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#### RESEARCH

# Comparison of Length-at-Date Criteria and Genetic Run Assignments for Juvenile Chinook Salmon Caught at Sacramento and Chipps Island in the Sacramento-San Joaquin Delta of California

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#### **ABSTRACT**

There are four distinct runs of Chinook Salmon (Oncorhynchus tshawytscha) in the Central Valley, named after their primary adult return times: fall, late-fall, winter, and spring run. Estimating the run-specific composition of juveniles entering and leaving the Sacramento–San Joaquin Delta is crucial for assessing population status and processes that affect juvenile survival through the Delta. Historically, the run of juvenile Chinook Salmon captured in the field has been determined using length-at-date criteria (LDC); however, LDC

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run assignments may be inaccurate if there is high overlap in the run-specific timing and size of juveniles entering and leaving the Delta. In this study, we use genetic run assignments to assess the accuracy of LDC at two trawl locations in the Sacramento River (Delta entry) and at Chipps Island (Delta exit). Fin tissues were collected from approximately 7,500 juvenile Chinook Salmon captured in trawl samples between 2007 and 2011. Tissues were analyzed using 21 microsatellites to determine genetic run assignments for individuals, which we compared with LDC run assignments. Across years, there was extensive overlap among the distributions of run-specific fork lengths of genetically identified juveniles, indicating that run compositions based on LDC assignments would tend to underestimate fall-run and especially late-fall-run compositions at both trawl locations, and greatly overestimate springrun compositions (both locations) and winterrun compositions (Chipps Island). We therefore strongly support ongoing efforts to include tissue sampling and genetic run identification of juvenile Chinook Salmon at key monitoring locations in the Sacramento-San Joaquin River system.

#### **KEY WORDS**

Chinook Salmon, length-at-date criteria, Sacramento–San Joaquin Delta, genetics, microsatellites

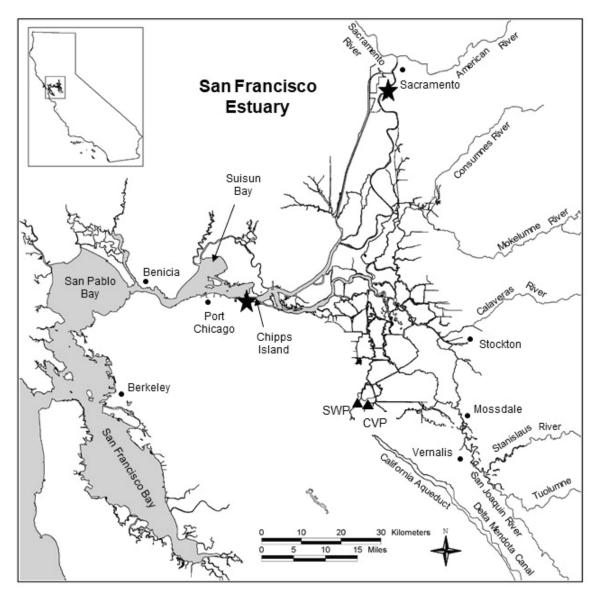
#### INTRODUCTION

The challenges of mixed stock salmon management extend not only to harvest in fisheries, but also to distinguishing stock of origin among juveniles migrating to sea. In the Central Valley of California, four distinct runs of Chinook Salmon (Oncorhynchus tshawytscha) are named after their primary adult return times: fall, late-fall, winter, and spring run (Fisher 1994; Yoshiyama et al. 1998). Juveniles of these runs intermix to various degrees during their seaward migrations in the lower Sacramento River and Sacramento-San Joaquin Delta (Figure 1; Yoshiyama et al. 1998; Williams 2006). Accurate run identification of juveniles at monitoring locations in tributaries and the Delta is crucial to understanding juvenile migration timing, movements, and distributions (e.g., Brandes and McLain 2001; del Rosario et al. 2013; Perry et al. 2016; Johnson et al. 2017), especially for the winter- and spring-run populations of the Sacramento River, which are listed as endangered and threatened, respectively, under the federal Endangered Species Act (Fed Regis 1994, 1999) and California Endangered Species Act (CESA, Title 14, Section 670.5). Many of the recovery (management) actions specified for the winter and spring runs target juvenile life stages (NMFS 2014), such as maintenance of instream flows, passage improvements, and restoration of riparian, wetland, and floodplain habitats. Juvenile monitoring studies with accurate run identification will be needed to evaluate and refine some of these various—and often costly—recovery actions (NMFS 2014; Peterson and Duarte 2020).

