FEATURE

Genetic Mixture Analysis Supports Recalibration of the Fishery Regulation Assessment Model

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Management of the commercially important Washington coastal Chinook Salmon *Oncorhynchus tshawytscha* troll fishery depends on the Chinook Salmon Fishery Regulation Assessment Model (FRAM). The Chinook Salmon FRAM uses historical and contemporary coded wire tag recoveries to estimate abundance and exploitation rates for particular indicator stocks. Those estimates are used to set limits on overall harvest and protect sensitive stocks. Current efforts are underway to implement a newer "base period" (time period on which exploitation rates are based). Our collaboration of science, management, and industry used genetic mixture modeling to provide independent stock composition estimates supporting FRAM recalibration. Genetic modeling suggested that total catch includes a much smaller proportion of a limiting Columbia River stock, a larger fraction of Canadian stocks, and an abundant Oregon coastal stock not previously included in the FRAM. Our results focus attention on particular stocks that will benefit from refinements in the Chinook Salmon FRAM.

INTRODUCTION

Commercial troll fishing for Chinook Salmon *Oncorhynchus tshawytscha* off the coast of Washington State began around 1912 and grew rapidly during World War I. By 1919, there were more than 1,000 boats in the fleet. Between 1935 and the early 1950s, harvest doubled from 200,000 to 400,000 fish/year. Harvest then declined dramatically in the late 1950s and early 1960s. Fewer than 100,000 fish were taken in 1965 (USDOC 1976). Harvest numbers have varied widely in recent years (from 8,636 in 2008 to 55,313 in 2015). Some stocks are still quite abundant and can sustain harvest, whereas others are severely depressed and are now protected under the U.S. Endangered Species Act (ESA). Despite those declines in some stocks, the Washington Chinook Salmon fishery overall remains an important economic asset to the state and the entire region (US$2.6 million ex-vessel value; TCW 2008), yet the troll fishery presents some acute management challenges. The 1976 environmental impact statement/preliminary fishery management plan for the troll salmon fishery of the Pacific coast described the difficulty inherent in managing this mixed-stock fishery and foretold the increasingly thorny problem of protecting sensitive stocks while targeting abundant stocks for harvest:

> The mobility of the troll fleets, plus the fact that the salmon stocks upon which the fleets fish are highly migratory, makes management of the fishery extremely complicated. This combination results in both the fisheries and the resources crossing interstate and international boundaries. In addition to the international problems, management of the salmon resource is further complicated by the presence of large net fisheries and sport fisheries also fishing on many of these same salmon stocks (U.S Department of Commerce 1976:12).

The commercial Chinook Salmon fishery off the U.S. West Coast, including Washington State, is managed using the Fishery Regulation Assessment Model (FRAM) as the primary analytical and evaluation tool (PFMC 2008). The FRAM is dependent on historical and contemporary coded wire tag (CWT) recoveries and provides a discrete time-step, age-structured, deterministic model that is used by the Pacific Fishery Management Council (PFMC) for annual pre-season and postseason estimates of the impacts of ocean and terminal fisheries on particular stock groups of Chinook Salmon and Coho Salmon *O. kisutch*. For Chinook Salmon, impacts are modeled for most stock groups from California's Central Valley (Sacramento River), the north-central Oregon coast, the Columbia River, Willapa Bay, the north Washington coast, Puget Sound, and southern British Columbia. The FRAM is used to evaluate proposed annual regulation scenarios in specific fisheries for compliance with harvest allocation, ESA compliance, and domestic and international legal obligations. The latter includes providing treaty tribes with the opportunity to harvest specific shares of individual Chinook Salmon stocks, as well as meeting obligations for stock-specific management associated with the Magnuson–Stevens Fishery Conservation and Management Act (16 U.S. Code 1801–1891[d], 2014). It is important to note that the FRAM and other CWT-based fishery management models used on the West Coast are integral elements of both international and regional management structure. tribal, state, provincial, and federal fishery management agencies in the eastern Pacific contribute to and benefit from the Regional Mark Information System database, the international repository of CWT marking and recovery data.

Fishery Regulation Assessment Model Base Period for Inference of Current Exploitation Rates

The Chinook Salmon FRAM depends on CWT recoveries to estimate contemporary stock-specific abundance and exploitation rates as inferred from a historical "base period" (see PFMC 2008 for a detailed quantitative description of the FRAM, including flow charts and formulas for individual processes). The base period 1979–1982 is a critical element of the Chinook Salmon FRAM and is currently being updated to the period 2007–2013. Contemporary postseason abundance and observed catches, applied to the base period data in the FRAM, produce annual exploitation rate estimates as well as stock composition estimates that are comparable to genetic mixture analysis. That comparison of stock composition estimates allows an independent evaluation of the Chinook Salmon FRAM. The base period is important because those historical exploitation rates are used to infer contemporary stock-specific exploitation. Managers then set regulations to allocate harvest and control exploitation rates on sensitive stocks.

Genetic Mixture Analysis

Genetic mixture analysis, also known as genetic stock identification (GSI), uses genetic data to infer the source populations that most likely contributed to a particular group of fish taken in a mixed-stock fishery (Milner et al. 1985). Genetic mixture modeling based on DNA microsatellite data has been extensively tested and validated in Atlantic Salmon *Salmo salar* and multiple Pacific salmon species (Beacham et al. 2003, 2008; Griffiths et al. 2010). There are generally two components to these studies: the unknown fishery mixture and the baseline data set of known-origin fish. Each of these data sets consists of a list of fish with their associated multilocus genotypes, typically coded as a string of paired character states (alleles) at each genetic locus (chromosomal location). Genetic stock identification is the process of fitting a model of potential source populations to the multilocus genotypes of the fish in the observed mixture (Koljonen et al. 2005).

Table 1. The total number of Chinook Salmon samples genotyped were randomly drawn from all those collected in Washington troll fisheries during 2012–2015 (genotyped/collected) and are listed by time (year) and area (Figure 1), along with total harvest (number of fish landed), numbers of boats participating in sampling (including percentage of the fleet represented by the samplers), and the Northwest Fisheries Science Center's Tissue Archive Accession Number (genotyping success rate ~98.6%).

	Spring		Summer						
Year	Area 2	Area 3 & 4	Area 2	Area 3 & 4	Total	Landings	Boats sampling	Approximate fleet representation (%)	Accession number
2012	495/543	371/489	188/223	355/403	1,409/1,658	36,855	15	44	90560
2013	479/514	120/127	492/552	220/226	1,302/1,419	40,090	9	26	90599
2014	348/555	470/703	469/743	93/175	1,387/2,176	38,707	11	32	90612
2015	619/1,489	270/612	191/430	166/435	1,246/2,966	55,313	13	38	90643
Total	1,932/3,101	1,238/1,932	1,340/1,948	834/1,239	5,344/8,219				

Our study had two principal goals: (1) to compare GSI and FRAM stock composition estimates for different times and areas in the commercial troll fishery for Chinook Salmon, and (2) to describe apparent trends or patterns in the spatial and temporal distribution of stocks. Our hope was that genetic results from this fishery would improve our understanding of stock distribution and contribute to the power and utility of current CWT-based fishery management as implemented using the FRAM. We examined the relative distribution of different stocks among time/area strata; however, our primary focus was on fishery impacts. Because stocks can have different exploitation rates, our fishery-dependent study design is ill suited to address the more academic question of how each stock is actually distributed at sea in time and space.

