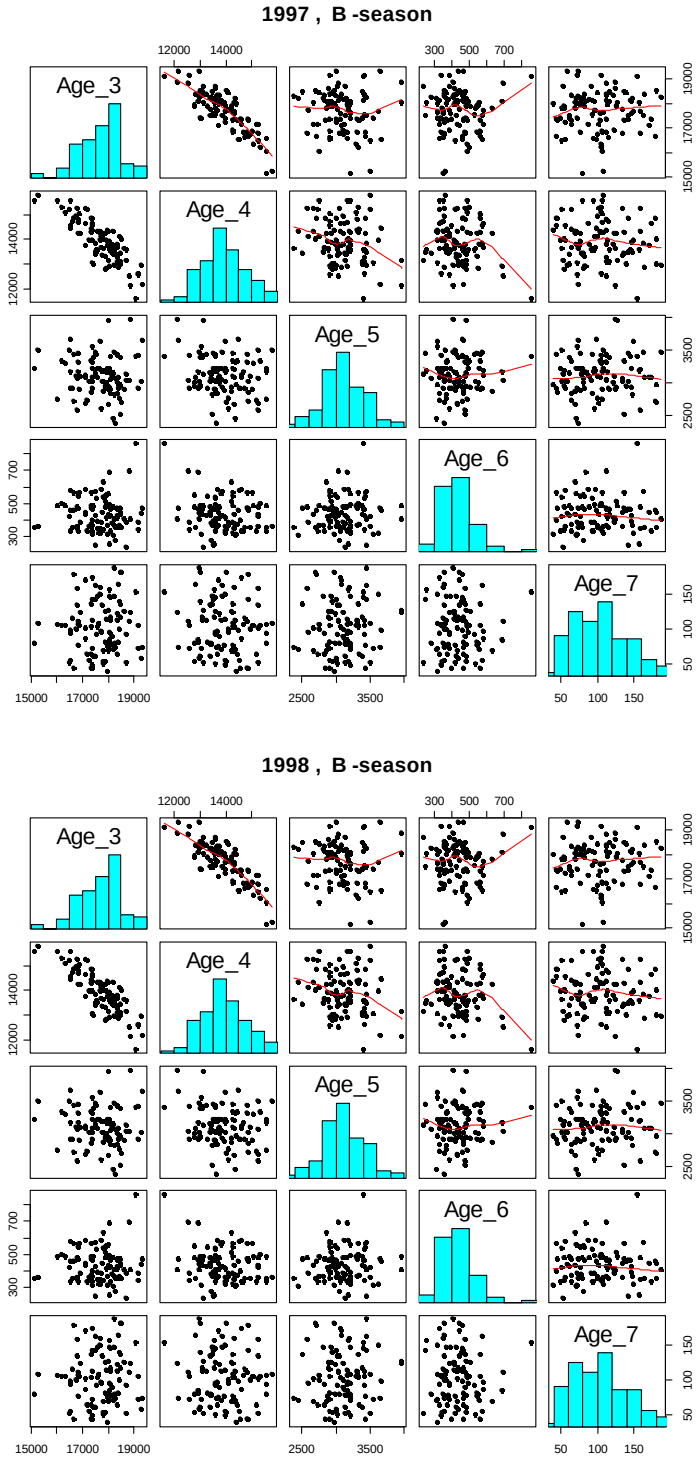

Fig. 3-4 Bootstrap estimates of Chinook salmon bycatch example showing correlation of bycatch at different ages for the B-season in 1997 (top) and 1998 (bottom).

