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MANAGEMENT BRIEF

Quantifying the Uncertainty of a Juvenile Chinook Salmon Race Identification Method for a Mixed-Race Stock

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Abstract

Expected daily FL ranges (length at date) of juvenile Chinook Salmon *Oncorhynchus tshawytscha* have been used throughout California's Central Valley to identify federally listed winter-run and spring-run juveniles in a mixed four-race stock. Accurate race identification is critical both to species recovery and to management of the water supply for 25 million people and a multibillion-dollar agricultural industry. We used genetic race assignment of 11,609 juveniles sampled over 6 years to characterize the accuracy of the length-at-date approach, specifically by testing two of its central assumptions: (1) juvenile FL distributions do not overlap between races on a daily basis; and (2) the growth rates that are used to project FL at date are accurate. We found that 49% of FLs for genetically identified juveniles occurred outside the expected length-at-date ranges for their respective races, and we observed a high degree of overlap in FL ranges among the four races. In addition, empirical growth rates were well below those from which length-at-date criteria were derived. Given the high degree of FL overlap between races, we conclude that modification of the length-at-date method will not substantially reduce identification error. Thus, we recommend that genetic assignment be used at least as a supplemental approach to improve Central Valley Chinook Salmon race identification, research, and management.

Management of rare species often requires decisions to be made based on inadequate data and suboptimal tools, thereby introducing uncertainty into risk assessment (Burgman 2005; Moore and Runge 2012); this uncertainty can lead to profound ecological and economic consequences (Gillespie et al. 2011; McGowan et al. 2011). Such is the case for California's Central Valley, where the monitoring of endangered Chinook Salmon *Oncorhynchus tshawytscha* populations and the legal restrictions on water exports to protect those populations depend in part on a juvenile race identification method of unknown accuracy, called the length-at-date method.

The Central Valley comprises the combined basins of California's two longest rivers, the Sacramento River and the San Joaquin River, and was once among the most productive systems for salmon on the U.S. Pacific coast. Although a 150-year history of mining, fishery exploitation, habitat loss, and water infrastructure development has led to a severe and continuing decline in Central Valley salmon (Yoshiyama et al. 1998; Katz et al. 2012), the Sacramento–San Joaquin River system remains the only river system that supports four distinct spawning races of Chinook Salmon: spring, fall, late fall, and the endemic winter run (Yoshiyama et al. 1998). While these run designations are based on a difference in the general timing of adult spawning migrations, the juvenile offspring of these races constitute a mixed population in the Central Valley basin, and there are no clear morphological or behavioral characteristics that can be used to distinguish an individual juvenile's race (Williams 2006; del Rosario et al. 2013). Winter-run Chinook Salmon were federally listed in 1990 as a threatened species under the Endangered Species Act (NMFS 1990), and the status was updated to endangered in 1994 (NMFS 1994); the spring run was subsequently listed as threatened in 1999 (NMFS 1999). After federal listing of these

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races, the inability to determine the race of juveniles proved problematic for management, particularly with regard to the assessment of losses at the primary pumping facilities of the California State Water Project and federal Central Valley Project. The two pumping facilities are located in the inland delta formed by the confluence of the Sacramento and San Joaquin rivers (hereafter, Sacramento–San Joaquin Delta) and supply water to 25 million people (8% of the U.S. population: Sommer et al. 2007) and a multibillion-dollar agricultural industry that produces nearly half of the fruits, nuts, and vegetables grown in the USA (CDFA 2013). However, these pumping facilities also entrain juvenile salmon (Kimmerer 2008; Brown et al. 2009).

To monitor the status and account for take of protected Chinook Salmon, the California Department of Fish and Wildlife developed a length-at-date approach in 1989 (Fisher 1992; Harvey 2011; del Rosario et al. 2013), which continues to be used as the primary method of identifying and enumerating the take of winter-run juveniles throughout the Central Valley (e.g., NMFS 2009; del Rosario et al. 2013). The length-at-date approach originated from the observation that the spawning seasons of the four Central Valley Chinook Salmon runs are somewhat segregated in time (Fisher 1992; Harvey 2011; del Rosario et al. 2013). Based on this observation, the calendar year was divided into four adjacent, nonoverlapping time spans; the earliest and latest dates of each time span represented the earliest and latest estimated spawning dates of each run. Emergence dates (estimated from spawning intervals), a standard emergence length of 34 mm FL, and a juvenile exponential growth rate of 6.57×10^{-3} $\log_e$(mm FL)/d were then applied to project the expected minimum and maximum FLs for juveniles of each run through time. Note that throughout this document, "growth rate" refers to "apparent growth rate," a term commonly used to describe growth estimates that are potentially confounded by the influence of factors in addition to individual growth, such as immigration, emigration, and size-selective mortality (e.g., Ricker 1942; Busacker et al. 1990). Within this construct, the FL of a juvenile Chinook Salmon sampled in the Central Valley on any given day of the calendar year could be compared with a table of length-at-date criteria to designate that juvenile's race (Fisher 1992; Harvey 2011; del Rosario et al. 2013).

Although the simplicity of the length-at-date approach fulfilled an immediate need for field identification, many biologists involved with the approach's development, adoption, and subsequent use recognized that the assumptions underlying the approach were oversimplified (Williams 2006; del Rosario et al. 2013). Therefore, development of a genetic-based assignment method was initiated in 1994 to validate and potentially supplant the length-at-date identification method. Since 1996, genetic race assignment has been routine for juveniles collected at fish screens on intakes (also known as "salvaged" juveniles) at state and federal water pumping facilities, although genetic-based assignment has not been adopted for take assessment. Although salvaged fish are not counted directly toward protected species take, the number salvaged is the primary input variable for calculation of take.

An informal analysis of initial genetic test results suggested that roughly half of juveniles identified as winter run by the length-at-date method were not in fact genetic winter run; this finding led in 1997 to a doubling of the Endangered Species Act take allowance and to the adoption of modified length criteria based on a higher assumed winter-run growth rate of 8.16×10^{-3} $\log_e$(mm FL)/d, which was intended to reduce misidentification of age-0 spring-run and fall-run fish as winter run (described by Harvey 2011). Subsequently, a similar evaluation of the original length criteria also found that roughly half of the winter-run-length juveniles collected at salvage facilities were not genetic winter run (Hedgecock 2002). These prior analyses were limited in several respects. The early genetic tests used in these evaluations identified only the winter run, with all other juveniles being termed "non-winter run," and thus the length-at-date error rate could only be estimated with respect to genetic winter run (i.e., the proportion of winter-run-length fish that were not genetic winter run; and the proportion of non-winter-run-length fish that were genetic winter run). The analyses also did not correct for a bias of genetic samples toward large, early migrating juveniles in the winter-run length range for years prior to 2004, during which a variety of size-stratified sampling protocols was employed without formal documentation. Perhaps most importantly from a regulatory standpoint, the two analyses evaluated the accuracy of the original length-at-date model but did not assess the modified growth rate model currently used at the salvage facilities.