METHODS

Sample collection

We genotyped Chinook Salmon tissue samples that were randomly drawn from all rayed fin clips collected by commercial fishers participating in Washington Chinook Salmon troll fisheries conducted during 2012–2015 (Table 1). On average, in each year we analyzed 3.2% of total harvest collected by roughly 35% of the fleet (range = 26–44%). Although there are approximately 150 permit holders, not all of them fish, and many of them fish only a small portion of the season. Most of our samplers caught their trip limits regularly, so based on review of trip limits caught per week over a 10-year period, 34 is a reasonable estimate of average fleet size for active commercial trollers on the Washington coast. Samples were collected opportunistically as time permitted and might not represent an ideal random sample. However, we offered a per-fish monetary incentive to ensure sampling during busy periods, so we believe that the collections represent a reasonable approximation of the fish taken in the fishery in each time and area. Collection location and date were recorded (GPS time stamp) as well as fork length and mark status (many hatchery-origin fish are marked with the removal of the adipose fin).

Fin-clip samples were folded in Whatman 3MM chromatography paper, dried, and stored in barcoded coin envelopes at ambient temperature. Samples were deposited into the National Oceanic and Atmospheric Administration (NOAA) Northwest Fisheries Science Center (NWFSC) Conservation Biology Division's Genetic Tissue Archive (accession numbers are listed in Table 1). Collection data were downloaded from GPS units provided to fishers and were transcribed from forms printed on the collection envelopes. Fin clips were collected each year during the normal commercial fishing season that occurred between May and September. In our analyses, we refer to the May–June period as spring and July–September as summer (Table 1). No Chinook Salmon harvesting is permitted at other times in the open ocean off Washington. Samples were analyzed from the southern Area 2 (Gray's Harbor Area: Leadbetter Point to the Queets River at 47.5° latitude on the Washington coast) and from the more northerly areas 3 (Quillayute Area) and 4 (Cape Flattery Area), which were cobined and are referred to as "Area 3 & 4" for our study (Queets River to the U.S.–Canadian border; Figure 1).

Genotyping and reference baseline

The Washington Department of Fish and Wildlife (WDFW) and the NWFSC cooperated in processing Chinook Salmon tissue samples. In 2012, samples were divided between the NWFSC and WDFW genetics laboratories. From 2013 to 2015, all genotyping was carried out by NWFSC. In both laboratories, DNA was extracted and purified by using Qiagen DNeasy membrane capture kits. Purified DNA samples were amplified and genotyped for 13 internationally standardized microsatellite loci (see below for interlaboratory genotyping standardization). Amplified microsatellite products were size fractionated on an Applied Biosystems 3730 Genetic Analyzer in the WDFW Molecular Genetics Laboratory and on an Applied Biosystems 3100 Genetic Analyzer at the NWFSC. Genotypic data produced by the WDFW and NWFSC were combined to create a single, 4-year data set for mixture analysis.

The genetic mixture models we employed depend on a complete representation in the baseline of all potentially contributing populations. In this study, we used the internationally standardized microsatellite baseline data set (same loci and allele designations; Moran et al. 2006) produced by the Genetic Analysis of Pacific Salmonids (GAPS) consortium (Moran et al. 2005; Seeb et al. 2007). This data set was designed explicitly for eastern Pacific coastal fishery mixtures, and geographic coverage is excellent for the fisheries examined here, including more than 20,000 known-origin fish from 167 representative populations. The GAPS Chinook Salmon baseline is the most comprehensive of its kind. The baseline includes all evolutionarily significant units and wildlife species listed under the ESA and its Canadian counterpart (i.e., Committee on the Status of Endangered Wildlife in Canada) and is believed to represent principal genetic lineages from all significant production areas over that geographic range. The GAPS Chinook Salmon database is thoroughly vetted with the salmon genetics research community on the Pacific coast of the USA and Canada (Seeb et al. 2007). The 13 microsatellite loci that make up the coastwide baseline are highly

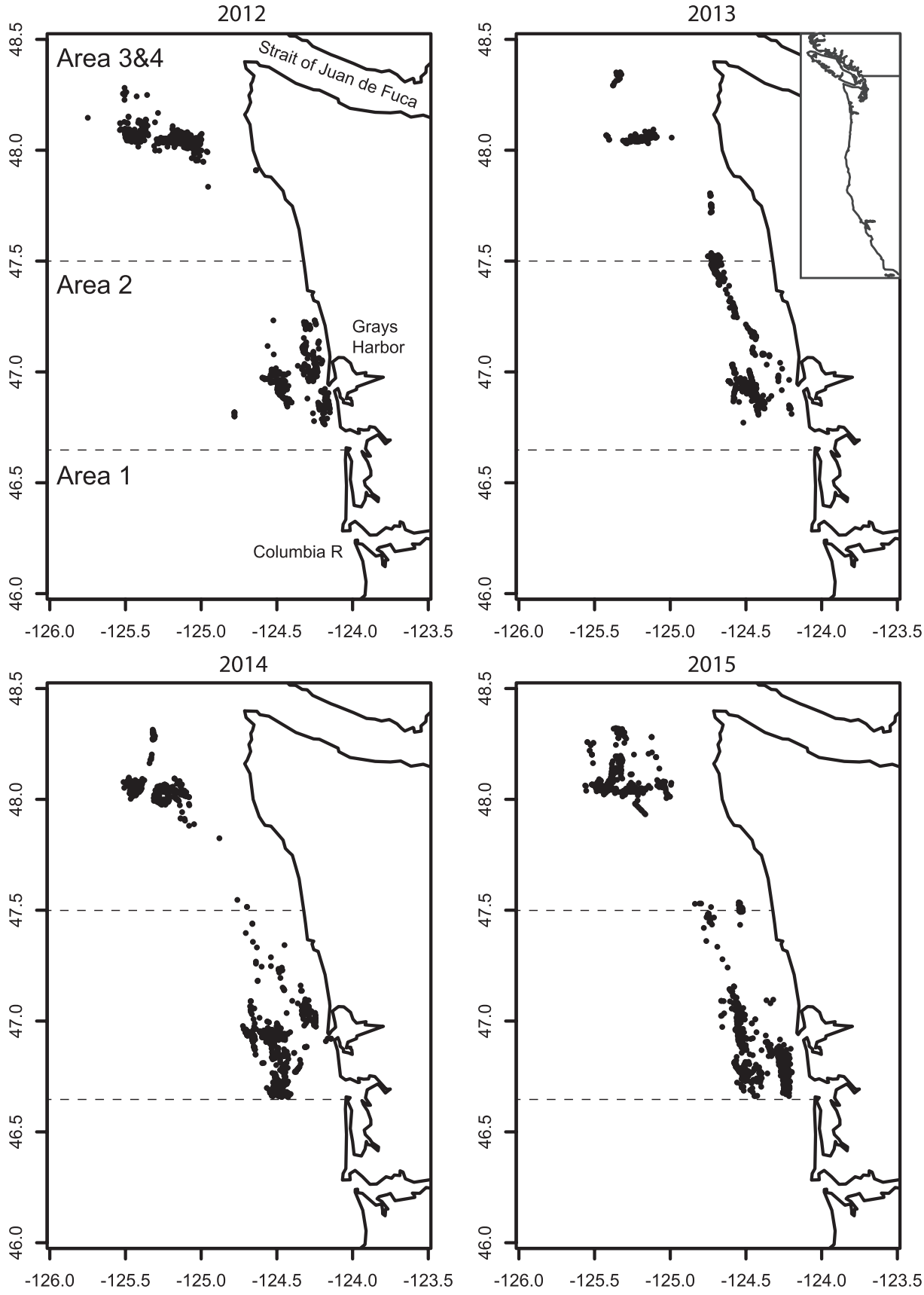

Figure 1. Collection locations of individual Chinook Salmon taken in the commercial troll fishery off the coast of Washington. Samples were separated between the Juan de Fuca Canyon in Area 3 & 4 north of latitude 47.5 and those taken to the south in Area 2 near Grays Harbor. These areas represent most of the Washington troll fishery.

variable, with almost 500 alleles observed. Extensive simulations and leave-one-out jackknife analyses showed excellent power to allocate mixed-stock fisheries to origin, either as single individuals or as modeled proportions (Seeb et al. 2007; Anderson et al. 2008). The GAPS Chinook Salmon baseline has been used widely in studies of harvest and bycatch impacts (Satterthwaite et al. 2014; Bellinger et al. 2015) as well as ecological genetic studies (e.g., Rhodes et al. 2011; Roegner et al. 2012; Johnson et al. 2013). The current study provides an opportunity to independently evaluate Chinook Salmon stock composition estimates from the FRAM over the 4-year period from 2012 through 2015.