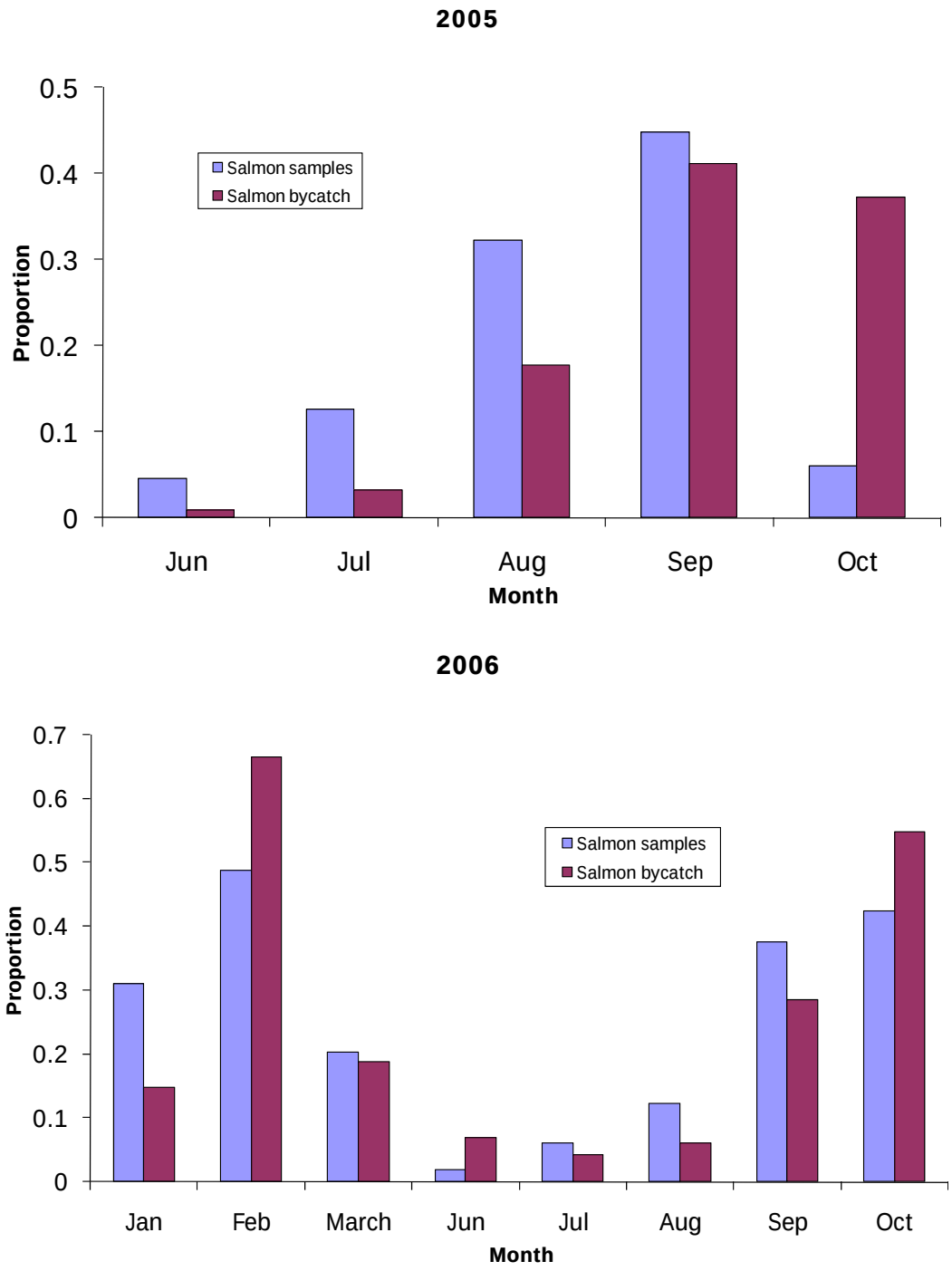

Fig. 3-5 Proportion of Chinook salmon samples collected for genetics compared to the proportion of bycatch by month for 2005 B-season only (top panel) and 2006 A and B season combined (bottom panel).