Therefore, we undertook an evaluation of the length-at-date method's accuracy, taking advantage of a greatly expanded data set, a more uniform sampling regime, improved genetic markers (Banks and Jacobson 2004), and improved analytical software (Kalinowski 2003, 2007), all of which allowed greater genetic test accuracy and race resolution. We specifically tested whether the length distributions of genetically assigned runs supported the two central assumptions of the length-at-date approach: (1) juvenile FL distributions do not overlap between races on a daily basis; and (2) the growth rates that are used to project FL at date are accurate.

METHODS

Fish that were salvaged at the state and federal pump intakes were regularly sampled (Kimmerer 2008; Grimaldo et al. 2009). The FLs of all juvenile Chinook Salmon in these samples were measured, and a subsample of juveniles was selected for nonlethal genetic analysis. Although most juveniles are salvaged between January and June in any given year, we considered a single "migration year" to encompass all juveniles that were salvaged from September of the previous year to August of the year of interest. Due to evidence of

size-biased sampling in some years, we limited most of our analyses to six migration years (2004 and 2006–2010); Kolmogorov–Smirnov and Anderson–Darling *K*-tests performed on pooled monthly FL distributions and on pooled annual sample date distributions for these migration years showed that distributions were not significantly different ($P > 0.05$ for both tests) between the subset of genetically tested juveniles and all salvaged juveniles (no more than 1 month with $P < 0.05$ for FL). However, our analysis of false-positive error rates for juveniles in the winter-run length-at-date range was extended to encompass the full 1996–2010 record because within this limited length range, unbiased sampling occurred during all years. Improper storage of tissue samples collected in 2005 precluded analysis of any samples from that year. Sampling, storage, DNA extraction, and genotyping of salvaged juveniles followed the protocol described by Banks et al. (2000). To determine genetic race assignment and to generate an estimated assignment probability (i.e., probability of correct genetic assignment) for each juvenile, we compared individual genotypes with the Central Valley Chinook Salmon HMSC16 baseline by using Genetic Mixture Analysis software (Kalinowski 2003) or its modified version, ONCOR (Kalinowski 2007).

An evaluation of genetic assignment accuracy performed on adult Chinook Salmon of known phenotypic run (Banks et al. 2014) revealed that Genetic Mixture Analysis and ONCOR software in combination with the HMSC16 baseline generated assignment probabilities that were overestimated and did not correlate well with actual misassignment rates, such that software-generated assignment probabilities were not useful for controlling genetic test error rate in our analysis. Therefore, we used all genetic assignments and qualified our conclusions based on the false-positive error rate of genetic tests for each race, as derived from Banks et al. (2014); the false-positive error rate was calculated as the number of misassigned fish divided by the total number of fish assigned to each race (Linn 2004).

Consistent with current practices at the salvage facilities, we used the modified length criteria for length-at-date assignment (Supplementary Table S.1 in the online version of this article). To visualize (1) juvenile FL conformity to ranges delineated by the length-at-date model and (2) the degree of overlap between races, we organized FL data into biweekly length frequency distributions according to sample month and day (years were combined), and we then overlaid these distributions with the length-at-date boundaries used to separate the races.

We also wanted to test whether FL distributions exhibited a more fundamental overlap between races, beyond merely an overlap in distribution tails. To accomplish this, we compared median FLs between the races within each biweekly period by using the nonparametric Kruskal–Wallis test followed by multiple comparisons with a nonparametric version of Tukey's honestly significant difference test (Siegel and Castellan 1988) as implemented in the R package "pgirmess" (R Development Core Team 2012; Giraudoux 2013). Age-0 and age-1 juveniles were visually distinguished from each other by using biweekly length frequency histograms and were compared separately. However, since early spawning for the winter run can occur soon after late spawning of the previous brood year's late-fall run and because the emigration period of age-0 winter-run juveniles coincides more with the emigration period of age-1 juveniles from the other races than with the emigration of age-0 fish from other races (Figure 1), we also compared the FLs of age-0 winter-run fish with the FLs of age-1 fish from the other races. Comparisons within each biweekly period were performed only for races with sample sizes of 10 or more FLs.

To compare empirical growth rates with the assumed growth rates of the length-at-date model, we used linear regression of $\log_e$(FL, mm) against the sample date of salvaged juveniles for each race and for each migration year; this regression approach was identical to that used in the original development of length-at-date growth rates based on juvenile Chinook Salmon raised in artificial rearing channels (Fisher 1992; Harvey 2011). For the fall, spring, and late-fall runs, which exhibited multiple migrant types, we performed separate regressions for (1) age-1 juveniles (distinguished from age-0 juveniles as previously indicated) and (2) early season fry migrants and late-season parr–smolt migrants within the age-0 class, which exhibited different growth trajectories. The transition point between the growth trajectories of fry migrants and parr–smolt migrants within the age-0 class were distinguished with segmented linear regression of $\log_e$(FL, mm) against salvage date (pooled across years for each run) using the R package "segmented" version 2.15.0 (Muggeo 2003, 2008; R Development Core Team 2012). Segmented linear regression also identified FLs in a transition period between the early season fry migrants and late-season parr–smolt migrants within the age-0 class. These FLs were not used in growth regressions because migrant type could not be distinguished. Growth rate regressions were performed only for sub-data sets containing 10 or more FLs.