Single-nucleotide polymorphisms (SNPs) have been used for other GSI studies (Narum et al. 2008; Hess et al. 2011). However, no current SNP baseline was available with the geographic breadth (from the Central Valley of California to Southeast Alaska) and depth (multiple-year samples from multiple populations from each genetic stock group) necessary to characterize the contributing populations observed in Washington coastal Chinook Salmon fisheries.

Data analysis

To estimate stock compositions, we used conditional maximum likelihood mixture modeling (CMLMM) as implemented in ONCOR software (Kalinowski et al. 2007), including bias correction (Anderson et al. 2008). Allele frequencies were estimated to assign nonzero, population-specific frequencies for all alleles observed in the mixture samples but not observed in the source populations (Rannala and Mountain 1997). The CMLMM uses the expectation maximization algorithm (Dempster et al. 1977) to estimate the most likely proportions of contributing populations. We used the CMLMM approach to derive modeled proportions because those are better suited to our application and are more robust than tallied individual assignments, especially where mixture proportions are nonuniform (Koljonen et al. 2005).

We first examined overall stock composition for each of the 4 years, irrespective of time and area. We estimated 95% confidence intervals around the point estimates for each stock using 100 bootstrap replicates, resampling both the mixture and the baseline (Kalinowski et al. 2007). We felt comfortable using this number of bootstrap replicates because preliminary analyses of 2012 and 2013 data demonstrated that 100 bootstrap replicates generated confidence limits that were indistinguishable from those obtained with 1,000 replicates. These estimates represent the proportional stock composition of fish in the mixture samples collected. Genetic stock composition estimates were compared to postseason estimates from FRAM (PFMC 2012–2016) that reflected all fishery-related mortality, including postrelease mortality of sublegal-sized fish. These comparisons imply that nonretention mortality was uniform across stocks. Departures from uniform mortality rates might result from stock-specific differences in age structure or size at age; however, these effects would be limited to sublegal encounters and were unlikely to be of sufficient magnitude to confound our results.

For each year, we stratified our stock composition estimates by time and area to facilitate comparisons with the FRAM. Forty-six genetic stock groups were aligned with 12 FRAM stocks (Appendix Table A.1). As stated earlier, we examined two areas off the Washington coast (Area 2 in the south; Area 3 & 4 in the north; Figure 1) and two time periods (spring and summer). Mean squared error (MSE) was used to evaluate the fit of FRAM stock composition estimates to those from GSI. Recognizing the bias for large contributing stocks, we also calculated mean absolute percentage error, which is more sensitive to small contributing stocks. Because results were similar, only MSE values are presented.

RESULTS

Sample Collection

Of the total 8,219 samples collected over the course of this study, most included complete and internally consistent collection data (e.g., time and location). However, we observed some problems with at-sea georeference data due to a malfunction with one of our GPS units, which resulted in a large number of duplicated waypoints (collection time and location). Additionally, some waypoints were from the Westport Boat Basin (Grays Harbor) or the site where the GPS units were configured in Olympia, Washington, an urban center 100 km inland from the study area. In total, 1,186 samples were missing valid latitude/longitude coordinates, so those specific location and time stamp data were omitted from analyses. Despite the discarding of faulty GPS data, sample batches allowed confident assignment to time period (spring or summer) and area stratum (Area 2 or Area 3 & 4). Finally, 45 samples were omitted that were found to have been collected outside the study area—that is, in Area 1 south of Leadbetter Point (Figure 1).

Laboratory Analysis

Sample quality was excellent. Only about 1.4% of processed samples were later omitted from analyses due to sparse genotypic data and excessive homozygosity, which are typical of degraded DNA from poor-quality tissue samples. For example, a sample scored as homozygous for three highly polymorphic loci but failing amplification for all others would be omitted. Of the remaining samples, more than 80% were successfully typed for all 13 loci, and more than 99% were typed for 10 or more loci. In each year, from one to five pairs of fish (12 pairs total) were observed with identical multilocus genotypes. The variability of the GAPS Chinook Salmon microsatellite loci is such that identical genotypes for six or more loci, with no mismatches, would almost certainly be the result of multiple tissue samples taken from the same individual (individual-specific DNA "fingerprints"). In our case, members of each pair occurred within the same time/area stratum; therefore, we omitted one member of each pair. Our final sample size after filtering was 5,344 fish taken as a random sample from a total of 8,219 tissue samples collected (Table 1).

Nearly half the samples were taken from fish marked with an adipose fin clip, which identified them with near certainty as hatchery-produced individuals. Unmarked fish can be either hatchery or wild origin, but almost no wild fish are marked by clipping the adipose fin. All except eight fish sampled were of legal size (>66 cm), and average fork length was 77.2 cm (SD = 6.4 cm).

Genetic Mixture Modeling

Genetic mixture analysis showed that the Washington Chinook Salmon troll fishery is primarily supported by two Columbia River fall-run stocks: Mid-Columbia River tule and Upper Columbia River bright. On average, 44% of our sample was attributed to those two stocks (27% and 17%, respectively; Figure 2). Other important contributors included the Lower Columbia River bright and tule stock (9.7%) and the Fraser River/West Coast Vancouver Island (WCVI)/Georgia Strait

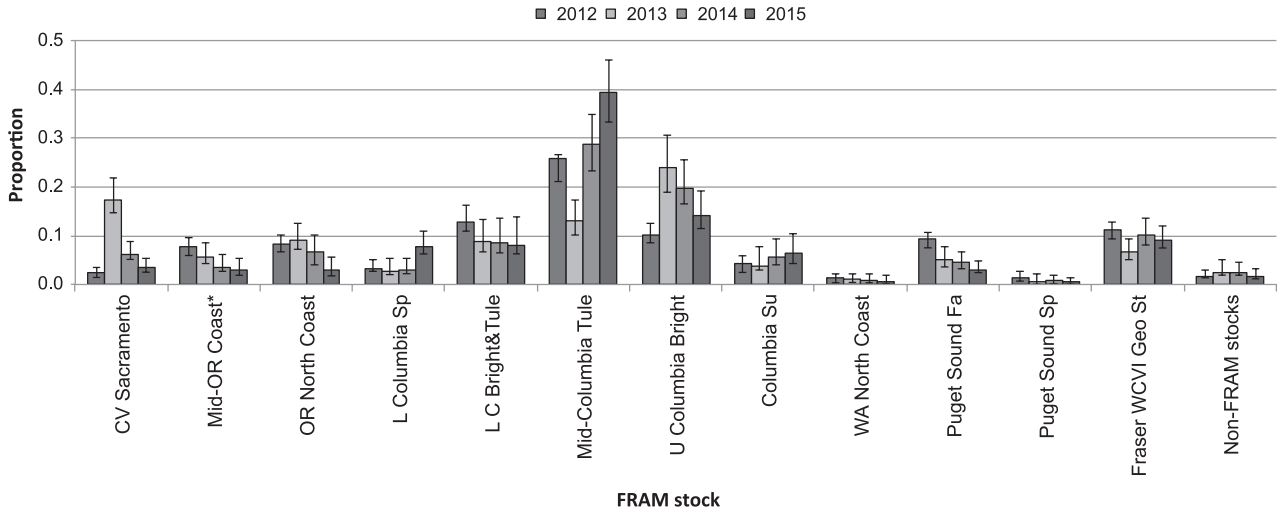

Figure 2. Genetic stock composition estimates and 95% confidence intervals for genetic stock groups of Chinook Salmon aligned to 11 Fishery Regulation Assessment Model (FRAM; coded wire tag) indicator stocks and the Mid-Oregon Coast stock (ordered from south to north), and a combined group of 22 non-FRAM stocks, 2012–2015 (Sp = spring, Su = summer, Fa = fall; CV = Central Valley; OR = Oregon; L = Lower; U = Upper; L C = Lower Columbia River; WA = Washington; WCVI = West Coast Vancouver Island; Geo St = Georgia Strait). The non-FRAM Mid-Oregon Coast stock (marked with an asterisk) is disaggregated from the other non-FRAM stocks because it made an unexpectedly large contribution in all 4 study years. See Appendix for stock descriptions.