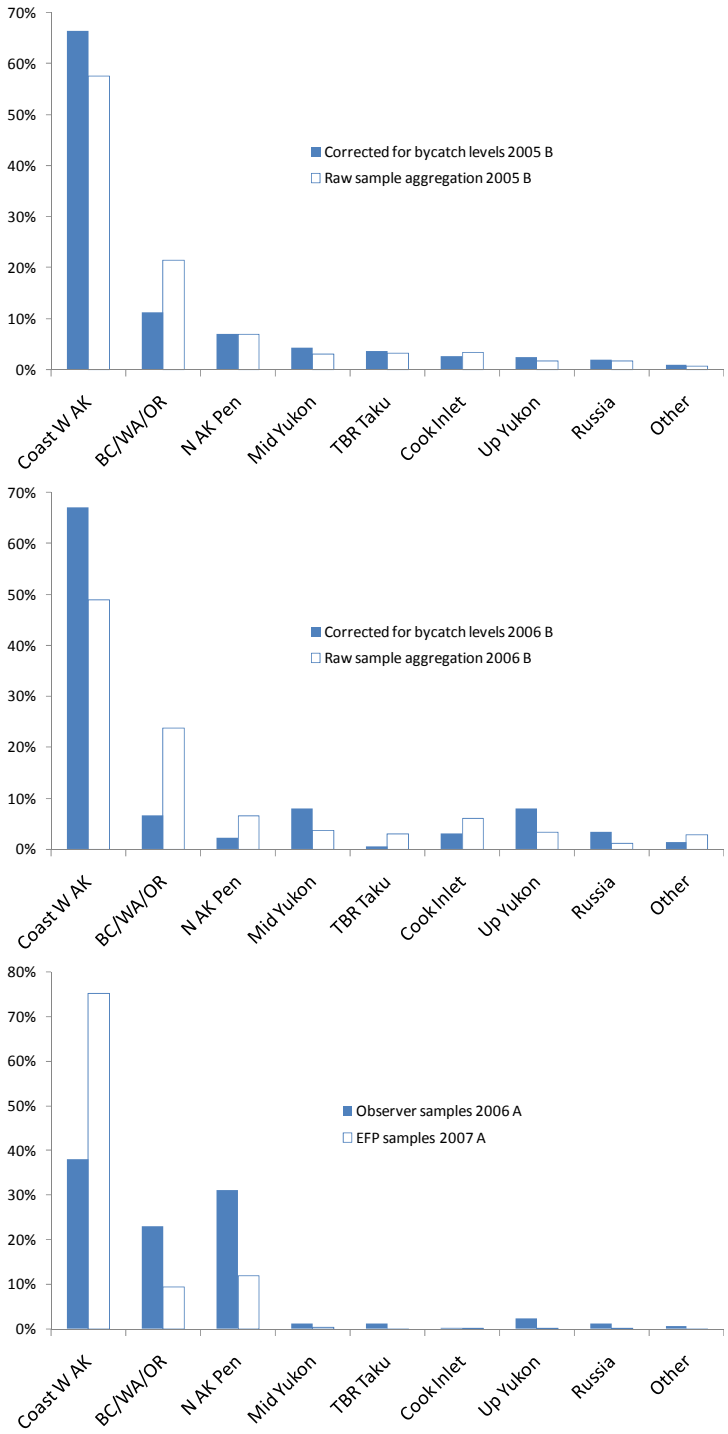

Fig. 3-6 Chinook salmon bycatch results by reporting region for 2005 B season (top), 2006 B season (middle), and the 2006 and (partial sample) of 2007 A seasons (bottom). The top two panels include uncorrected results where bycatch differences between regions (east and west of 170°W) are ignored (empty columns).

3.3.3 Estimating adult equivalence

The impact of bycatch on salmon runs is the primary output statistic. This measure relates the historical bycatch levels relative to the subsequent returning salmon run *k* in year *t* as:

$$u_{t,k} = \frac{AEQ_{t,k}}{AEQ_{t,k} + S_{t,k}} \qquad (1)$$

where $AEQ_{t,k}$ and $S_{t,k}$ are the adult-equivalent bycatch and stock size (run return) estimates of the salmon species in question, respectively. The calculation of $AEQ_{t,k}$ includes the bycatch of salmon returning to spawn in year *t* and the bycatch from previous years for the same brood year (i.e., at younger, immature ages). This latter component needs to be decremented by ocean survival rates and maturity schedules. The impact of current year and previous years bycatch on salmon returning (as adult equivalents in year *t*) can be expressed in expanded form (without stock specificity) as:

$$\begin{aligned}
AEQ_t = & \sum_{a=3}^{7} c_{t,a}\gamma_a + \\
& \gamma_4(1-\gamma_3)s_3 c_{t-1,3} + \\
& \gamma_5(1-\gamma_4)(1-\gamma_3)s_3 s_4 c_{t-2,3} + \\
& \gamma_6(1-\gamma_5)(1-\gamma_4)(1-\gamma_3)s_3 s_4 s_5 c_{t-3,3} + \\
& \gamma_7(1-\gamma_6)(1-\gamma_5)(1-\gamma_4)(1-\gamma_3)s_3 s_4 s_5 s_6 c_{t-4,3} + \\
& \\
& \gamma_5(1-\gamma_4)s_4 c_{t-1,4} + \\
& \gamma_6(1-\gamma_5)(1-\gamma_4)s_4 s_5 c_{t-2,4} + \\
& \gamma_7(1-\gamma_6)(1-\gamma_5)(1-\gamma_4)s_4 s_5 s_6 c_{t-3,4} + \\
& \\
& \gamma_6(1-\gamma_5)s_5 c_{t-1,5} + \\
& \gamma_7(1-\gamma_6)(1-\gamma_5)s_5 s_6 c_{t-2,5} + \\
& \\
& \gamma_7(1-\gamma_6)s_6 c_{t-1,6}
\end{aligned} \qquad (2)$$