The annual false-positive error rate for winter-run length-at-date assignment was calculated in similar fashion as the false-positive error rate for genetic tests. For each migration year, the false-positive error rate was the number of genetic non-winter-run fish that were within the length-at-date range for winter run divided by the total number of juveniles in the winter-run length range. This method for calculating false-positive error differs from the more common statistical approach for type I error rate but is more appropriate for expressing accuracy of the length-at-date approach as applied to the target salvage population (Linn 2004). Before calculating daily false-positive error rate, data were smoothed by averaging both the number of genetic winter-run juveniles and the number of all juveniles in the winter-run length range over the 3 d before

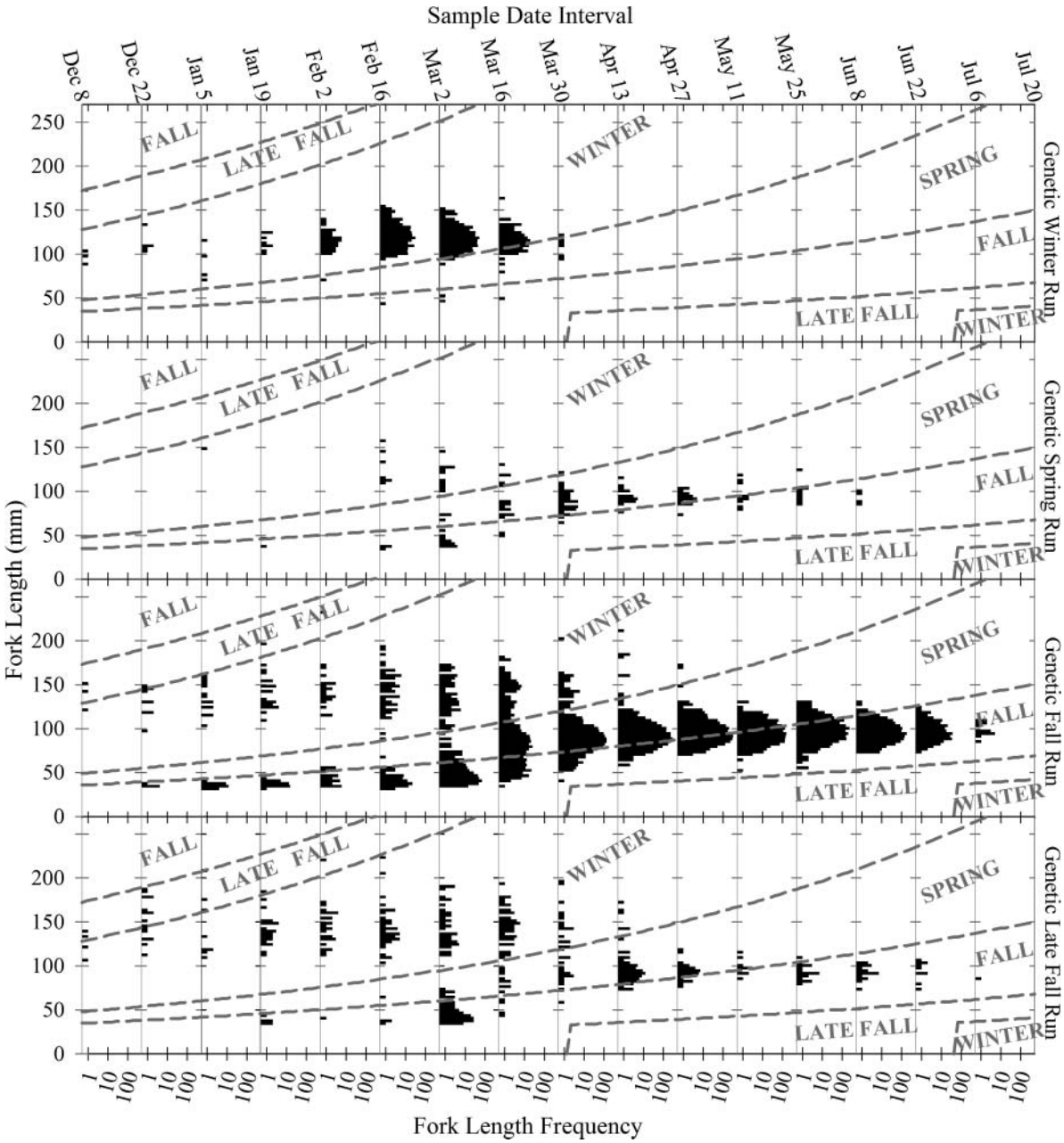

FIGURE 1. Length frequency distributions (mm FL; black bars and text), overlaid with length-at-date size criteria boundaries (gray dashed lines and text), for genetically identified winter, spring, fall, and late-fall Chinook Salmon juveniles (<270 mm) sampled over biweekly intervals at the intake canals for California State Water Project and federal Central Valley Project export facilities located in the inland Sacramento–San Joaquin Delta. Note that FL frequency is depicted on a modified $\log_{10}$ scale and that frequency distributions for most runs spread well beyond the corresponding predicted length-at-date ranges for each biweekly interval (as indicated by the intersection of dashed lines and *y*-axes).

and after each calendar day (i.e., 7-d running average). Daily rates were then averaged across years for each day of the year. All confidence intervals (CIs) for average values presented in figures and text are 95% CIs calculated from the sample from which the average was derived. All other statistical tests were performed in R (R Development Core Team 2012).

RESULTS

During our study years, 11,069 salvaged juvenile Chinook Salmon of unknown origin were assigned to race with genetic tests: 86.7% to the fall run, 7.1% to the winter run, 4.7% to the late-fall run, and 1.4% to the spring run (Table 1). There was substantial overlap of biweekly FL distributions among the

TABLE 1. Number of juvenile Chinook Salmon from each genetically assigned race that were assigned (based on FL) to each length-at-date race. Tissue was nonlethally sampled and FL was measured from fish that were collected (salvaged) at California State Water Project and federal Central Valley Project pump intakes in the Sacramento–San Joaquin Delta during 2004 and 2006–2010.

Length-at-date race assignment[a]	Genetic late-fall run	Genetic winter run	Genetic spring run	Genetic fall run
Late fall	9	0	0	3
Winter	218	749	22	287
Spring	116	56	95	4,629
Fall	193	5	45	4,915

[a] Length-at-date race was assigned using modified size criteria specific to salvage facilities (i.e., criteria were based on a higher assumed winter-run growth rate relative to the original criteria).

four genetic runs throughout the juvenile migration season. In particular, genetic fall-run, late-fall-run, and spring-run fish were broadly distributed across length ranges for all runs such that genetic assignments for nearly half (49%) of all juveniles differed from the corresponding length-at-date assignments (Figure 1). The greatest discrepancy was that 4,777 (47%) genetic fall-run juveniles fell within the spring-run length-at-date range, thus composing 95% of spring-run-length juveniles. Other large discrepancies were the 276 (3%) genetic fall-run fish and 211 (40%) genetic late-fall-run fish that fell within the winter-run length-at-date range, together constituting 39% of winter-run-length juveniles. In addition, 192 (36%) genetic late-fall-run fish fell within the fall-run length-at-date range, and 151 (44%) genetic spring-run individuals fell within either the fall-run or the winter-run length-at-date range.