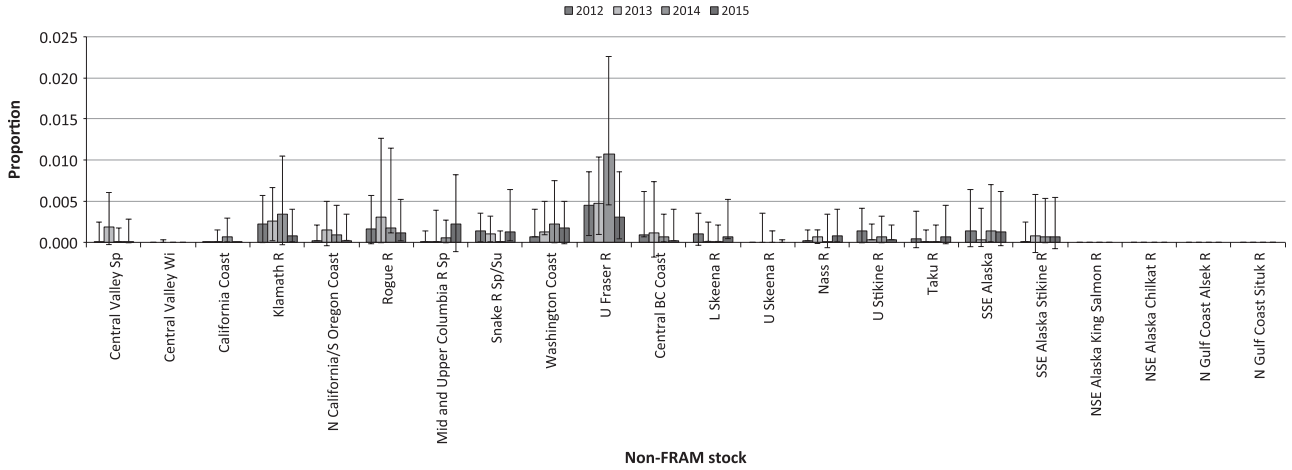

Figure 3. Genetic stock composition estimates and 95% confidence intervals for 22 non-FRAM (Fishery Regulation Assessment Model) stocks of Chinook Salmon (ordered from south to north; Sp = spring, R = river, Su = summer, Wi = winter; L = Lower; U = Upper; BC = British Columbia, SSE = southern southeast, NSE = northern southeast, N = north). The non-FRAM Mid-Oregon Coast stock was included with the FRAM stocks in Figure 2 rather than in this figure due to its much larger contribution in relation to other non-FRAM stocks. See Appendix for stock descriptions.

stock (a FRAM stock comprised of three genetically distinct regions; 9.5%). With the exception of 2013, overall stock composition showed little variation among years. Despite that relative uniformity, there was a general trend toward increasing abundance of the Mid-Columbia River tule stock through time, resulting in a narrower distribution of contributing stocks. Stock composition in 2013 was unusual in having a very high percentage of Central Valley–Sacramento River fall-run stock (14% in 2013; 2–7% in other years studied) and a smaller contribution from the Mid-Columbia River tule stock (14% in 2013; 31–50% in other years studied).

Comparison of Genetic Stock Identification and the Fishery Regulation Assessment Model

When the Chinook Salmon FRAM was developed, Mid-Oregon Coast populations were poorly represented among CWT releases. Those populations were not thought to contribute substantially to the Washington coastal troll fishery and therefore were not included in the model. In our study, however, GSI estimates for the Mid-Oregon Coast stock were unexpectedly large (Figures 2, 3) and were substantially larger than the estimated FRAM contribution of all non-FRAM stocks (Figure 4). The Mid-Oregon Coast stock contributed up to 29% of the harvest in Area 3 & 4 during summer 2012, and GSI estimates were generally an order of magnitude greater than the FRAM estimates for all non-FRAM contributors combined (which should have included the Mid-Oregon Coast stock; Figure 5). With the Mid-Oregon Coast stock disaggregated from the non-FRAM GSI estimate, FRAM and GSI estimates for the remaining non-FRAM-stock contributors were similarly low (GSI ~2%; Figure 2). Other than the Mid-Oregon Coast stock, the largest non-FRAM contributor

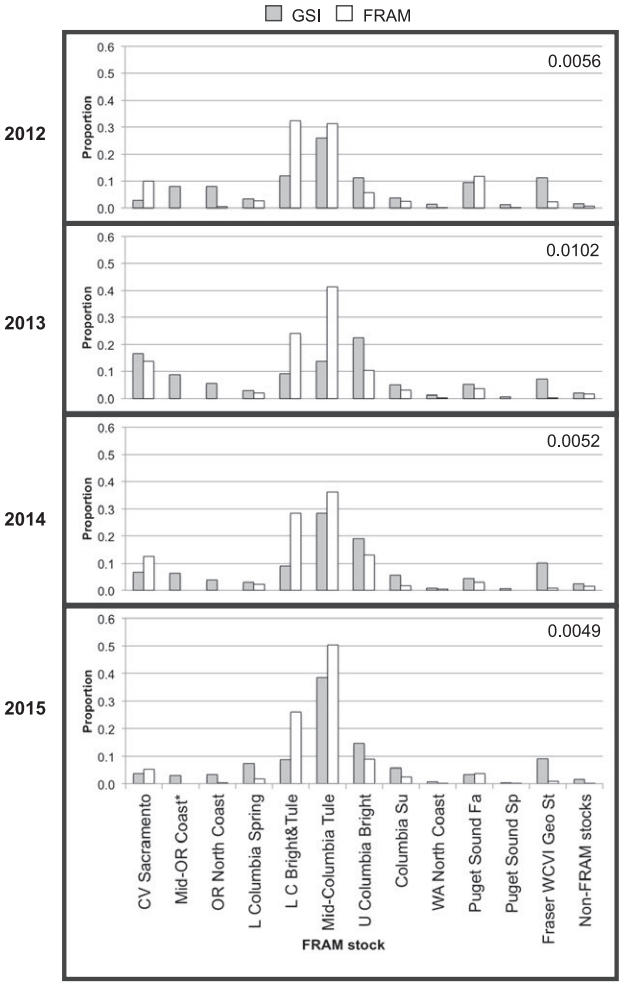

Figure 4. Genetic stock identification (GSI) and Fishery Regulation Assessment Model (FRAM) stock composition estimates for Chinook Salmon belonging to 11 FRAM stocks and the Mid-Oregon Coast stock (ordered from south to north), and an aggregate of 22 non-FRAM stocks (Sp = spring, Su = summer, Fa = fall; CV = Central Valley; OR = Oregon; L = Lower; U = Upper; L C = Lower Columbia River; WA = Washington; WCVI = West Coast Vancouver Island; Geo St = Georgia Strait). Because of its large contribution, the non-FRAM Mid-Oregon Coast stock is shown disaggregated from the non-FRAM GSI estimate and is instead included with the FRAM stocks. See Appendix for stock descriptions. Differences between FRAM and GSI were quantified by mean squared error (upper right corner of each panel).

was the Upper Fraser River stock, which averaged 0.6% of the troll fishery (range = 0.3–1.1%).

