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RESEARCH

Genetic Assessment of Floodplain Habitat Use by Juvenile Chinook Salmon

Sara Hugentobler[1], J. Louise Conrad[2], Alisha Goodbla[3], Ted Sommer[4], Mariah Meek[1]

ABSTRACT

Climate change is having widespread negative effects on freshwater environments, including an increasing frequency and severity of droughts. Drought conditions present unique challenges for the federally listed Central Valley Chinook Salmon (*Oncorhynchus tshawytscha*), which use the already limited floodplain in the Central Valley as rearing habitat. In this study, we examined how differing hydrologic conditions influence the run composition of juvenile Chinook Salmon in the floodplain (Yolo Bypass) vs. the mainstem of the Sacramento River. Juvenile Chinook Salmon from the Yolo Bypass and areas along the Sacramento River were identified to the genetically distinct runs (fall, late-fall, winter, and spring) from 2013 to 2019. We found overwhelmingly that length-at-date methods are misclassifying fish, particularly late-fall- and spring-run fish, and winter-run fish in the bypass. Using this genetic run-timing, we found that the abundances of endangered runs (spring and winter) are reduced during low flow periods in both the bypass and Sacramento River. Even during drought conditions, juvenile Chinook Salmon rearing in the Yolo Bypass attained significantly larger sizes than those in the Sacramento River. When comparing fish growth across time, during wet years fish in the bypass start smaller and get significantly larger over the course of the year, compared to drought years; while during both wet and dry years fish in the Sacramento River largely attain a smaller size than the Yolo Bypass fish. This suggests that floodplain habitat is critical to maintaining diversity in juvenile Chinook Salmon.

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Corresponding author: *hugentob@msu.edu*

1 Michigan State University College of Natural Science
Integrative Biology
East Lansing, Michigan 48823 USA

2 California Department of Water Resources
West Sacramento, CA 95691 USA

3 University of California Davis
Department of Animal Science
Davis, CA 95616 USA

4 Independent Consultant
Davis, CA 95616 USA

KEY WORDS

Chinook Salmon, genetics, monitoring, drought, floodplain, life history diversity, Yolo Bypass, Sacramento River

INTRODUCTION

Climate change presents a distinct threat to freshwater systems, because these systems often lack of connectivity between habitats, making it impossible for species to migrate to more favorable environments. The rise in temperature in freshwater basins is likely to lead to changes in habitat quality and quantity, and conditions are predicted to worsen (Woodward et al. 2010; Ficklin et al. 2014). Overall, changing water conditions (such as increase in temperature or habitat fragmentation) have already greatly reduced some freshwater population sizes, likely altering the overall amount of biodiversity and biocomplexity in these systems (Ficke et al. 2007; Brucet et al. 2012). Maintaining genetic and phenotypic diversity is necessary for population resiliency in the face of these fluctuations, and loss of biocomplexity further reduces any given population's ability to respond to climatic change and drought (Crozier et al. 2008).

The Central Valley of California is predicted to become one of the most water-scarce areas in the world as a result of climate change and increasing water use (Famiglietti et al. 2011). Recently, the Central Valley experienced one of the longest and most severe droughts in California history, spanning the years from 2012 to 2016 (Xiao et al. 2017). During this time, water in the largest watershed in California—the Sacramento River watershed—was at an all-time low, with the worst period of drought occurring in 2015. This led to vastly reduced connectivity between Sacramento River and its adjacent floodplain habitats, which extensive development and channelization have already negatively affected (James and Singer 2008). Reduced access to floodplain habitat is particularly troubling because seasonally flooded habitats in the Sacramento River are critically important, providing important spawning, rearing, and feeding opportunities for native freshwater species (Sommer et al. 2001a; van Dyke and Wasson 2005). For example, the Yolo Bypass (YBY)—one of the few remaining large-scale seasonal floodplain habitats in the upper San Francisco estuary—provides habitat for 45 different animal species and flood protection for the lower Sacramento Valley (Salcido 2012).