Historically, run assignments of juvenile Chinook Salmon captured at tributary and Delta monitoring sites have been determined using the river model length-at-date criteria (LDC) developed by Fisher (1992) and later refined to daily criteria (1992 memorandum report from S. Greene to R. L. Brown, unreferenced, see "Notes"; Harvey 2011; del Rosario et al. 2013). These non-overlapping criteria, which were based on observations of run-specific spawning times and assumed juvenile growth rates, define the expected fork-length range of juveniles of each run across the calendar year (Harvey et al. 2011).

A modified version of the river model LDC, called the Delta model LDC, has been used since 1997 to estimate incidental take of winter- and springrun juveniles at the fish salvage facilities of the two water export facilities in the Central Valley (Figure 1): the California State Water Project (SWP) and the federal Central Valley Project (CVP) (Harvey 2011; Harvey et al. 2014). While the river and Delta LDCs have somewhat different winterrun length ranges, it has been long recognized that the tenuous assumptions that underlie both LDCs, coupled with evidence of overlapping juvenile length distributions, cast doubt on the reliability of all LDC run assignments in the lower Sacramento River and Delta (Williams 2006; Harvey 2011; Harvey et al. 2014). Consequently, genetic approaches were investigated in the 1990s (Hedgecock et al. 2001), leading to the development of assignment methods based on microsatellites and a baseline collection of Central Valley Chinook Salmon (Banks et al. 2000; Banks and Jacobson 2004). Using this methodology, Harvey et al. (2014) compared genetic run assignments with those based on the Delta model LDC for juvenile Chinook Salmon obtained at the SWP and CVP, and found that 49% of genetically identified juveniles had fork lengths outside their run-specific LDC. It is unclear, however, if such inaccuracies in LDC assignments occur at other monitoring sites in the lower Sacramento River and Delta.

In this paper, we use genetic run assignments to assess the accuracy of the river model LDC for juvenile Chinook Salmon sampled from trawl catches during 2007 through 2011 in the Sacramento River and at Chipps Island (Figure 1). These trawl locations, each with several decades of standardized data collection, are two key sites monitored by the Delta Juvenile Fish Monitoring Program of the US Fish and Wildlife Service (USFWS). We use the river model LDC in this study because it has been typically used for all river monitoring sites (conducted by several agencies) in the Central Valley, and those sampled in the river and Delta by USFWS. Trawling the Sacramento River captures juveniles just as they enter the Delta, while trawling at Chipps Island captures juveniles as they exit the Delta



**Figure 1** The San Francisco Estuary in California, which includes the Sacramento–San Joaquin Delta. The cities of Sacramento and Mossdale are the north and south boundaries of the Delta, respectively, whereas Chipps Island is the western boundary. The State Water Project (SWP) and federal Central Valley Project (CVP) water export facilities are located in the southwest of the Delta (*triangles*). *Stars* denote the locations of the Sacramento and Chipps Island trawls.

(Figure 1). As detailed in Johnson et al. (2017), having accurate run identification at these two trawl locations is a critical step toward developing robust run-specific estimates of relative or absolute juvenile abundance and, potentially, estimates of survival through the Delta. For the imperiled winter and spring runs, having reliable estimates of population abundance at Delta entry and exit are viewed as key metrics to inform freshwater and Delta management actions (Johnson et al. 2017), and to support the

development of life-cycle models for these runs (e.g., Hendrix et al. 2014; Cordoleani et al. 2020).

#### **METHODS**

We took tissue samples from approximately 7,500 unmarked juvenile Chinook Salmon caught in trawl sampling in the Sacramento River and near Chipps Island between October 2007 and June 2011 (these years reflect the time-period funded by the Delta Science Program). The USFWS

conducted the trawling as part of the Interagency Ecological Program (IEP). Trawls in the Sacramento River were conducted in an upstream direction and in the middle of the channel of a roughly 6.4-km reach, with the northernmost boundary at the south end of the City of Sacramento. A midwater trawl was used in the Sacramento River between April and September; a Kodiak trawl was used between October and March to increase catch of larger Chinook juveniles (McLain 1998). Trawling at Chipps Island was conducted using a midwater trawl within a 3-km section of river upstream of the western tip of Chipps Island (Brandes and McLain 2001). Chipps Island trawls were conducted in three channel locations (north, south, and middle), and both upstream and downstream, depending on tidal conditions.

At both locations, trawling was typically conducted 2 to 3 days per week using ten 20-minute tows per day during morning hours. Occasionally, the number or duration of tows at Chipps Island was reduced as a result of inclement weather, mechanical problems, or excessive catch of Delta Smelt, which were listed in 1993 as a threatened species under the Federal and California State Endangered Species Acts (Fed Regist 1993). For example, between February 5 and March 10 of 2008, trawling at Chipps Island was curtailed because of concerns that incidentaltake limits for Delta Smelt might be exceeded. Trawling in the Sacramento River was more regular and not disrupted by incidental catch of Delta Smelt; however, tissue sampling there did not begin until late March of 2008.