where $c_{t,a}$ is the bycatch of age *a* salmon in year *t*, s_a is the proportion of salmon surviving from age *a* to *a+1*, and γ_a is the proportion of salmon at sea that will return to spawn at age *a*. Since this model is central to the calculation of *AEQ* values, an explanatory schematic is given in Fig. 3-7. Maturation rates vary over time and among stocks detailed information on this is available from a wide variety of sources. For the purpose of this study, an average over putative stocks was developed based on a variety of studies (Table 3-13). Note that there is a distinction between the distribution of mature age salmon found in rivers (Table 3-13) and the expected age-specific maturation rate of oceanic salmon ($\gamma_{a,k}$) used in this model. However, given ocean survival rates the values for $\gamma_{a,k}$ can be solved which satisfy the age-specific maturation averaged over different stocks (bottom row of Table 3-13).

Appendix 5: High resolution stock identification for migratory studies of Chinook salmon (Available at http://www.adfg.alaska.gov/static/fishing/PDFs/research/Chinook_Coastwide_SNPs_09.pdf)

High-Resolution Stock Identification for Migratory Studies of Chinook Salmon

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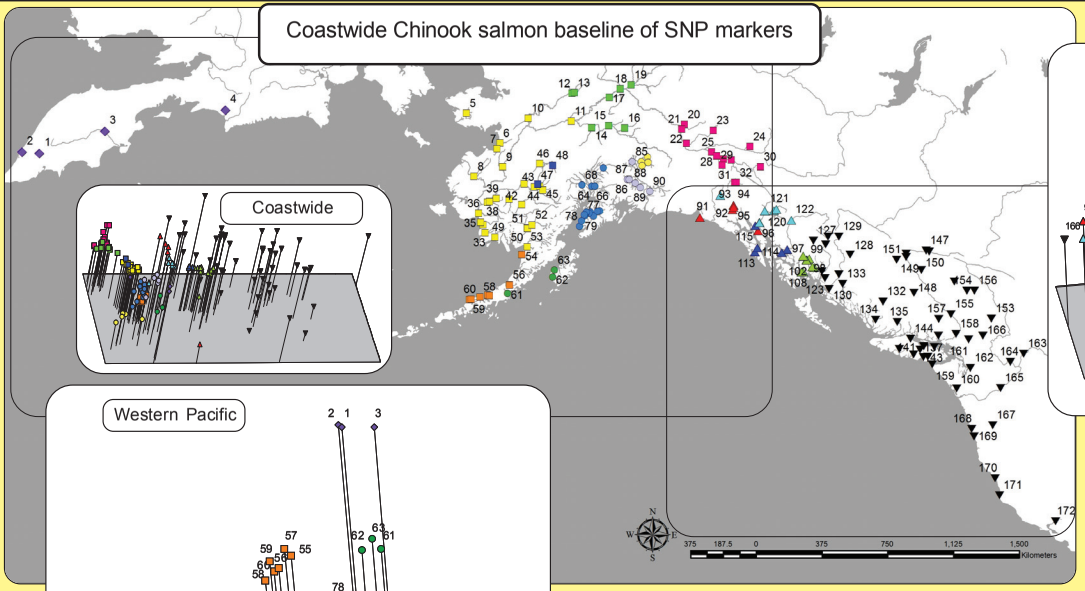
Introduction

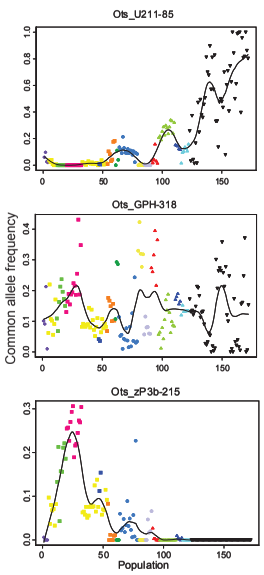
Little is known of the oceanic migration patterns and relative survival of individual stocks of Chinook salmon. Until recently, investigation of the effects of fluctuating marine conditions on the abundance and distribution of Chinook salmon has only been approachable through the sporadic collection of tagged individuals and analysis of scale patterns. Here we present a baseline of genetic markers based on 45 single nucleotide polymorphisms (SNPs) surveyed in 172 populations across the species range in the North Pacific. This baseline provides the foundation for the application of genetic stock identification for high-resolution exploration of the distribution of Chinook salmon in marine waters. Initial results indicate that 15 broad-scale groups can be identified in mixed stock analysis of high seas samples, an increase in the available resolution.