Some similarities in stock composition estimates were found between GSI and FRAM, but in most cases, we saw substantial differences. High concordance was observed between GSI and FRAM in only 4 of 16 time/area strata; all four were in Area 2 during spring 2012, spring and summer 2014, and spring 2015 (MSE < 0.0043; Figure 5). Genetic stock identification and FRAM usually diverged more substantially in Area 3 & 4 for both spring and summer time strata. Despite similar numbers of contributing stocks, FRAM estimated narrower, less diverse distributions of contributing stocks in essentially every stratum relative to GSI, especially in the more northerly Area 3 & 4.

Consistent, directional departures between GSI and FRAM were observed for particular stocks across time/area strata and across years (Figure 5). Relative to GSI, FRAM estimates were consistently low for the Oregon North Coast stock and for the Fraser River/WCVI/Georgia Strait stock. The FRAM estimates were also lower for the Upper Columbia River bright stock, especially in the spring fishery. The FRAM estimates were consistently lower than GSI for Columbia River summer and Washington North Coast stocks, although absolute contributions were small with both methods. By contrast, FRAM estimates for the ESA-listed Puget Sound fall-run stock were consistently higher than GSI estimates. Genetic stock identification showed smaller changes in stock composition between time strata than did FRAM but showed larger differences between areas (Figure 5). The most extreme mismatch between methods, other than the Mid-Oregon Coast issue described above, was in estimates of the Lower Columbia River bright and tule stock and the Mid-Columbia River tule stock. In every stratum, FRAM estimates for the Lower Columbia River bright and tule stock were greater than comparable GSI estimates. For the Mid-Columbia River tule stock, FRAM estimates were greater than GSI in 13 of 16 time/area strata (Figure 5).

DISCUSSION

Potentially Informative Differences Between Genetic Stock Identification and the Fishery Regulation Assessment Model

Stock composition estimates from GSI often differed dramatically from comparable FRAM estimates. These differences were apparent in northern and southern areas and spring and summer time periods but especially in northern Area 3 & 4. In particular, FRAM estimates were consistently greater than GSI estimates for the sensitive, ESA-listed Lower Columbia River tule stock. Although our genetic analysis did not discriminate Lower Columbia River tules from Lower Columbia River brights, FRAM results suggested the bright contribution was very small, and most of the fish in this combined group were likely from the Lower Columbia River tule stock. This difference in stock composition between methods is particularly important because the Lower Columbia River tule stock is the limiting stock in the coastal troll fishery (and is also protected as threatened under the ESA). Our results suggest that the stock might be consistently overestimated under the current management regime. The PFMC attempts to structure fisheries between Cape Falcon (Oregon) and the Canadian border to limit marine and freshwater exploitation rates on Lower Columbia River natural tule populations to no greater than 41% (PFMC 2015). That objective was the primary constraint for ocean fisheries in this area between 2012 and 2015. It might be that tule contributions estimated from GSI were less than those predicted by FRAM because these stocks were less abundant than current FRAM estimates or because exploitation rates were lower than those estimated by the FRAM. Preliminary FRAM composition estimates using the updated base period appear to be closer to current GSI estimates—for example, lower estimates for tule stocks and Puget Sound stocks but greater estimates for Upper Columbia River brights (based on ongoing recalibration efforts). It is not clear whether improved concordance is a result of updated exploitation rates that might be more accurate or is due to other factors, including chance. Estimated proportions for the Fraser River/WCVI/Georgia Strait stock are slightly greater

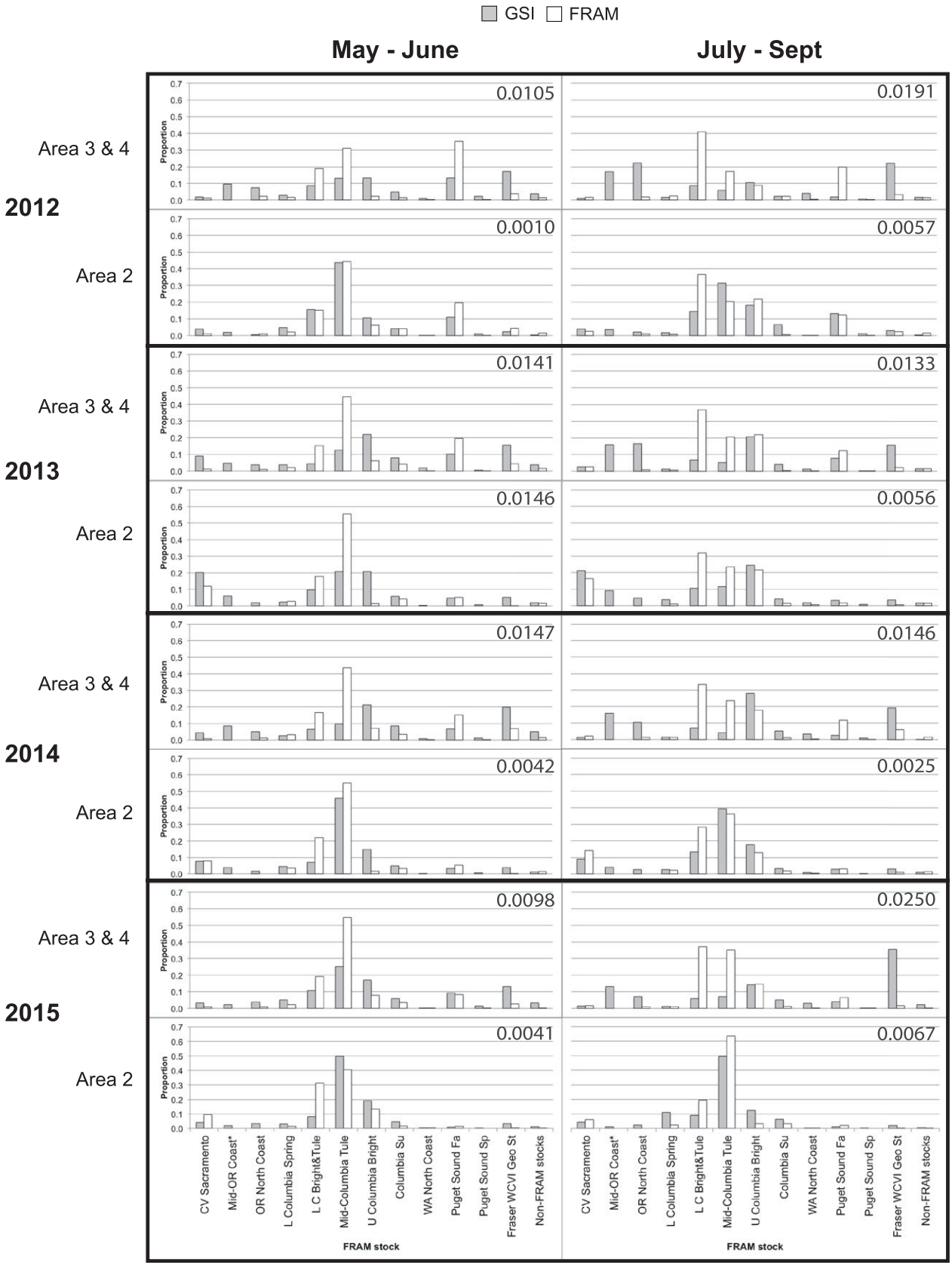

Figure 5. Time/area-stratified genetic stock identification (GSI) and Fishery Regulation Assessment Model (FRAM) stock composition estimates for Chinook Salmon belonging to 11 FRAM stocks and the Mid-Oregon Coast stock (ordered from south to north), in addition to an aggregate of 22 non-FRAM stocks (Sp = spring, Su = summer, Fa = fall; CV = Central Valley; OR = Oregon; L = Lower; U = Upper; L C = Lower Columbia River; WA = Washington; WCVI = West Coast Vancouver Island; Geo St = Georgia Strait). Mean squared error values appear in the upper right corner of each panel. See Table 1 for sample sizes and Appendix for stock descriptions.