We classified juvenile salmon to their run in the field using the river model LDC (hereafter referred to simply as "LDC"). We made attempts to sample tissues from all juvenile salmon caught in the trawl, though sub-sampling of the fall-run LDC was incorporated during late April and early May, when many unmarked fall-run hatchery fish were assumed to be in the catch, based on the number of tagged hatchery fish caught. During those periods, we sampled tissue from only five juveniles per tow (50 per day) in the fall-run LDC.

Sampling protocols for collecting tissues were similar to those used at the SWP and CVP fish facilities (Harvey et al. 2014), except that we placed samples on filter paper and allowed them to air dry instead of using a buffer solution. In the field, we took a 1 × 2-mm or 2 × 4-mm triangular piece of tissue from the top or bottom lobe of the caudal fin shortly after a juvenile was caught. We placed the tissue on filter paper, folded the filter paper over twice, and inserted it into a labeled coin envelope. We then dried the tissues in the laboratory and placed them into plastic bags for storage. We gave the samples a unique ID number and linked them to individuals in the trawl database.

## **Genetic Run Assignments**

Details of the molecular and statistical methodology used to determine genetic run assignments are provided in Banks et al. (2014) and references therein. In brief, we characterized samples using the 21-microsatellite panel for the Hatfield Marine Science Center baseline, denoted HMSC21 (Banks et al. 2014). HMSC21 includes the following loci: Ots-104, -107 (Nelson and Beacham 1999); Ots-201b, -208b, -209 -211, -212, -215 (Greig et al. 2003); Ots-G78b, -G83b, -G249, -G253, -G311, -G422, -G409 (Williamson et al. 2002); Ost515 (Naish and Park 2002); and five microsatellites derived from research characterizing alternate copies of the circadian rhythm transcription factor Cryptochome, including Cry2b.1, Cry2b.2, Cry3 (O'Malley et al 2010), Ots-701 (GeneBank accession # KF163438), and Ots-702 (GeneBank accession # KF163440). Alternate microsatellite alleles were resolved through electrophoresis using an Applied Biosystems (AB) 3730xl DNA analyzer and scored using AB GeneMapper software (Version 4).

We assessed data for the 21 microsatellites from each sample from the Sacramento River or Chipps Island against the HMSC21 baseline using the "assign individual to baseline population" option of the population assignment program ONCOR (Kalinowski et al. 2007) to determine the most likely sub-population origin. The baseline data comprised five primary sub-populations as described in Banks et al. (2000): fall, late-fall, winter, and two genetically distinct assemblages

of spring run from (1) Butte Creek, and (2) neighboring Mill and Deer creeks. The fall-run sub-population includes mainstem spawning populations from throughout the Sacramento and San Joaquin rivers, as well as both early (putative spring) and late (putative fall) returns to the Feather River (spring run) because of difficulty in resolving sub-structure between these latter two stocks (Banks et al. 2000; Hedgecock et al. 2001). Although the late-fall run is considered part of the fall-run ESU (evolutionary significant unit), it has a distinct life history and genetic differences (Yoshiyama et al. 1998; Williams 2006), as well as management concerns, and so we report separate results for genetic assignments of the fall and late-fall runs.

The genetic run assignments used here can be uncertain and sometimes incorrect (Banks et al. 2014). Blind test data that quantify falsepositive and false-negative error rates (Banks et al. 2014) can be used to estimate run-assignment "corrections" that adjust run numbers within a given sample (e.g., for a discrete sampling period and size class of individuals), as done by del Rosario et al. (2013) for winter run and Pyper et al. (2013) for all runs (using the Chipps Island assignments presented here). However, the methodology is complex when applied to all runs, contains arbitrary decisions (e.g., defining discrete periods for pooling samples), and most importantly, does not generally lead to substantively different conclusions regarding run compositions compared to using raw (uncorrected) genetic assignments (Pyper et al. 2013). Thus, for the sake of brevity, we use raw genetic assignments for comparisons with LDC assignments and note in the discussion where key uncertainties and differences are expected, as found by Pyper et al. (2013).