One species that utilizes the YBY is Chinook Salmon (*Oncorhynchus tshawytscha*), which includes two federally listed Evolutionarily Significant Units (ESUs) (Sommer et al. 2001a). Many juvenile Chinook within the Sacramento River basin use the YBY as feeding and rearing habitat as they make outward migrations to the Pacific Ocean. For fish migrating from the Sacramento Valley, the primary route is the mainstem of the Sacramento River (LSR), which is extremely channelized and has high water velocities (Sommer et al. 2001b). This mainstem habitat is often sub-optimal for Chinook Salmon rearing and is correlated with high mortality (Michel et al. 2015). In contrast, off-channel habitats often provide more favorable conditions in the form of increased food resources and shelter from predators (Jeffres et al. 2008; Limm and Marchetti 2009).

Within the YBY, more favorable habitat conditions are correlated with an increase in the overall abundance and size of juvenile Chinook (Katz et al. 2013; Hellmair et al. 2018). Furthermore, evidence suggests that the YBY facilitates increased biocomplexity in the form of variation in juvenile size at out-migration, which can significantly affect ocean survival (MacArthur 1955; Schindler et al. 2010; Woodson et al. 2013; Goertler et al. 2018a). Evidence from other off-channel habitats in the Central Valley suggest that areas like the YBY can provide a "shifting habitat mosaic," which leads to differing growth rates during differing hydrological conditions (Cordoleani et al. 2022). This diversity of habitats across space and time is important for maintaining biocomplexity, leading to an overall portfolio effect (Greene et al. 2009). This can lead to some life-history traits performing better under different conditions, providing population buffering and overall stability of the species (Sturrock et al. 2015).

In addition to the portfolio effect provided by variation in size, the Central Valley is the only location within the Chinook Salmon range that has four distinct Chinook Salmon spawning life histories (runs), named for the time they return from the ocean to freshwater rivers to spawn (Meek et al. 2014). It is widely accepted that this life-history diversity provides the important biocomplexity necessary to mitigate adverse effects of changing environmental conditions on any one population (Hilborn et al. 2003; Carlson and Satterthwaite 2011). However, the spring and winter-run are experiencing population declines in excess of 90%, and the US Fish and Wildlife Service (USFWS) currently lists them as threatened and endangered, respectively, under the US Endangered Species Act, with winter-run also being listed as endangered under the California Endangered Species Act (Bergman et al. 2012; NOAA Fisheries 2014). The loss of either or both the spring and winter-run would represent an extreme loss of the biocomplexity of the region. Intensifying drought conditions in the Central Valley have led to extremely low water, increasing temperatures, and reduced flow rates that may reduce its ability to provide adequate habitat for all runs.

Currently, we do not know to what extent the YBY supports juvenile Chinook of the different runs in terms of abundance or residence time. Many of the natural resource agencies that work in the Central Valley have used non-genetic methods to identify juveniles to run type, mainly using a Length at Date (LAD) model (Harvey 2011). These criteria were introduced in the 1970s and incorporate fork length and date of capture to determine a classification. Although this method is expedient for use in the field, there is evidence the classifications are highly inaccurate (Harvey et al. 2014).

The purpose of this study was to examine the differences (if any) in run biocomplexity between the two habitat types—YBY and LSR—by addressing the following questions:

- Do genetic methods and the LAD model show similar patterns of run composition across the YBY and adjacent LSR?
- Do genetically determined run and size distributions differ between the YBY and LSR?

Understanding these questions can help inform how best to provide habitat for out-migrating juvenile Chinook salmon to support population-scale biocomplexity, a known factor that contributes to species resilience in this region (Carlson and Satterthwaite 2011). On a more regional level, this study provides insights into the degree to which different run identification methods (LAD vs. genetic) are usable in different habitats (e.g., floodplain vs. channel).