The only consistent differences in the central tendency of FL distributions were between the winter run and the other runs during the four biweekly intervals from February 2 to March 29, a period in which 97% of the genetic winter-run juveniles were detected in salvage. Median FLs for the winter run were larger than median FLs for age-0 fry migrants from the other runs and were smaller than median FLs for age-1 fall-run and late-fall-run juveniles (Table 2).

Across all years and runs, we performed 12 regressions to estimate the growth rate of non-winter-run age-1 juveniles. Even when α was not corrected for multiple comparisons, only 1 of the 12 regressions exhibited a significant positive trend at $P < 0.05$ (fall run in 2007: growth rate $= 1.37 \times 10^{-3}$ $\log_e$[mm FL]/d; Figure 2). Similarly, only 5 of 15 regressions for non-winter-run parr–smolt migrants had significant FL trends at $P < 0.05$, one of which was negative (range $= -0.75 \times 10^{-3}$ to 7.47×10^{-3} $\log_e$[mm FL]/d), whereas winter-run migrants had two positive and two negative significant FL trends out of the 6 years tested (range $= -2.85 \times 10^{-3}$ to 2.13×10^{-3} $\log_e$[mm FL]/d; $P < 0.05$; Figure 2). Three of the five regressions for fry migrants had significant trends, all of which were positive (range $= 8.54 \times 10^{-3}$ to 21.05×10^{-3} $\log_e$[mm FL]/d; $P < 0.05$; Figure 2). Even among strictly the significant positive FL trends, the average rate of increase for non-winter-run age-1 migrants and age-0 parr–smolt migrants (mean $= 3.82 \times 10^{-3}$ $\log_e$[mm FL]/d; CI $= \pm 2.98 \times 10^{-3}$) was only about half the rate from which length-at-date criteria were derived (6.57×10^{-3} $\log_e$[mm FL]/d). For the winter run, the average of the positive trends (mean $= 1.98 \times 10^{-3}$ $\log_e$[mm FL]/d; CI $= \pm 1.97 \times 10^{-3}$) was less than a quarter of the winter-run growth rate assumed in the length-at-date approach (8.16×10^{-3} $\log_e$[mm FL]/d). In contrast, the average rate of increase for fry migrants (mean $= 15.61 \times 10^{-3}$ $\log_e$[mm FL]/d; CI $= \pm 15.90 \times 10^{-3}$) was more than double the length-at-date-assumed rate for non-winter-run fish (6.57×10^{-3} $\log_e$[mm FL]/d).

The yearly false-positive error rate for length-at-date winter-run assignments from 1996 to 2010 exhibited a downward trend (linear regression: $F_{2,\ 12} = 12.57$, $P < 0.01$; Figure 3b). Average yearly error rate over this period (mean error rate $=$ 0.56; CI $= \pm 0.11$) was higher than the single error rate (0.47) derived from data pooled across all years (not accounting for unequal distribution of sample sizes between years).

The proportion of genetic non-winter-run juveniles within the winter-run length range varied considerably over the juvenile migration season and between years as depicted by the CIs of daily false-positive error (Figure 4b). From December 1 through approximately the third week in January, the average daily false-positive error rates were highly variable, although on average they were over 0.50. Thereafter, average error rate declined, falling below 0.50 from the second week of February through the second week of March (a period of 5 weeks), and then rose rapidly to 1.0 by mid-April. However, the lower 95% confidence limit fell below 0.50 from the first week of February through the third week of March (a period of 7 weeks).

DISCUSSION

Using genetics as a validation tool, we have now characterized the uncertainty of the length-at-date method for assigning race to individual juvenile Chinook Salmon, particularly with respect to winter-run juveniles. The two central assumptions of the length-at-date approach (i.e., segregated FL ranges between races and a constant shared growth rate among races) were not supported by the FL data for genetically identified

TABLE 2. Comparison of median FL between genetically identified races of juvenile Chinook Salmon (F = fall run; L = late-fall run; W = winter run; S = spring run) sampled within the same biweekly date ranges (month and day) during 2004 and 2006–2010 at California State Water Project and federal Central Valley Project pumping plants in the Sacramento–San Joaquin Delta. Young-of-the-year (age-0) winter-run juveniles were compared with (1) age-0 juveniles of other races and (2) age-1 and older (age-1+) juveniles of other races (Kruskal–Wallis median test followed by multiple comparison tests where applicable). Races with fewer than 10 FLs in a biweekly group were not considered. Significantly different medians for races within each comparison are denoted by different lowercase letters.

Date range	Genetic race	*N*	Median FL (mm)	χ^2	df	*P*
Age-0 winter run and age-0 non-winter run						
Feb 2–15	F z	23	42	42.803	1	<0.001
	W y	39	115			
Feb 16–Mar 1	F z	74	39	168.640	1	<0.001
	W y	241	119			
Mar 2–15	F z	330	44	611.805	2	<0.001
	L z	111	42			
	W y	380	117			
Mar 16–29	F z	301	78	238.261	3	<0.001
	L z	13	77			
	W y	13	80			
	S y	126	115			
Mar 30–Apr 12	F	974	88	0.392	2	0.822
	L	12	89			
	S	33	90			
Apr 13–26	F	1,781	91	2.641	2	0.267
	L	63	92			
	S	19	92			
Apr 27–May 10	F	2,053	93	0.083	2	0.959
	L	32	93.5			
	S	18	93			
May 11–24	F	1,180	95	0.064	1	0.800
	S	10	94.5			
May 25–Jun 7	F y	1,494	98	8.751	1	0.003
	L z	21	92			
Jun 8–21	F	1,021	95	1.458	1	0.227
	L	20	92			
Age-0 winter run and age-1+ non-winter run						
Jan 19–Feb 1	F	23	135	0.0709	1	0.790
	L	24	139.5			
Feb 2–15	F y	21	142	43.770	2	<0.001
	L y	26	144			
	W z	39	115			
Feb 16–Mar 1	F y	55	145	96.739	2	<0.001
	L y	40	138			
	W z	241	119			
Mar 2–15	F y	63	135	114.574	3	<0.001
	L y	43	136			
	W z	12	117.5			
	S z	380	117			
Mar 16–29	F y	54	148	133.139	2	<0.001
	L y	49	146			
	W z	126	115			
Mar 30–Apr 12	F	32	143.5	0.885	1	0.347
	L	20	142.5			