#### **Comparisons**

We compared LDC and genetic run assignments at both trawl locations for the 4 "field" years in which data were collected (2008 through 2011), where field year comprised samples collected from September through August of the subsequent calendar year (e.g., field year 2008 ran from September 1, 2007 through August 31,

2008). The data consisted of only those individuals for which a genetic assignment was made. We first report comparisons of LDC and genetic run assignments pooled across field years, which demonstrate the key differences between the two assignment methods at each trawl site. We then compare annual run assignments, which highlight among-year variation in differences between the two assignment methods. In our comparisons, we assume that genetic run assignments represent the "true" run of each juvenile sampled; however, as noted above and in the discussion, genetic assignments are not without error. For each run type, we used Pearson's chi-square test (i.e., analysis of  $2 \times 2$ contingency tables; Zar 1999) to assess the statistical difference in run proportions based on LDC assignments vs. genetic assignments.

#### **RESULTS**

Across field years 2008 through 2011, genetic run assignments were made for 2,565 juvenile Chinook Salmon collected from the Sacramento River and 5,108 juveniles collected at Chipps Island (Table 1; Figure 2). Differences in acrossyear tabulations of genetic and LDC assignments by run type were statically significant ( $\chi^2 > 45.0$ ; p < 0.0001) in all cases except for winter run in the Sacramento River ( $\chi^2 = 0.11$ ; p = 0.75).

Two key discrepancies between genetic and LDC assignments were evident at both trawl locations. First, LDC assignments were lower for fall run and much higher for spring run compared to genetic assignments because genetic fall run dominated the spring-run LDC (Table 1; Figure 2). For example, from the Sacramento River, 436 (17.0% of total) juveniles that were genetic fall run were assigned to the spring-run LDC, and similarly at Chipps Island (985 or 19.3%; Table 1). Consequently, genetic fall run comprised 80.9% of the spring-run LDC from the Sacramento River (436 of 539 juveniles), and 78.2% at Chipps Island (985 of 1,259 juveniles). Thus, LDC assignments underestimated the fall-run fraction of juveniles compared to the genetic fraction (77.0% LDC vs. 87.1% genetic from the Sacramento River; 69.9% LDC vs. 84.8% genetic at Chipps Island), and

**Table 1** Run assignments for juvenile Chinook Salmon based on length-at-date criteria (LDC; rows) versus genetic assignments (columns) across field years 2008 through 2011 for Sacramento River and Chipps Island trawls. Shaded cells denote matching runs for the two assignment methods.

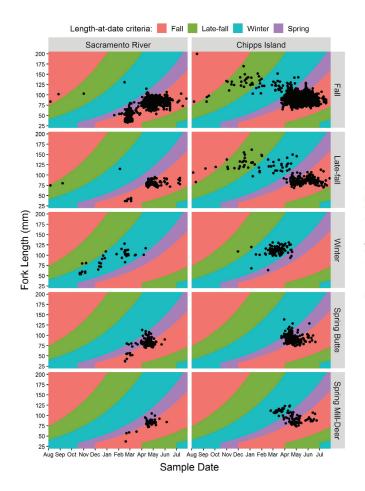
		Genetic					
Location	LDC	Fall	Late-fall	Winter	Spring Butte	Spring Mill/Deer	LDC total
Sacramento	Fall	1795	96	0	54	30	1975
	Late-fall	1	2	3	0	0	6
	Winter	2	1	38	4	0	45
	Spring	436	15	1	71	16	539
	Genetic total	2234	114	42	129	46	2565
Percent of total	Fall	70.0	3.7	0.0	2.1	1.2	77.0
	Late-fall	0.0	0.1	0.1	0.0	0.0	0.2
	Winter	0.1	0.0	1.5	0.2	0.0	1.8
	Spring	17.0	0.6	0.0	2.8	0.6	21.0
	Genetic total	87.1	4.4	1.6	5.0	1.8	100.0
Chipps Island	Fall	3263	194	0	71	42	3570
	Late-fall	29	22	3	0	0	54
	Winter	53	27	98	20	27	225
	Spring	985	29	4	210	31	1259
	Genetic total	4330	272	105	301	100	5108
Percent of total	Fall	63.9	3.8	0.0	1.4	0.8	69.9
	Late-fall	0.6	0.4	0.1	0.0	0.0	1.1
	Winter	1.0	0.5	1.9	0.4	0.5	4.4
	Spring	19.3	0.6	0.1	4.1	0.6	24.6
	Genetic total	84.8	5.3	2.1	5.9	2.0	100.0

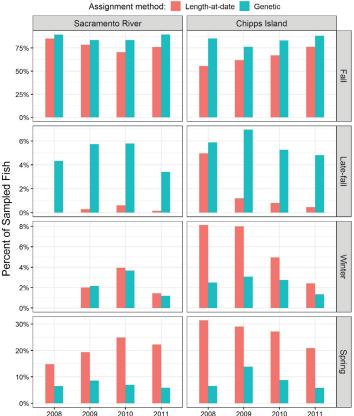
greatly overestimated the spring-run fraction (21.0% LDC vs. 6.8% genetic from the Sacramento River; 24.6% LDC vs. 7.9% genetic at Chipps Island; Table 1 with genetic fractions summed across the spring sub-populations).