METHODS

Study Site

The YBY is a managed floodplain that provides flood control for the city of Sacramento. The 24,000-ha region is one of the only remaining floodplain habitats within the Sacramento River basin. Habitat in the YBY includes grasslands, managed wildlife areas, agriculture, tidal wetlands and channels, and perennial ponds (Sommer et al. 2001a; Sommer et al. 2005). Water enters the bypass from a few sources, creating access points for juvenile Chinook Salmon (Figure 1). Downstream migrating Chinook Salmon can most easily enter the YBY when the Sacramento River overtops the Fremont Weir, located at the northern part of the YBY (Sommer et al. 2001a). When water overtops the weir, water fans out across the YBY, creating suitable Chinook rearing habitat (Katz et al. 2017; Takata et al. 2017). During dry periods when the Sacramento River does not spill over the Fremont Weir, there are still substantial tidal river flows in YBY from its base near Rio Vista, allowing young salmon to access the region (Goertler et al. 2018a). During these periods, additional flow inputs from smaller westside tributaries (e.g., Putah and Cache creeks) enter a perennial channel called the “toe drain.” Consequently, juvenile salmon can access the region in both flood and non-flood years, but connectivity between the YBY and Sacramento River is greatest in wet years (Sommer et al. 2005). In contrast, the adjacent Sacramento River channel is a deep and fast-flowing river system, with water reaching depths of >5 m and flows as high as ~311 m^3s^{-1}, with little vegetation (Sommer et al. 2001b). This channel is always available for juvenile Chinook Salmon, but provides almost no opportunities for rearing, feeding, and protection from predators (May and Brown 2002; Brown and Bauer 2010).