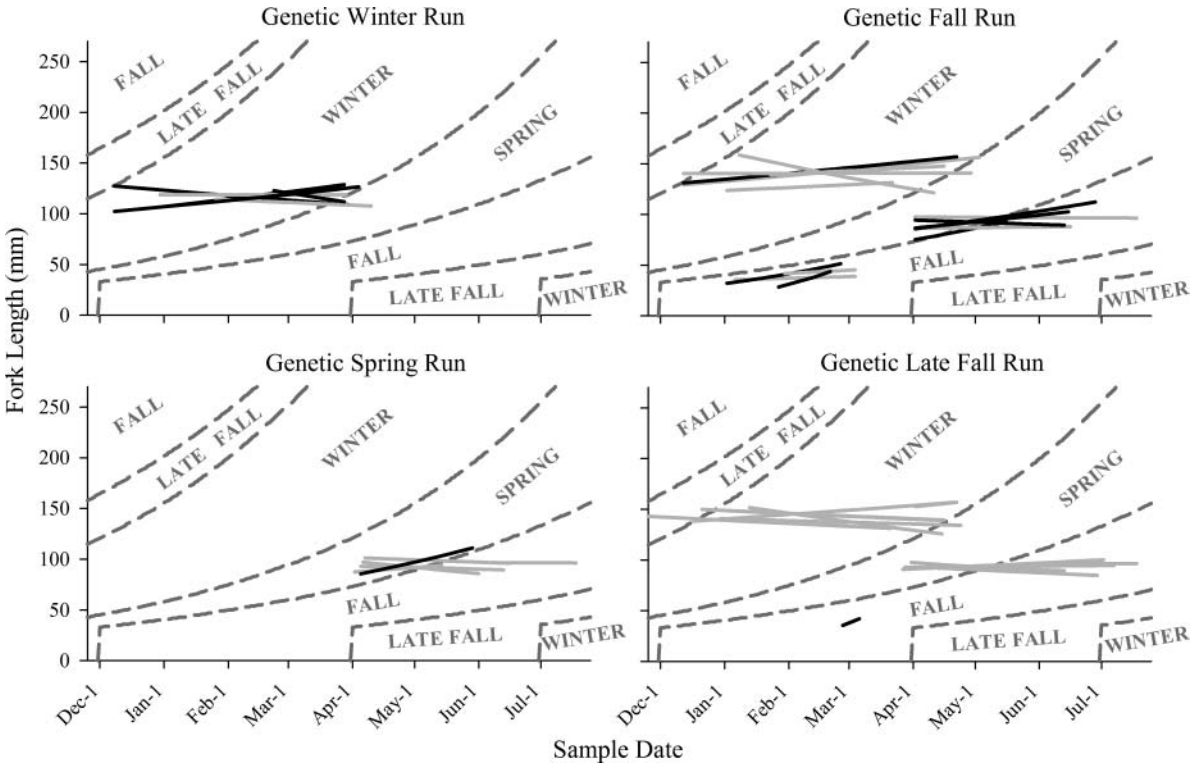

FIGURE 2. Fork length–calendar date regression lines for 2004 and 2006–2010 (solid black = $P < 0.05$; solid gray = $P > 0.05$), overlaid with length-at-date size criteria boundaries (dashed gray lines and gray text), for genetically identified Chinook Salmon juveniles (<270 mm). For the spring, fall, and late-fall runs, separate regressions were performed for age-1 juveniles (upper left in each panel), age-0 fry migrants (lower left in each panel), and age-0 parr–smolt migrants (right side of each panel) for years with 10 or more data points. Length-at-date size criteria boundaries (gray dashed lines and text) are equivalent to predicted apparent growth rates.

juveniles. Fork length ranges of the individual runs were not segregated and were widely distributed across length-at-date categories (Table 1; Figure 1), and the FL trends for all runs did not consistently exhibit the constant growth rates used to generate length-at-date criteria (Figure 2). In fact, there was so little distinction among the FL distributions of juvenile spring-run, fall-run, and late-fall-run Chinook Salmon that the median FL did not significantly differ among these runs (Table 2). The lack of distinction between FL distributions, coupled with the lack of consistent FL trend (i.e., growth rate), indicates that a simple refinement of length criteria based on modified growth rates—or even based on length ranges fitted to genetically identified races—will not produce more accurate run assignments.

Owing to the early focus on the winter run by the Central Valley salmon genetics program and because genetic tests for assigning fish to the winter run are highly accurate (genetic test error rates are <1%; Banks et al. 2014), the genetic assignment record for the winter run is the longest and most reliable among the four Central Valley races, and thus genetic validation of the length-at-date method is most robust for this race. Over the period 1996–2010, the annual proportion of genetic non-winter-run juveniles within the winter-run length range varied substantially from 23% to 89%, with a generally downward trend that was driven primarily by increasing numbers of salvaged genetic winter-run fish.

Within each year, genetic winter-run juveniles exhibited the most concentrated and segregated salvage timing of the four races. Relative to the other races, genetic winter-run fish migrated through the Sacramento–San Joaquin Delta earlier and within a shorter time frame, primarily between February 1 and April 1 (Figure 1). Although the majority of winter-run-length fish were also sampled at the salvage facilities during this time frame, the proportion of genetic non-winter run among these winter-run-length fish—and therefore the false-positive error rate—was lowest and most consistent during this period (Figure 4). However, before February 1 and after April 1, well over 50% and often closer to 80% of salvaged juveniles in the winter-run length range were not genetic winter run, thus inflating the false-positive error rate. In addition, pulses of winter-run emigrants during December and January of some years resulted in a highly variable error rate in those months.