The second key discrepancy at both trawl locations occurred for late-fall run. Juveniles identified as genetic late-fall run were mostly found in the fall-run LDC (Table 1; Figure 2). Consequently, LDC assignments greatly underestimated the late-fall-run fraction of juveniles compared to the genetic fraction (0.2% LDC vs. 4.4% genetic from the Sacramento River; 1.1% LDC vs. 5.3% genetic at Chipps Island; Table 1).

For winter run, differences between LDC and genetic assignments were minimal for the Sacramento River but larger for Chipps Island (Table 1; Figure 2). At Chipps Island, most genetic winter run were within the winter-run LDC (98 of 105 juveniles; Table 1); however, relatively large numbers of genetic fall (53), late-fall (27), spring Butte (20), and spring Mill/Deer (27) juveniles were also within the winter-run LDC (Table 1; Figure 2). Consequently, the fraction of winter run based on LDC assignments (4.4%) was more than double the fraction based on genetic assignments (2.1%; Table 1) at Chipps Island.

At both trawl locations, genetic spring-run assignments to the Butte Creek sub-population were roughly three times greater than those





**Figure 2** Scatterplot of genetic run assignments (*rows*) for juvenile Chinook Salmon caught in the Sacramento River trawl (*left column*) and Chipps Island trawl (*right column*) as a function of fork length and sample date across field years 2008-2011. The *color regions* correspond to the length-at-date criteria (LDC) for run assignment. Adapted from Johnson et al. (2017).

**Figure 3** Percent of total juvenile Chinook Salmon by field year assigned to each run (*rows*) based on length-at-date criteria (LDC) versus genetic analysis for the Sacramento River trawl (*left column*) and Chipps Island trawl (*right column*). Adapted from Perry et al. (2016).

for Mill and Deer creeks (Table 1). In addition, genetic spring-run Mill/Deer juveniles tended to fall outside of the spring-run LDC to a greater extent than genetic spring-run Butte juveniles (Figure 2; Table 1). From the Sacramento River, only 16 (35%) of 46 genetic spring-run Mill/Deer juveniles were in the spring-run LDC (the remaining 30 were in the fall-run LDC), compared to 71 (55%) of 129 genetic spring-run Butte juveniles (Table 1). Similarly, at Chipps Island, only 31 (31%) of 100 genetic spring-run Mill/Deer juveniles were in the spring-run LDC (the remaining were in the fall and winter-run LDCs),

compared to 210 (70%) of 301 genetic spring-run Butte juveniles.

There were also notable differences between LDC and genetic assignments among field years, particularly for juveniles collected at Chipps Island (Figure 3). Annual numeric assignments for the Sacramento River and Chipps Island are provided in Tables 2 and 3, respectively. Annual differences in genetic and LDC assignments by run type were statically significant ( $\chi^2 > 6.0$ ; p < 0.015) in most cases, except for fall run from the Sacramento River in 2008 ( $\chi^2 = 1.96$ ; p = 0.16), late-fall run at Chipps Island in 2008 ( $\chi^2 = 0.35$ ;

**Table 2** Run assignments for juvenile Chinook Salmon based on length-at-date criteria (LDC; *rows*) versus genetic assignments (*columns*) by field year for the Sacramento River trawl. Shaded cells denote matching runs for the two assignment methods.

		Genetic					
Field Year	LDC	Fall	Late-fall	Winter	Spring Butte	Spring Mill/Deer	LDC total
2008	Fall	214	10	0	8	4	236
	Late-fall	0	0	0	0	0	0
	Winter	0	0	0	0	0	0
	Spring	33	2	0	5	1	41
	Genetic total	247	12	0	13	5	277
2009	Fall	476	37	0	27	7	547
	Late-fall	0	0	2	0	0	2
	Winter	1	0	13	0	0	14
	Spring	106	3	0	22	4	135
	Genetic total	583	40	15	49	11	698
2010	Fall	206	15	0	8	3	232
	Late-fall	1	1	0	0	0	2
	Winter	0	1	12	0	0	13
	Spring	68	2	0	9	3	82
	Genetic total	275	19	12	17	6	329
2011	Fall	899	34	0	11	16	960
	Late-fall	0	1	1	0	0	2
	Winter	1	0	13	4	0	18
	Spring	229	8	1	35	8	281
	Genetic total	1129	43	15	50	24	1261

p=0.55), and for winter run from the Sacramento River in all years ( $\chi^2 < 0.3$ ; p > 0.60). For these comparisons, we are most interested in how relative differences in annual run proportions (fractions) between LDC and genetic assignments vary across years (Figure 3). For example, for spring run, ratios of the LDC fraction vs. genetic fraction from the Sacramento River ranged from a low of 2.25 in 2009 (19.3% LDC vs. 8.6% genetic) to a high of 3.80 in 2011 (22.3% LDC vs. 5.9% genetic; Figure 3). Differences for spring run were broader at Chipps Island, with ratios ranging from a low of 2.10 in 2009 (29.1% LDC vs. 13.9% genetic) to a high of 4.79 in 2008 (31.4% LDC vs. 6.6% genetic; Figure 3).