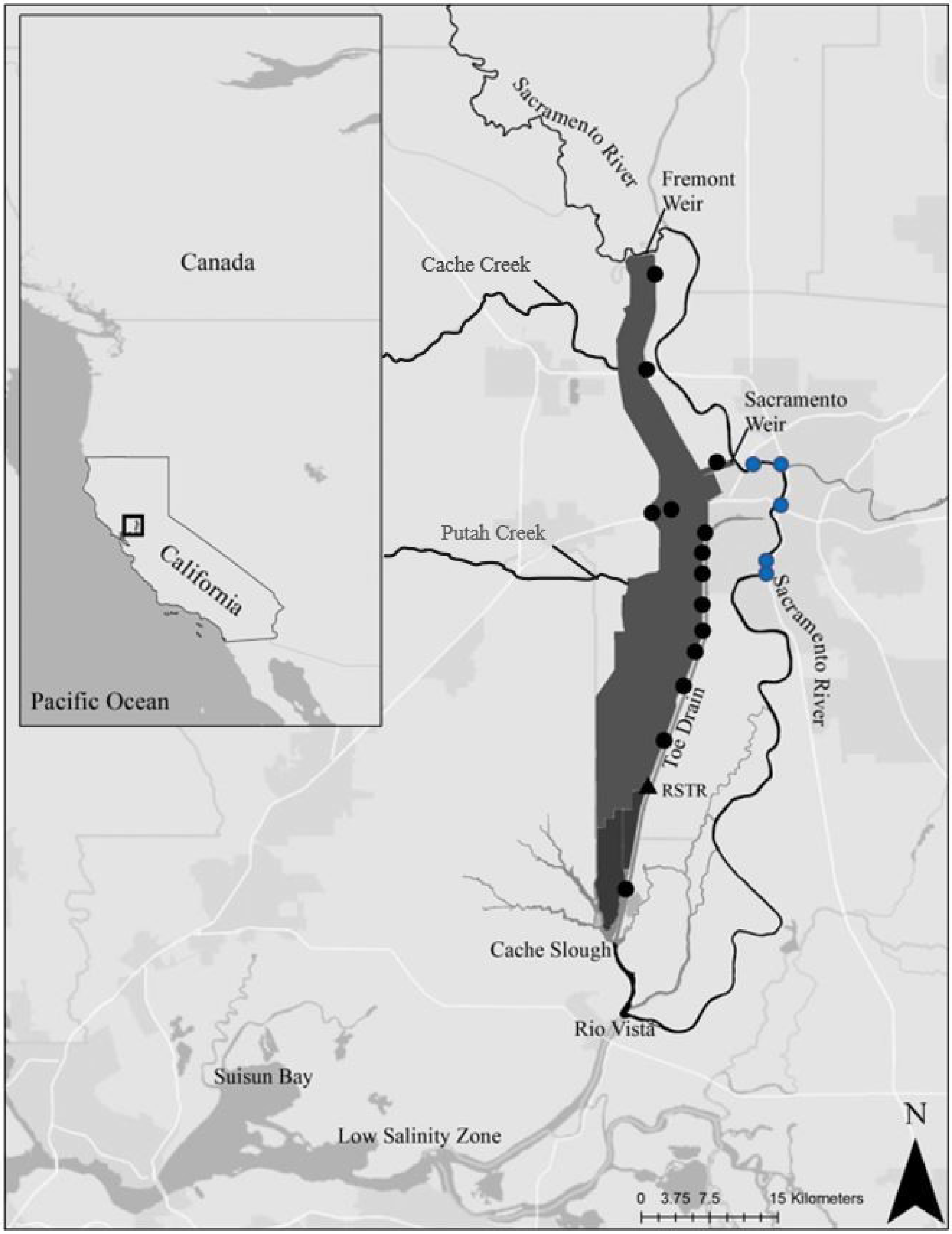

Figure 1 Map of the sampling region. *Black symbols* indicate juvenile Chinook Salmon sampling locations within the Yolo Bypass, collected by CDWR. *Blue symbols* indicate sampling locations collected by the USFWS. *Source:* Adapted from Goertler et al. 2018b.

Sampling

Morphometric data, DNA samples, and environmental water conditions were obtained from monitoring projects that operate within the Sacramento River from both the California Department of Water Resources (CDWR), which operates the Yolo Bypass Fish Monitoring Program (Pien and Kwan 2022), and the USFWS, which operates the Delta Juvenile Fish Monitoring Program (Mahardja et al. 2019).

In the YBY, sampling occurred during winter and spring by two main methods: a rotary- screw trap and beach seines, a program operated by CDWR that started in 1998. The rotary- screw trap sits at the base of the toe drain of the YBY and is approximately 2.6 meters in diameter. It was operated and fished 5 to 7 days a week, depending on water conditions. Beach seines measuring 7.62 by 1.22 m were towed parallel to the shoreline in 17 spots along the YBY, with ten spots along the toe drain, three perennial ponds, and four high flow sites. These sampling events occurred once every other week as water conditions allowed (Sommer et al. 2001b; Goertler et al. 2018a; Schreier et al. 2018).

The USFWS collected samples from the LSR using three different methods.

1. In the tidal Sacramento River at Sherwood Harbor, a Kodiak trawl operated from October to March and was towed between two boats (Brandes and Mclain 2001; del Rosario et al. 2013).

2. During April and September, a midwater trawl was used and towed with one boat. Sampling by both trawls was at the surface and usually consisted of ten tows per day, 3 days per week.

3. The third method used beach seines, conducted at two sites downriver from the Fremont Weir entrance to the YBY and adjacent to sampling seines in the bypass (Figure 1). Sample sites in the YBY and LSR were largely adjacent, and efforts were made to catch juveniles at the same point in their migration.

Table 1 Summary of fish sampled per location and year reported here form all sampling sites mentioned in Figure 1. YBY = Yolo Bypass and LSR = lower Sacramento River.