Another dimension of management concern regarding the accuracy of race assignment is the false-negative error rate. Because the calculation of false-negative error rate relies on equal detection probability of genetic winter-run juveniles across the length-at-date ranges for all races, it was only

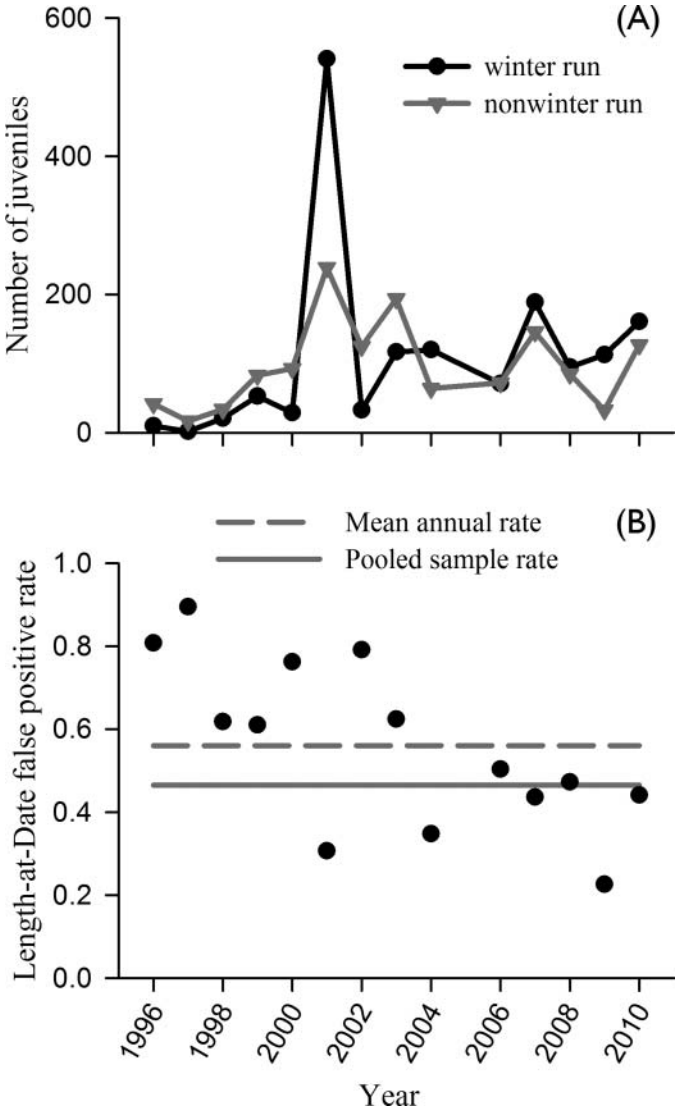

FIGURE 3. **(A)** Number of genetic winter-run fish (black) and genetic non-winter-run fish (gray) among genetically tested juveniles in the winter-run length-at-date range for Chinook Salmon salvaged at state and federal water projects; and **(B)** yearly proportion of genetic non-winter-run fish in the winter-run length-at-date range (i.e., false-positive error rate). The dashed horizontal line is the false-positive error rate calculated as an average of annual error rates (circles); the solid horizontal line is the single error rate calculated from data pooled across all years.

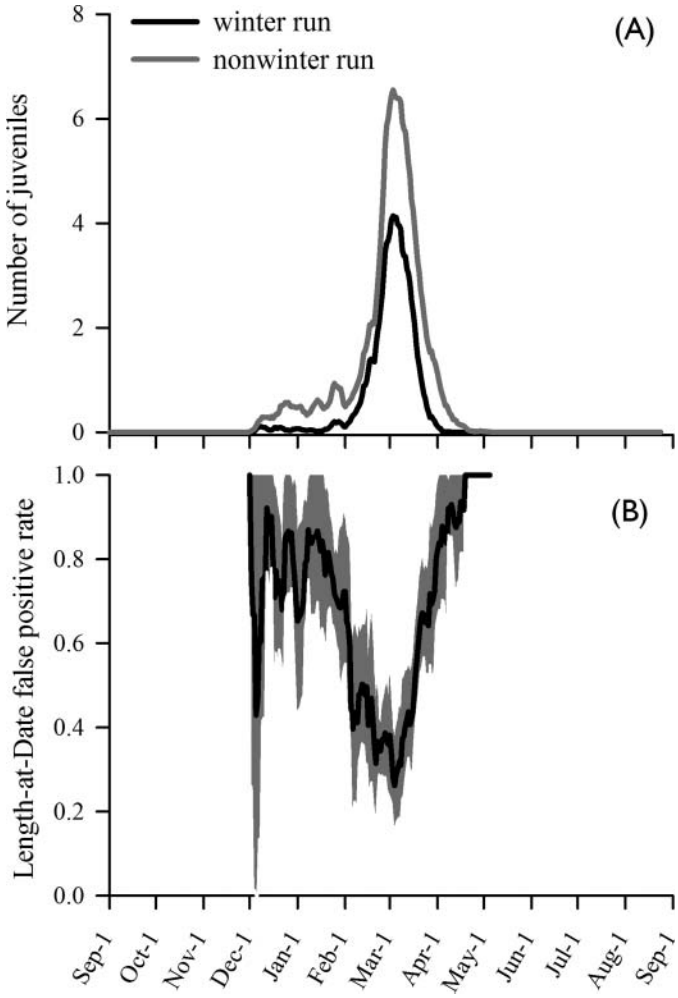

FIGURE 4. For genetically tested juvenile Chinook Salmon salvaged at state and federal water projects during 1996–2010: **(A)** average daily count of all juveniles (gray line) and genetic winter-run juveniles (black line) in the winter-run length-at-date size range; and **(B)** the average daily proportion of juveniles in the winter-run length-at-date size range that were identified as not genetic winter run (i.e., false-positive error rate). Daily count was smoothed with a 7-d running average before averaging across years. False-positive rate in panel B (black line) is shown with the 95% confidence interval (gray-shaded area).

appropriate to examine genetic assignments from 2004 and later years, when genetic samples were not biased by size-selective sampling. Although a large proportion of genetic non-winter-run fish occurred within the winter-run length range (as reflected by the false-positive rate discussed above), the majority of genetic winter-run individuals were also effectively encapsulated within the winter-run length criteria. Between 2004 and 2010, only 8% of salvaged genetic winter-run fish occurred outside the winter-run length criteria; this is double the 4% false-negative rate reported by Hedgecock (2002) but is still below 10%. The success of the length-at-date method in identifying genetic winter run did not appear to be at the cost of misidentifying large numbers of fish from the other races, as the FLs of the other genetic runs were widely distributed across the winter-run length range and broadly overlapped the genetic winter-run size distributions (Figure 1). In other words, another slight shift in the borders of the winter-run length range would probably not have substantially altered the false-negative error rate.