For the other runs, annual differences in run fractions were most pronounced for assignments at Chipps Island (Figure 3). Ratios of the LDC fraction vs. genetic fraction for fall run at Chipps Island ranged from a low of 0.65 in 2008 (55.5% LDC vs. 85.1% genetic) to a high of 0.87 in 2011 (76.3% LDC vs. 88.1% genetic). For late-fall run, ratios varied widely from a low of 0.10 in 2011 (0.5% LDC vs. 4.8% genetic) to a high of 0.85 in 2008 (5.0% LDC vs. 5.9% genetic). Lastly, ratios for winter run ranged from a low of 1.81 in 2010 (5.0% LDC vs. 2.7% genetic) to a high of 3.27 in 2008 (8.1% LDC vs. 2.5% genetic).

The most notable difference between the Sacramento River and Chipps Island occurred

**Table 3** Run assignments for juvenile Chinook Salmon based on length-at-date criteria (LDC; *rows*) versus assignments based on genetic analysis (*columns*) by field year for Chipps Island trawl. Shaded cells denote matching runs for the two assignment methods.

		Genetic					
Field Year	LDC	Fall	Late-fall	Winter	Spring Butte	Spring Mill/Deer	LDC total
2008	Fall	229	11	0	5	1	246
	Late-fall	14	8	0	0	0	22
	Winter	11	5	11	1	8	36
	Spring	123	2	0	13	1	139
	Genetic total	377	26	11	19	10	443
2009	Fall	401	32	0	24	6	463
	Late-fall	3	4	2	0	0	9
	Winter	15	12	20	2	11	60
	Spring	152	4	1	55	6	218
	Genetic total	571	52	23	81	23	750
2010	Fall	810	49	0	31	15	905
	Late-fall	7	4	0	0	0	11
	Winter	13	7	37	3	7	67
	Spring	293	11	0	48	15	367
	Genetic Total	1123	71	37	82	37	1350
2011	Fall	1823	102	0	11	20	1956
	Late-fall	5	6	1	0	0	12
	Winter	14	3	30	14	1	62
	Spring	417	12	3	94	9	535
	Genetic total	2259	123	34	119	30	2565

for winter run assignments (e.g., Figure 3). Across years, the winter-run LDC was clearly the best performing LDC at depicting genetic run assignments (e.g., Figure 2), with 38 (90%) of 42 genetic winter run found in the winter-run LDC from the Sacramento River and 98 (93%) of 105 at Chipps Island (Table 1). However, numerous juveniles of other genetic runs were found within the winter-run LDC at Chipps Island, while only seven such fish were found at Sacramento (two fall, one late-fall, and four spring run from Butte Creek; Table 1). Consequently, annual differences between LDC and genetic assignments of winter run from the Sacramento River were relatively small (e.g., less than 9%; Figure 3). More generally, however, this relates to another

discrepancy observed between locations: it appears that numerous fall, late-fall, and springrun yearlings (age-1 juveniles) were caught at Chipps Island from October through March but very few from the Sacramento River. From October 2008 through March 2011, when trawl effort and tissue sampling were comparable between locations, fork-length distributions of non-genetic-winter run were strongly bimodal, with presumed yearlings above 92 mm and sub-yearlings (age-0 fish) below 82 mm. Using this designation and time-period, a total of 76 yearlings captured at Chipps Island had fall, latefall, and spring-run genetic assignments, 48 of which were found inside the winter-run LDC (e.g., Figure 2). In contrast, only three such yearlings

were captured at Sacramento, with two found inside the winter-run LDC.

#### **DISCUSSION**

Our comparisons of LDC versus genetic run assignments for juvenile Chinook Salmon caught in trawl samples from the Sacramento River and at Chipps Island indicate that, across a given field season, run compositions based on the river model LDC are likely to contain two key biases at both trawl locations. First, fall-run compositions will be underestimated, and springrun compositions strongly overestimated (e.g., 2to 5-fold overestimates) because large proportions of genetic fall-run juveniles have fork lengths within the spring-run LDC. Second, compositions of late-fall run will be highly underestimated because most genetic late-fall-run juveniles have fork lengths within the fall-run LDC, while comparatively few juveniles of any run will be found in the late-fall-run LDC. In addition, at Chipps Island, we expect winter-run compositions to be strongly overestimated by LDC (e.g., 2- to 3-fold overestimates) because many yearlings from the other genetic runs will have fork lengths within the winter-run LDC.