under the new FRAM base period, but those estimates are still substantially less than GSI estimates. The FRAM estimates of Canadian stocks are important because total harvest is first allocated between nations, then between tribal and nontribal fishers, next between sport and commercial fishers, and finally among time/area sectors. Errors made in allocating the total catch between the United States and Canada are propagated downward and influence the equitable distribution of this important cultural and economic resource among all fishers.

Differences Not Due to Misalignment of Genetic Groups and Fishery Regulation Assessment Model Stocks

To make comparisons between GSI and FRAM stock composition estimates, we had to align FRAM stocks to our 167 genetic baseline populations comprising reference samples of known-origin individuals (Appendix Table A.1). In most cases, alignment was a straightforward process because hatchery collections in our baseline were often exactly the same FRAM indicator stocks. However, in some cases, different FRAM stocks are genetically similar and cannot be easily distinguished—even stocks that show morphological differences (e.g., Lower Columbia River bright versus Lower Columbia River tule stocks). In other cases, FRAM stocks are made up of multiple individual populations that belong to genetically distinct groups (e.g., Canadian stocks in Georgia Basin). After years of hatchery stock transplantation and propagation of mixed-origin broodstocks, some populations have been partially homogenized and genetic differences have been diminished. Incongruities between GSI baseline populations and FRAM stock groups were mitigated partly by the allocate-sum procedure used in genetic mixture analysis to aggregate local populations into population groups (Wood et al. 1987). In this procedure, proportional allocations to local populations are summed hierarchically to estimate the contributions of population aggregates. Ideally, population aggregates are based on genetic similarity (Wood et al. 1987), so population allocation errors occur primarily within aggregates and not among them. Whereas some genetically similar local populations were aggregated into separate groups to satisfy nongenetic FRAM stocks, resulting allocation errors should have been restricted to the implicated FRAM groups. We do not think that there are substantial misallocation errors in our data, although we are aware of two potential sources of this type of error. First, allocation estimates for the FRAM Oregon North Coast stock might have decreased due to misallocation of Siuslaw River Chinook Salmon (GSI: Mid-Oregon Coast; FRAM: Oregon North Coast) to other populations in the Mid-Oregon Coast GSI stock, which was not included in the FRAM. Second, allocation estimates for the FRAM Upper Columbia River summer/fall stock might have been decreased due to misallocation of Hanford Reach Chinook Salmon (GSI: Upper Columbia River summer/fall; FRAM: Upper Columbia fall bright) to other populations in the Upper Columbia River GSI stock. Neither of these misallocation errors to FRAM group would substantially change our findings.

Opportunities and Limitations for Genetic Stock Identification and Refined Time/Area Management

We hoped that results from our GSI study would increase the power and utility of current CWT-based Chinook Salmon fishery management as implemented using the FRAM. We succeeded in a number of important ways. Overall, our results support current recalibration of the Chinook Salmon FRAM to a more recent base period. This is important to management because the base period is used to determine stock abundance and exploitation and, by extension, postseason stock composition. One of our most important findings was the contribution of Mid-Oregon Coast populations to harvests. Previously, those populations were not thought to contribute substantially to Washington commercial troll harvest, and they were not originally included in the Chinook Salmon FRAM when it was developed. Because genetic data showed a substantial contribution from Mid-Oregon Coast populations, we reviewed historical data for this fishery and found tag recoveries that supported the results of genetic mixture analysis. Unfortunately, the options for CWT release programs in this region are extremely limited. The only tagging program with a sufficient time series is in the Elk River, which is at the southern end of the Mid-Oregon Coast region and, according to our genetic data, is not necessarily representative of other populations in the region in terms of overall contribution to the fishery. The Elk River contributes less than 7% of all Mid-Oregon Coast fish, whereas the Umpqua River contributes 41%.

Stock composition analysis is used to monitor and evaluate fishery impacts on Chinook Salmon stocks and to increase understanding of the spatiotemporal distribution of these stocks, including their associations with oceanographic conditions. Our efforts were focused on fishery impacts and improving the ability of resource managers to allocate harvest of abundant stocks among fisheries while protecting sensitive stocks, especially those listed under the ESA. However, because abundant and sensitive stocks co-occur in coastal ocean fisheries, more detailed information on sensitive stock distribution might not improve managers' abilities to increase harvests of abundant stocks while still holding impacts on sensitive stocks to acceptable levels. Nevertheless, improved distributional information will provide more accurate estimates of relative impacts and should better inform safe harvest levels.

Genetic stock identification provides a powerful, independent opportunity for cross validation of the Chinook Salmon FRAM. With GSI, every fish is genetically marked and can be included in the mixture model. With CWTs, tag recoveries vary in each fishery depending on the stocks contributing to the fishery and the tagging rates for hatchery releases, which can vary between 0% (none tagged) and 100% (all tagged). Expanding CWT stock composition estimates to include wild fish would require information not available for this complex fishery, including age-specific escapement and exploitation rates of wild populations. Therefore, the number of tagged fish in a mixed-stock fishery is not easily related to the total number of fish originating from natural production areas surrounding hatcheries that tag fish. In contrast to CWT retrieval, GSI sampling is nonlethal, although some delayed mortality undoubtedly results from capture and handling. Non-lethality provides an opportunity to sample nonretained, sublegal-sized fish and to obtain empirical, stock-specific estimates of those encounters. Genetic stock identification estimates of stock origin for individual fish also include assignment error that has been well characterized (Anderson et al. 2008).

Unlike CWT-based methods, neither conventional GSI mixture modeling nor individual assignment provides age-specific exploitation rates or discrimination of different hatchery release groups (e.g., different ages or experimental

treatments) among fish from the same or genetically similar populations. Age can be inferred from otoliths or scales, but collection and analysis require significant additional effort and expense. Age is also obtainable using an alternative genetic method referred to as parentage-based tagging (PBT), which requires genotyping all (or nearly all) potential parents in a "marked" population so that offspring can be assigned to specific parent pairs. Parentage-based tagging is often used for characterizing relative reproductive success of hatchery fish spawning in the wild (Ford et al. 2012), and it can provide nearly all of the information currently obtained from CWTs, including the time and location where the parents were spawned as well as family-specific performance (Hankin et al. 2005; Anderson and Garza 2006). Although PBT has been proposed as an alternative to CWTs (Anderson et al. 2012; Steele et al. 2013), it is thought to be logistically intractable and cost prohibitive on a coastwide scale (Hankin et al. 2015). Instead, managers have suggested using radio-frequency identification (RFID) micro tags to replace or augment CWTs (Hankin et al. 2015). However, after considering results of a contracted study on the issue, the Pacific Salmon Commission decided that "transition to the current generation of RFID tags (microchips or PIT tags) is not warranted" (Pacific Salmon Commission 2017). A common sentiment among managers is that "investigation of new technological approaches to provide data for salmon fishery management diverts monies that can be used to maintain the existing CWT program" (Pacific Salmon Commission Joint CWT Implementation Team 2015). Multiple reports leave open the possibility of reconsidering RFID tags in 3–5 years, but for the near future, CWT-based harvest models will remain the cornerstone of West Coast salmon management.