In a system such as the Central Valley, where protected races must be distinguishable from coexisting unprotected races and where no single tool can distinguish between them, a hybrid approach may provide the most reliable estimates for

monitoring and take assessment. A hybrid approach is currently in use at the salvage facilities, where winter-run take is based on length-at-date assignment modified by an assumed annual 50% false-positive error rate (NMFS 2009). However, incorporation of genetic analyses and updated information on the accuracy of the length-at-date method can potentially improve this hybrid system. Genetic testing could be used to monitor and assess take of the most accurately identifiable stocks (i.e., winter-run and select spring-run stocks). During the lag time between field sampling and genetic assignment, which currently varies from several days to many weeks, the interim take of winter-run fish could be estimated with a modified length-at-date approach by using a seasonally adjustable false-positive error rate (Figure 4b) and by incorporating error rate uncertainty into take assessments. Alternative genetic approaches may be applied for protected stocks that are not identifiable with current Central Valley genetic baselines, such as proportions of the spring-run population that cannot be separated from the formerly allopatric fall run due to limited recent hybridization. One such approach is parental-based genetic tests that link juveniles directly to individual spawners that have been sampled in the field (i.e., to their parents; Anderson and Garza 2006). However, parental-based genetic testing requires rigorous estimation of both juvenile production and the proportion of the adult population that is genetically analyzed—expensive and labor-intensive processes that will limit the use of this method in situations other than hatcheries.

Although the growth rates of juvenile Chinook Salmon salvaged at the fish screens were derived in the same manner as the length-at-date growth rates, it is important to note that growth was not actual growth. More accurately, the FL of salvaged fish represented juvenile length at the point of emigration from freshwater. As the most intensive program for sampling fish communities in the Sacramento–San Joaquin Delta, salvage is arguably the most comprehensive existing record of juvenile Chinook Salmon presence and FL distribution at emigration. The most marked feature of this distribution was a general convergence of fall-run, late-fall-run, and spring-run FLs to a narrow and constant range of 80–110 mm after mid-April (Figure 1). Before mid-April, winter-run juveniles and (to a lesser extent) age-1 juveniles from the other runs also exhibited narrow-range, nontrending FL distributions through time (Figures 1, 2). These distributions suggest that within the 2–4-month emigration period for each migrant type, the cues for juvenile emigration from the delta may depend more on a juvenile size or age threshold than on calendar date or environmental cues. In addition, the broad and overlapping FL ranges of the spring, fall, and late-fall runs demonstrated a diversity of juvenile emigration timing and length within all three runs. Recent analyses suggest that a portfolio of life history strategies historically existed within the Central Valley runs, lending resilience to salmon populations in California's variable and unpredictable climate (Lindley et al. 2009; Carlson and Satterthwaite 2011). Fish screen salvage data support otolith studies (Miller et al. 2010) indicating that a range of alternative emigration strategies persist despite hatchery and water management activities that strongly favor a narrowing of life history diversity (Lindley et al. 2009).

Any effort to replace the length-at-date approach will have to contend with the same issue that originally led to adoption of this method; there is no alternative approach currently available that will fulfill the requirements of expedient, nonlethal identification with low false-positive and false-negative error rates for all protected races. Genetic tests are not a panacea for problematic race assignment. Current genetic tests cannot distinguish between fall, late-fall, and spring runs at an acceptable level of accuracy, and any solution that incorporates genetic testing will need to address the lag time between sample collection and the availability of genetic test results. Nevertheless, for management of Central Valley Chinook Salmon and water resources, these genetic analyses offer a substantial improvement over historical race identification methods based on growth models, and we recommend that genetic tools be used at least as a supplemental approach to race identification and management. Based on the successful application of genetic tools to other salmon stocks and other rare fishes (e.g., Green Sturgeon *Acipenser medirostris*: Israel et al. 2004), these approaches will probably be increasingly valuable in the management of mixed stocks, both for direct identification of protected populations and as a tool to assess the uncertainty of nongenetic monitoring strategies.

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REFERENCES

Anderson, E. C., and J. C. Garza. 2006. The power of single-nucleotide polymorphisms for large-scale parentage inference. Genetics 172:2567–2582.

Banks, M. A., and D. P. Jacobson. 2004. Which genetic markers and GSI methods are more appropriate for defining marine distribution and migration of salmon? North Pacific Anadromous Fish Commission Technical Note 5:39–42.

Banks, M. A., D. P. Jacobson, I. Meusnier, C. A. Greig, V. K. Rashbrook, W. R. Ardren, C. T. Smith, J. Bernier-Latmani, J. Van Sickle, and K. G. O'Malley. 2014. Testing advances in molecular discrimination among Chinook Salmon life histories: evidence from a blind test. Animal Genetics 45:412–420.

Banks, M. A., V. K. Rashbrook, M. J. Calavetta, C. A. Dean, and D. Hedgecock. 2000. Analysis of microsatellite DNA resolves genetic structure and diversity of Chinook Salmon (*Oncorhynchus tshawytscha*) in California's Central Valley. Canadian Journal of Fisheries and Aquatic Sciences 57:915–927.

Brown, L. R., W. Kimmerer, and R. Brown. 2009. Managing water to protect fish: a review of California's environmental water account, 2001–2005. Environmental Management 43:357–368.

Burgman, M. 2005. Risks and decisions for conservation and environmental management. Cambridge University Press, Cambridge, U.K.

Busacker, G. P., I. R. Adelman, and E. M. Goolish. 1990. Growth. Pages 363–387 *in* C. B. Schreck and P. B. Moyle, editors. Methods for fish biology. American Fisheries Society, Bethesda, Maryland.

Carlson, S. M., and W. H. Satterthwaite. 2011. Weakened portfolio effect in a collapsed salmon population complex. Canadian Journal of Fisheries and Aquatic Sciences 68:1579–1589.

CDFA (California Department of Food and Agriculture). 2013. California agricultural statistics review, 2012–2103. CDFA, Sacramento. Available: http://www.cdfa.ca.gov/statistics/. (October 2014).

del Rosario, R. B., Y. J. Redler, K. Newman, P. L. Brandes, T. Sommer, K. Reece, and R. Vincik. 2013. Migration patterns of juvenile winter-run sized Chinook Salmon (*Onchorhynchus tschawytscha*) through the Sacramento–San Joaquin delta. San Francisco Estuary and Watershed Science 11(1).