Our results are consistent with previous comparisons of LDC and genetic run assignments of juvenile Chinook Salmon recovered at the SWP and CVP fish salvage facilities (Hedgecock 2002; Harvey et al. 2014). For example, Harvey et al. (2014) compared Delta model LDC and genetic assignments for over 11,000 juveniles across years 2004 and 2006 through 2010, and collectively, found that 47% of genetic fall-run juveniles were within the spring-run LDC, nearly all genetic latefall-run juveniles were found outside their LDC, and 39% of juveniles within the winter-run LDC were from other genetic runs. The biases in the Delta model LDC run compositions implied by these results are similar to those found at Chipps Island (e.g., Figure 2). In addition, Harvey et al. (2014) report considerable year-to-year variation in the differences between LDC and genetic compositions for winter run, as we found across years at Chipps Island (Figure 3).

Our analyses, as well as those of Harvey et al. (2014), assume that genetic run assignments represent the true run of juveniles. However, the genetic assignments used here can be uncertain and are best validated using blind tests (Banks et al. 2014) in which fish of known run origin (either juveniles or adults) are genetically assigned to a run. For a given run (e.g., fall run), blind tests yield the number of correct assignments as well as false-positive errors (e.g., fish of other runs incorrectly assigned to fall run) and false-negative errors (e.g., fall-run fish incorrectly assigned to a different run). The blind-test error rates can then be used to derive corrected estimates of genetic run assignments for a given sample, as done by Pyper et al. (2013) for the raw assignments at Chipps Island reported here.

Although the use of corrected assignments would not alter the conclusions of this paper, it is important to acknowledge uncertainties in genetic run assignments. The blind-test results of Banks et al. (2014) indicated low error rates for genetic assignments of fall run and winter run, and, hence, corrected assignments for these runs were very similar to the raw assignments reported here for Chipps Island (Pyper et al. 2013). In contrast, late-fall run were associated with a high false-negative error rate (e.g., 52% of true late-fall-run fish were incorrectly assigned to fall run) and a seemingly small yet crucial falsepositive error rate, whereby 1.8% of true fall run were incorrectly assigned to late-fall run (Pyper et al. 2013). These error rates resulted in highly uncertain estimates of corrected assignments for late-fall run, and either increases or decreases in corrected vs. raw assignments, depending on the run composition of samples (Pyper et al. 2013). The largest annual difference occurred in 2011, with 74 corrected assignments for late-fall run at Chipps Island instead of the 123 shown in Table 3 (i.e., a 39.8% decrease using corrected assignments). Nevertheless, the same general conclusion about LDC versus genetic assignments holds: run compositions of late-fall run are likely to be highly underestimated when based on LDC assignments.

For spring run, few fish of known origin were included in the blind tests, with 13 fish for Butte Creek and only two fish for Mill and Deer creeks (Banks et al. 2014). Pyper et al. (2013) pooled these data to compute error rates for each sub-population (and their total) and found that corrected assignments were very similar to the raw assignments reported here for Chipps Island; however, spring-run assignments should be viewed as somewhat uncertain and potentially biased, given the lack of blind test data available. Because genetic assignments at Chipps Island and the Sacramento River were based on the same methodology, the strong coherence observed between raw and corrected genetic assignments for fall, winter, and spring run at Chipps Island (Pyper et al. 2013) would also be expected for assignments made for the Sacramento River. Another source of uncertainty in our genetic assignments relates to the Feather River spring run. As a result of introgression, the spring and fall runs in the Feather River are genetically similar (Banks et al. 2000; Hedgecock et al. 2001), and hence some small (but unknown) fraction of the genetic fall run assignments presented here was likely composed of Feather River spring run.

For the Sacramento River and Chipps Island, LDC run assignments appear generally unreliable, and as noted by Harvey et al. (2014), refinements to the mutually exclusive, run-specific LDCs would not substantively improve LDC assignments, given the broad overlap in juvenile fork lengths observed across runs for genetically identified individuals (e.g., Figure 2). In addition, it is unlikely that observed ratios of LDC vs. genetic assignments could be used to develop useful "corrections" for LDC assignments in years without genetic data, given the high variation in differences between LDC and genetic assignments observed across years for most runs (e.g., Figure 3; see also Harvey et al. 2014). In short, high fork-length overlap and potentially large annual differences in run-specific juvenile abundance, migration timing, and growth rates—particularly for the numerically dominant fall run-make LDC assignments at Sacramento and Chipps Island untenable in most cases.