Future Directions

For various historical, logistical, and financial reasons, the U.S. West Coast fishery harvest management community has generally resisted genetic methods (Pacific Salmon Commission 2008). This is in distinct contrast to fisheries farther north in Canada and Alaska, where genetic mixture modeling is central to harvest management. West Coast salmon harvest management has instead evolved toward exploitation rate evaluation rather than stock composition estimates in individual fisheries (Morishima and Henry 2000). Exploitation rate estimation from CWT recoveries is a straightforward calculation, but estimates from GSI data would require all fisheries to be sampled, which is unlikely with current budget constraints on existing programs. Nevertheless, GSI provides a superior method for many stock composition comparisons in selected fisheries, such as the Washington coastal troll fishery. Until now, stock composition estimates from GSI dating back to the 1980s (Milner et al. 1985; Utter et al. 1987) were not used in fishery management because of the large investment in CWT assessment methods. Although it is unlikely that GSI, PBT, or RFID tags will soon replace CWTs (Pacific Salmon Commission 2008, 2015), we expect that genetic methods will increasingly be used to help mitigate problems associated with mark-selective fisheries. These problems and others include violating the assumption of similar exploitation rates between wild populations and hatchery indicator stocks, total marking of hatchery fish (complicating tag recovery), lethal sampling to recover CWTs, and potential mismatch between wild populations and their hatchery indicator stocks with respect to habitat use or migration timing, resulting in different exploitation rates. Following the guidance of the Pacific Salmon Commission (2008), our study offers an example of the valuable role genetics can play in supporting the established management structure built around coded-wire tags.

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BIOGRAPHIES

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APPENDIX

Table A.1. Listing of Genetic Analysis of Pacific Salmonids (GAPS) consortium Chinook Salmon baseline populations, with corresponding genetic stock groups (Seeb et al. 2007) and Chinook Salmon Fishery Regulation Assessment Model (FRAM) stocks (adult return times characteristic of particular stocks: sp = spring, su = summer, fa = fall, and wi = winter; L = lower; U = upper; EF = East Fork; WF = West Fork; NF = North Fork, M= middle, SSE = South southeast, NSE = North southeast, N = North, S = South, W = West, E = East. WCVI = West Coast Vancouver Island; Geo St = Georgia Strait).

GAPS population	Genetic stock group	FRAM stock
Mill Creek sp	Central Valley sp	Not included in the FRAM
Butte Creek sp	Central Valley sp	Not included in the FRAM
Deer Creek sp	Central Valley sp	Not included in the FRAM
Feather Hatchery sp	Central Valley fa[a]	Central Valley–Sacramento
Stanislaus River	Central Valley fa	Central Valley–Sacramento
Butte Creek fa	Central Valley fa	Central Valley–Sacramento
Feather Hatchery fa	Central Valley fa	Central Valley–Sacramento
Battle Creek	Central Valley fa	Central Valley–Sacramento
Sacramento Hatchery	Central Valley wi	Not included in the FRAM
Russian River	California Coast	Not included in the FRAM
Eel River	California Coast	Not included in the FRAM
Trinity Hatchery fa	Klamath River	Not included in the FRAM
Trinity Hatchery sp	Klamath River	Not included in the FRAM
Klamath River fa	Klamath River	Not included in the FRAM
Chetco River	N California/S Oregon Coast	Not included in the FRAM
Cole Rivers Hatchery	Rogue River[b]	Not included in the FRAM
Applegate Creek	Rogue River	Not included in the FRAM
Umpqua Hatchery	Mid-Oregon Coast	Not included in the FRAM
Millicoma River	Mid-Oregon Coast	Not included in the FRAM
Coos Hatchery	Mid-Oregon Coast	Not included in the FRAM
S Coos Hatchery	Mid-Oregon Coast	Not included in the FRAM
Elk Hatchery	Mid-Oregon Coast	Not included in the FRAM
Sixes River	Mid-Oregon Coast	Not included in the FRAM
S Umpqua Hatchery	Mid-Oregon Coast	Not included in the FRAM
Coquille River	Mid-Oregon Coast	Not included in the FRAM
Siuslaw River	Mid-Oregon Coast	Oregon North Coast
Alsea River	N Oregon Coast	Oregon North Coast
Nehalem River	N Oregon Coast	Oregon North Coast
Siletz River	N Oregon Coast	Oregon North Coast
Kilchis River	N Oregon Coast	Oregon North Coast
Necanicum Hatchery	N Oregon Coast	Oregon North Coast
Nestucca Hatchery	N Oregon Coast	Oregon North Coast
Salmon River fa	N Oregon Coast	Oregon North Coast
Trask River	N Oregon Coast	Oregon North Coast
Wilson River	N Oregon Coast	Oregon North Coast
Yaquina River	N Oregon Coast	Oregon North Coast
Cowlitz Hatchery sp	W Cascade sp	Lower Columbia sp
Kalama Hatchery sp	W Cascade sp	Lower Columbia sp
Lewis Hatchery sp	W Cascade sp	Lower Columbia sp
Sandy River	W Cascade fa	Lower Columbia bright and tule
Cowlitz Hatchery fa	W Cascade fa	Lower Columbia bright and tule
Lewis River fa	W Cascade fa	Lower Columbia bright and tule
McKenzie Hatchery	Willamette River	Lower Columbia sp
N Santiam Hatchery	Willamette River	Lower Columbia sp

(Continues)

Table A.1 (Continued)

GAPS population	Genetic stock group	FRAM stock
Spring Creek Hatchery	Spring Creek Group tule	Mid-Columbia tule
U Yakima Hatchery	Mid and U Columbia River sp	Not included in the FRAM
Warm Springs Hatchery	Mid and U Columbia River sp	Not included in the FRAM
Wenatchee River sp	Mid and U Columbia River sp	Not included in the FRAM
Wenatchee Hatchery sp	Mid and U Columbia River sp	Not included in the FRAM
Carson Hatchery	Mid and U Columbia River sp	Not included in the FRAM
John Day River	Mid and U Columbia River sp	Not included in the FRAM
U Deschutes River	Deschutes River fa	Upper Columbia fall bright
L Deschutes River	Deschutes River fa	Upper Columbia fall bright
Methow River	U Columbia River su/fa	Columbia su
Wells Hatchery	U Columbia River su/fa	Columbia su
Wenatchee River su/fa	U Columbia River su/fa	Columbia su
Hanford Reach	U Columbia River su/fa	Upper Columbia fall bright
Minam River	Snake River sp/su	Not included in the FRAM
Rapid River Hatchery	Snake River sp/su	Not included in the FRAM
Secesh River	Snake River sp/su	Not included in the FRAM
Tucannon Hatchery	Snake River sp/su	Not included in the FRAM
Tucannon River	Snake River sp/su	Not included in the FRAM
Newsome Creek	Snake River sp/su	Not included in the FRAM
WF Yankee Fork	Snake River sp/su	Not included in the FRAM
EF Salmon River	Snake River sp/su	Not included in the FRAM
Imnaha River	Snake River sp/su	Not included in the FRAM
Lyons Ferry Hatchery	Snake River fa	Upper Columbia fall bright
Queets River	Washington Coast	Washington North Coast
Sol Duc Hatchery	Washington Coast	Washington North Coast
Forks Creek Hatchery	Washington Coast	Washington North Coast
Hoh River	Washington Coast	Washington North Coast
Humptulips Hatchery	Washington Coast	Not included in the FRAM
Makah Hatchery	Washington Coast	Washington North Coast
George Adams Hatchery	Hood Canal	Puget Sound fa
Hamma Hamma River	Hood Canal	Puget Sound fa
Elwha Hatchery	Juan de Fuca	Puget Sound fa
Elwha River	Juan de Fuca	Puget Sound fa
Dungeness River	Juan de Fuca	Puget Sound fa
Voights Hatchery	S Puget Sound fa	Puget Sound fa
Soos Hatchery	S Puget Sound fa	Puget Sound fa
White Hatchery	S Puget Sound sp	Puget Sound sp
Hupp Springs Hatchery	S Puget Sound sp	Puget Sound sp
Clear Creek Hatchery	S Puget Sound fa	Puget Sound fa
S Prairie Creek	S Puget Sound fa	Puget Sound fa
Skagit River	Whidbey Basin	Puget Sound sp
U Skagit River	Whidbey Basin	Puget Sound sp
U Sauk River	Whidbey Basin	Puget Sound sp
L Sauk River	Whidbey Basin	Puget Sound sp
Suiattle River	Whidbey Basin	Puget Sound sp
Marblemount Hatchery sp	Whidbey Basin	Puget Sound sp
Marblemount Hatchery su	Whidbey Basin	Puget Sound sp
U Cascade River	Whidbey Basin	Puget Sound sp