Fisher, F. W. 1992. Chinook Salmon, *Oncorhynchus tshawytscha*, growth and occurrence in the Sacramento–San Joaquin River system. California Department of Fish and Game, Inland Fisheries Division, draft office report, Redding.

Gillespie, G. R., M. P. Scroggie, J. D. Roberts, H. G. Cogger, M. J. Mahony, and K. R. McDonald. 2011. The influence of uncertainty on conservation assessments: Australian frogs as a case study. Biological Conservation 144:1516–1525.

Giraudoux, P. 2013. pgirmess: data analysis in ecology. R package version 1.5.8. Available: http://perso.orange.fr/giraudoux. (October 2014).

Grimaldo, L. F., T. Sommer, N. Van Ark, G. Jones, E. Holland, P. B. Moyle, B. Herbold, and P. Smith. 2009. Factors affecting fish entrainment into massive water diversions in a tidal freshwater estuary: can fish losses be managed? North American Journal of Fisheries Management 29:1253–1270.

Harvey, B. N. 2011. Length-at-date criteria to classify juvenile Chinook Salmon in the California Central Valley: development and implementation history. Interagency Ecological Program Newsletter 24(3). Available: http://www.water.ca.gov/iep/newsletters/2011/IEPNewsletterFinalSummer2011.pdf. (October 2014).

Hedgecock, D.. 2002. Microsatellite DNA for the management and protection of California's Central Valley Chinook Salmon (*Oncorhynchus tshawytscha*). University of California–Davis, Bodega Marine Laboratory, Final Report to the California Department of Water Resources, Amendment to Agreement B-59638, Bodega.

Israel, J. A., M. Blumberg, J. F. Cordes, and B. May. 2004. Geographic patterns of genetic differentiation among western U.S. collections of North American Green Sturgeon (*Acipenser medirostris*). North American Journal of Fisheries Management 24:922–931.

Kalinowski, S. T. 2003. Genetic mixture analysis 1.0. Montana State University, Department of Ecology, Bozeman. Available: http://www.montana.edu/kalinowski. (October 2014).

Kalinowski, S. T. 2007. ONCOR: a computer program for genetic stock identification. Montana State University, Department of Ecology, Bozeman. Available: http://www.montana.edu/kalinowski/Software/ONCOR.htm. (October 2014).

Katz, J., P. B. Moyle, R. M. Quinones, J. A. Israel, and S. Purdy. 2012. Impending extinction of salmon, steelhead, and trout (Salmonidae) in California. Environmental Biology of Fishes 96:1169–1186.

Kimmerer, W. J. 2008. Losses of Sacramento River Chinook Salmon and Delta Smelt to entrainment in water diversions in the Sacramento–San Joaquin delta. San Francisco Estuary and Watershed Science 6(2).

Lindley, S. T., C. B. Grimes, M. S. Mohr, W. Peterson, J. Stein, J. T. Anderson, L. W. Botsford, D. L. Bottom, C. A. Busack, T. K. Collier, J. Ferguson, J. C. Garza, A. M. Grover, D. G. Hankin, R. G. Kope, P. W. Lawson, A. Low, R. B. MacFarlane, K. Moore, M. Palmer-Zwahlen, F. B. Schwing, J. Smith, C. Tracy, R. Webb, B. K. Wells, and T. H. Williams. 2009. What caused the Sacramento River fall Chinook stock collapse? NOAA Technical Memorandum NMFS-SWFSC-447.

Linn, S. 2004. A new conceptual approach to teaching the interpretation of clinical tests. Journal of Statistics Education [online serial] 12(3).

McGowan, C. P., M. C. Runge, and M. A. Larson. 2011. Incorporating parametric uncertainty into population viability analysis models. Biological Conservation 144:1400–1408.

Miller, J. A., A. Gray, and J. Merz. 2010. Quantifying the contribution of juvenile migratory phenotypes in a population of Chinook Salmon *Oncorhynchus tshawytscha*. Marine Ecology Progress Series 408:227–240.

Moore, J. L., and M. C. Runge. 2012. Combining structured decision making and value-of-information analyses to identify robust management strategies. Conservation Biology 26:810–820.

Muggeo, V. M. R. 2003. Estimating regression models with unknown breakpoints. Statistics in Medicine 22:3055–3071.

Muggeo, V. M. R. 2008. segmented: an R Package to fit regression models with broken-line relationships. R News 8(1). Available: http://cran.r-project.org/doc/Rnews/. (October 2014).

NMFS (National Marine Fisheries Service). 1990. Endangered and threatened species; Sacramento River winter-run Chinook Salmon; final rule. Federal Register 55:214(5 November 1990):46515.

NMFS (National Marine Fisheries Service). 1994. Endangered and threatened species; threatened status for two Chinook Salmon evolutionarily significant units (ESUs) in California; final rule. Federal Register 59:2(4 January 1994):440, 450.

NMFS (National Marine Fisheries Service). 1999. Endangered and threatened species; threatened status for two Chinook Salmon evolutionarily significant units (ESUs) in California; final rule. Federal Register 64:179(16 September 1999):50394–50415.

NMFS (National Marine Fisheries Service). 2009. Biological opinion and conference opinion on the long-term operations of the Central Valley Project and State Water Project. Endangered Species Act Section 7 consultation. National Ocean and Atmospheric Administration, National Marine Fisheries Service, Southwest Region, Long Beach, California.

R Development Core Team. 2012. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna.

Ricker, W. E. 1942. The rate of growth of Bluegill sunfish in lakes of northern Indiana. Indiana University, Department of Conservation, Indianapolis.

Siegel, S., and N. J. Castellan Jr. 1988. Nonparametric statistics for the behavioral sciences, 2nd edition. McGraw-Hill, New York.

Sommer, T., C. Armor, R. Baxter, R. Breuer, L. Brown, M. Chotkowski, S. Culberson, F. Feyrer, M. Gingras, B. Herbold, W. Kimmerer, A. Mueller-Solger, M. Nobriga, and K. Souza. 2007. The collapse of pelagic fishes in the upper San Francisco Estuary. Fisheries 32:270–277.

Williams, J. G. 2006. Central Valley salmon: a perspective on Chinook and steelhead in the Central Valley of California. San Francisco Estuary and Watershed Science 4(3):Article 2.

Yoshiyama, R. M., F. W. Fisher, and P. B. Moyle. 1998. Historical abundance and decline of Chinook Salmon in the Central Valley region of California. North American Journal of Fisheries Management 18:487–521.