An important exception, however, may be for LDC assignments of winter run at Sacramento, which were reasonably consistent with genetic assignments across years (e.g., Figure 3). At Sacramento, most genetic winter-run juveniles were caught across a protracted period from late October through early March and tended to have much higher fork lengths than the juveniles of other genetic runs caught during this period (e.g., Figure 2). At Chipps Island, most genetic winter run were caught between February and early April, with lengths consistent with their LDC; however, numerous juveniles of other runs (i.e., genetic fall, late-fall, and spring) were also caught between January and April, with lengths within the winter-run LDC (Figure 2), most of which were apparent yearlings. Thus, on one hand, our results suggest that LDC assignments of winter run from the Sacramento River may be suitable for developing a long-term index of relative abundance (trawling in the Sacramento River began in 1988), though more years of genetic data should be assessed to verify this finding (e.g., our Sacramento River data set contained only 3 years and 45 juveniles within the winter-run LDC; Table 2). On the other hand, the presence of numerous fall, late-fall, and spring-run yearlings at Chipps Island during October through March, vs. their relative absence in the Sacramento River, begs explanation.

There are several possible reasons for the observed lack of yearlings from the Sacramento River. These include sampling error (chance), low trawl efficiency for yearlings from the Sacramento River compared to Chipps Island (e.g., from systematic differences in turbidity conditions or trawl avoidance abilities), or the presence of fall-run yearlings from the San Joaquin River basin, which would be available for capture at Chipps Island but not from the Sacramento River. While systematic differences in trawl efficiencies between locations are likely, parallel fishing of the Kodiak and midwater trawls in the Sacramento River (McLain 1998) showed that the Kodiak trawl was more effective at catching larger juveniles, consistent with its intended use during winter months. Instead, we hypothesize that the primary mechanism

relates to differences in diel movement patterns. For example, Chapman et al. (2012) studied movements of acoustic-tagged late-fall yearlings in the Sacramento River and found downstream migrations to be primarily nocturnal within the river but much less so in the estuary. Similar patterns have been found for emigrating Sockeye Salmon smolts (Furey et al. 2016). It has been extensively documented that Atlantic Salmon juveniles exhibit predominantly nocturnal foraging and migration behaviors during winter months (e.g., at water temperatures <10-12 °C) but show little diel preference at warmer temperatures (e.g., Fraser and Metcalfe 1997; Johnston et al. 2004; Ibbotson et al. 2006). Thus, we postulate that during winter (and shoulder) months, yearlings of the fall, late-fall, and spring runs are much less vulnerable to daytime capture at Sacramento than at Chipps Island as a result of diel differences in downstream movements (or channel positions) between locations. Conversely, we postulate that such diel differences are less evident among winter-run juveniles, which are uniquely adapted for early sub-yearling migration. To this end, we recommend additional trawl studies at Sacramento to evaluate potential seasonal differences in diel patterns of catch, as first suggested by Wilder and Ingram (2006).

#### CONCLUSIONS

We strongly support ongoing efforts to include tissue sampling and genetic run identification of juvenile Chinook Salmon at key monitoring locations in the Sacramento-San Joaquin River system, as advocated by others (del Rosario et al. 2013; Harvey et al. 2014; Johnson et al. 2017). At the Sacramento and Chipps Island trawl locations, the combination of accurate run identification and innovative methods for estimating trawl efficiency may allow run-specific juvenile abundances to be estimated (Johnson et al. 2017). Having reliable abundance estimates at these two key life stages—as juveniles enter the Delta (Sacramento) and exit the Delta (Chipps Island) could yield valuable insight into the efficacy and performance of the many tributary and Delta recovery actions specified for the imperiled winter and spring runs (NMFS 2014; Johnson et

al. 2017; Peterson and Duarte 2020). Since the time of our genetic analyses via microsatellites, there have been advances in genetic assignment methods for Central Valley Chinook Salmon using single nucleotide polymorphisms (SNPs; Clemento et al. 2014; Meek et al. 2016; Meek et al. 2020), which are becoming the marker of choice given their density throughout the genome, ease of detection, and high-throughput capabilities (Meek et al. 2016). In particular, the SNP panel used by Meek et al. (2020) provided highly accurate identification of true winter run, fall run, late-fall run, and the distinct spring-run populations of Butte Creek, Mill/Deer creeks, and the Feather River. These advancements bode well for a potential broad-scale implementation of genetic run identification for juvenile Chinook Salmon at monitoring locations in the lower Sacramento River and the Delta.

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## **NOTES**

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