(Continues)

Table A.1 (Continued)

GAPS population	Genetic stock group	FRAM stock
Samish Hatchery	S Puget Sound fa	Puget Sound fa
Snoqualmie River	S Puget Sound fa	Puget Sound fa
Wallace Hatchery	Whidbey Basin	Puget Sound sp
Skykomish River	Whidbey Basin	Puget Sound sp
NF Stillaguamish Hatchery	Whidbey Basin	Puget Sound sp
NF Nooksack Hatchery	Nooksack	Puget Sound sp
Birkenhead Hatchery	L Fraser River	Canada (Fraser River/WCVI/Geo St)
W Chilliwack Hatchery	L Fraser River	Canada (Fraser River/WCVI/Geo St)
Maria Slough	L Fraser River	Canada (Fraser River/WCVI/Geo St)
Nicola Hatchery	L Thompson River	Canada (Fraser River/WCVI/Geo St)
Spius Hatchery	L Thompson River	Canada (Fraser River/WCVI/Geo St)
M Shuswap Hatchery	S Thompson River	Canada (Fraser River/WCVI/Geo St)
L Adams Hatchery	S Thompson River	Canada (Fraser River/WCVI/Geo St)
L Thom River	S Thompson River	Canada (Fraser River/WCVI/Geo St)
Raft River	N Thompson River	Canada (Fraser River/WCVI/Geo St)
Deadman Hatchery	N Thompson River	Canada (Fraser River/WCVI/Geo St)
Clearwater River	N Thompson River	Canada (Fraser River/WCVI/Geo St)
Louis Creek	N Thompson River	Canada (Fraser River/WCVI/Geo St)
Nechako River	Mid Fraser River	Canada (Fraser River/WCVI/Geo St)
Quesnel River	Mid Fraser River	Canada (Fraser River/WCVI/Geo St)
Stuart River	Mid Fraser River	Canada (Fraser River/WCVI/Geo St)
U Chilcotin River	Mid Fraser River	Canada (Fraser River/WCVI/Geo St)
Chilko River	Mid Fraser River	Canada (Fraser River/WCVI/Geo St)
Morkill River	U Fraser River	Not included in the FRAM
Salmon River sp	U Fraser River	Not included in the FRAM
Swift River	U Fraser River	Not included in the FRAM
Torpy River	U Fraser River	Not included in the FRAM
Big Qualicum Hatchery	E Vancouver Island	Canada (Fraser River/WCVI/Geo St)
Quinsam Hatchery	E Vancouver Island	Canada (Fraser River/WCVI/Geo St)
Nanaimo Hatchery fa	E Vancouver Island	Canada (Fraser River/WCVI/Geo St)
Puntledge Hatchery fa	E Vancouver Island	Canada (Fraser River/WCVI/Geo St)
Cowichan Hatchery	E Vancouver Island	Canada (Fraser River/WCVI/Geo St)
Marble Hatchery	W Vancouver Island	Canada (Fraser River/WCVI/Geo St)
Nitinat Hatchery	W Vancouver Island	Canada (Fraser River/WCVI/Geo St)
Robertson Hatchery	W Vancouver Island	Canada (Fraser River/WCVI/Geo St)
Sarita Hatchery	W Vancouver Island	Canada (Fraser River/WCVI/Geo St)
Tahsis River	W Vancouver Island	Canada (Fraser River/WCVI/Geo St)
Tranquil River	W Vancouver Island	Canada (Fraser River/WCVI/Geo St)
Conuma Hatchery	W Vancouver Island	Canada (Fraser River/WCVI/Geo St)
Porteau Cove Hatchery	S British Columbia Mainland	Canada (Fraser River/WCVI/Geo St)
Klinaklini River	S British Columbia Mainland	Canada (Fraser River/WCVI/Geo St)
Wannock Hatchery	Central British Columbia Coast	Not included in the FRAM
Atnarko Hatchery	Central British Columbia Coast	Not included in the FRAM
Kitimat Hatchery	Central British Columbia Coast	Not included in the FRAM
Ecstall River	L Skeena River	Not included in the FRAM
L Kalum River	L Skeena River	Not included in the FRAM
Bulkley River	U Skeena River	Not included in the FRAM
Sustut River	U Skeena River	Not included in the FRAM

(Continues)

Table A.1 (Continued)

GAPS population	Genetic stock group	FRAM stock
Babine Hatchery	U Skeena River	Not included in the FRAM
Owegee River	Nass River	Not included in the FRAM
Damdochax River	Nass River	Not included in the FRAM
Kincolith River	Nass River	Not included in the FRAM
Kwinageese River	Nass River	Not included in the FRAM
L Tahltan River	U Stikine River	Not included in the FRAM
Nakina River	Taku River	Not included in the FRAM
Tatsatua Creek	Taku River	Not included in the FRAM
U Nahlin River	Taku River	Not included in the FRAM
Kowatua Creek	Taku River	Not included in the FRAM
Chickamin/White Hatchery	SSE Alaska	Not included in the FRAM
Chickamin River	SSE Alaska	Not included in the FRAM
Chickamin Hatchery	SSE Alaska	Not included in the FRAM
Clear Creek	SSE Alaska	Not included in the FRAM
Cripple Creek	SSE Alaska	Not included in the FRAM
Keta River	SSE Alaska	Not included in the FRAM
King Creek	SSE Alaska	Not included in the FRAM
Andrew Creek	SSE Alaska Stikine River	Not included in the FRAM
Andrew/Mac Hatchery	SSE Alaska Stikine River	Not included in the FRAM
Andrew/Med Hatchery	SSE Alaska Stikine River	Not included in the FRAM
Andrew/Cry Hatchery	SSE Alaska Stikine River	Not included in the FRAM
King Salmon River	NSE Alaska King Salmon River	Not included in the FRAM
Tahini River	NSE Alaska Chilkat River	Not included in the FRAM
Tahini/Mac Hatchery	NSE Alaska Chilkat River	Not included in the FRAM
Big Boulder Creek	NSE Alaska Chilkat River	Not included in the FRAM
Klukshu River	N Gulf Coast Alsek River	Not included in the FRAM
Situk River	N Gulf Coast Situk River	Not included in the FRAM

[a] Mixture allocation to Central Valley fall genetic stock group will include fish from the extensively hybridized Feather River Hatchery "spring-run" brood stock.
[b] Mixture allocation to the Rogue River genetic stock group also includes fish from the closely related Select Area Fishery Evaluation hatchery program propagated in the lower Columbia River.