Coastwide Chinook salmon baseline of SNP markers



Measuring Genetic Variation

Genetic variation is measured by identifying locations along the genome (markers) where differences exist. Variant forms of these markers are called alleles. Single nucleotide polymorphisms (SNPs) are markers where two different nucleotides (alleles) have been found at the same location. The frequency of alleles at each SNP can vary widely between populations and population groups. The frequency variations at many SNPs can be used to distinguish populations and groups of populations in mixtures (e.g. juvenile samples, bycatch, or commercial harvest).



Reporting Groups

- Russia
- Coastal Western Alaska
- Middle Yukon River
- Upper Yukon River
- Upper Kuskokwim River
- North Alaska Peninsula
- South Alaska Peninsula
- Cook Inlet
- Upper Copper River
- Lower Copper River
- Northern SE Alaska
- Coastal SE Alaska
- Andrew Creek
- Transboundary Taku
- BC/WA/OR/CA

Estimated population contributions to mixtures of salmon were combined into broad-scale reporting groups. Reporting groups in this study were defined based on genetic similarity, geographic proximity, and management needs. Geographic organization can be seen on the maps and genetic organization can be seen using multidimensional scaling to represent genetic distances among populations in three dimensions. Clusters of populations in these plots indicate genetic similarities between the component populations. By comparing these plots with the maps potential reporting groups can be identified.

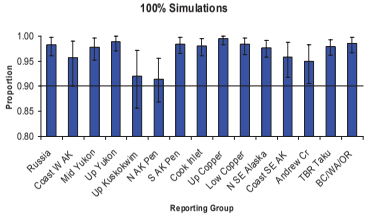
Coastwide
Three major groups of populations were identified: two within the Eastern Pacific populations (including Southeast Alaska) and a Western group (including Russia, Yukon River, and coastal Alaska to Copper River).

Eastern Pacific
British Columbia, Washington, Oregon, Idaho, and California populations are combined into a single genetically diverse reporting group because current representation is insufficient to allow further subdivision. Southeast Alaska and transboundary populations cluster into four groups.

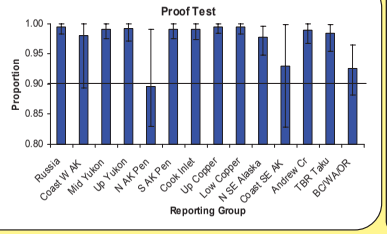
Western Pacific
Populations within this major group exhibit strong geographic and genetic clustering with the exception of the Coastal Western Alaska group, where populations are geographically dispersed, but genetically similar.

Testing the Baseline

100% Simulations
The first step to investigate the precision and accuracy possible for mixed stock analysis using this baseline involves simulated mixtures of hypothetical salmon in which all the individuals belong to a single reporting group. These 100% simulations are repeated 1,000 times. If the mixed stock analysis works perfectly then 100% of mixture would be attributed to the correct reporting group and any deviation would indicate error in the estimation process. Generally, 90% mean correct assignment indicates a high degree of genetic identifiability. All 15 reporting groups show correct allocations above the 90% thresh hold.



Known Sample Tests
The second step to investigate the precision and accuracy possible involves removing individual salmon from the baseline and using them to create a mixture of real salmon. This is a more stringent test than the simulations because the information in the baseline is reduced and real (not hypothetical) genotypes are used. As previously, these mixtures were composed entirely of individuals from the same reporting group. The results indicate that all groups are identifiable at or above the 90% thresh hold. Insufficient individuals were available from the Upper Kuskokwim reporting group to allow for inclusion in this test.



Conclusions

- The baseline of SNP markers demonstrates significant genetic variation among Chinook salmon populations.
- Genetic variation in Chinook salmon on a coastwide scale is closely associated with geographic features.
- Mixed stock analysis using genetic markers can identify 15 reporting groups on a coastwide basis.

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