Sample numbers		
Year	**YBY n**	**LSR n**
2013	60	139
2014	211	165
2015	23	67
2016	199	289
2017	983	632
2018	42	249
2019	453	517

Juveniles in both regions were then measured for fork length (mm) and assigned to run by their respective agencies, across the years of 2013 to 2019 (Table 1). The primary method currently used by many management agencies to assign individuals to run in both systems is the LAD method (Fisher 1992). This model uses fork length and date of capture to assign individuals to run. The CDWR uses the "Delta" version of the model to classify samples caught in the YBY, and the USFWS uses the "River model" for identification in the mainstem Sacramento River samples. The primary difference between these models is based on different algorithms for length-at-date calculation (Fisher 1992; Harvey et al. 2014).

Because we were interested in the ecology of the wild populations in the Central Valley, we excluded all known hatchery fish by excluding fish that lacked an adipose fin. Throughout the Sacramento River system, hatcheries clip the adipose fin of Chinook Salmon juveniles of all runs to signify hatchery origin, clipping 100% of late-fall-, spring-, and winter-run hatchery-origin fish. Only 25% of fall-run fish raised in hatcheries have their adipose fin clipped, therefore it is possible that some fall-run hatchery-origin fish are included in our dataset. However, during the period of our study, there was an increasing trend of releasing hatchery fish downstream in the Delta, particularly in drought years, to increase survival (Sturrock et al. 2019). Because of the predominant practices of transporting hatchery fish to the Delta (a site downstream of our study area) to increase survival, it is unlikely there were many hatchery-origin fall-run fish included in our analyses (Table 2).

Genotyping and Run Assignment

We collected fin clips for genetic analyses from ten randomly sampled fish per LAD run classification per sampling site per day. Tissue samples were placed in 95% ethanol and transported back to the lab. We extracted DNA from fins using the DNeasy® Blood and Tissue extraction kit (Qiagen, Valencia, CA). Samples were then genotyped using a Fluidigm Single Nucleotide Polymorphism (SNP) assay of 80 run-type informative markers that followed the protocol of Meek et al. 2016. This assay was developed using adult Chinook populations of known run throughout the Central Valley. We then assigned samples to run using ONCOR and the baseline described in the previous study (Kalinowski et al. 2008; Meek et al. 2016). We assigned a genetic run to samples with 80% or greater probability of assignment to a particular run, while those below that threshold were assigned as “unknown.” Samples that were “unknown” by genetic methods were not included in the analysis.

Statistical Analyses

To assess the accuracy of LAD identification, we assigned all samples a value of 0 or 1, 1 indicating a match between LAD and genetic run assignment, and 0 indicating a mismatch between LAD and genetic run assignment. We then separated samples by run (fall, late-fall, spring, and winter) and assessed them for mean accuracy employing bootstrap methods that used the ‘*boot*’ function in the R program boot (Canty et al. 2022). In this code, means from a random sample of the assigned values were calculated 1,000 times.

To evaluate if there were differences in proportion of run among individual years in the YBY vs. the Sacramento mainstem, we ran a chi-squared test of independence in R using the *‘chisq.test’* function. We then used the R package “corrplot” to evaluate the residuals in each year and run to determine which values were contributing the most to the overall statistic. Each year is classified to a hydrologic classification based on the Sacramento Valley water year Hydrologic Classification Indices (Whitney 2007; CDWR c2024a). Within this system there are five different classifications: Critical (C), Dry (D), Below Normal (BN), Above Normal (AN), and Wet (W). This metric is determined by taking into account the levels of unimpaired runoff and the previous year’s index (Davis et al. 2000).

Next, we analyzed size differences in the YBY vs. the LSR fork length and date of fall-run fish by putting these data into a linear regression and using the ‘*glm*’ function in R. We separated the data by year and location (YBY vs. LSR), assuming a normal distribution. We then evaluated these models for statistical differences between years by using a two-sided t-test to compare the difference between the relative slopes. We compared each slope within 1 year individually and by each location. In both these analyses, we only used fall-run fish to reduce the chance that differences in size were the result of life-history characteristics present in other runs. Additionally, fall-run was the only population with large enough sample sizes to provide meaningful and statistically sound comparisons.

To further evaluate differences between size among juveniles in different hydrological regimes, we compared all mean fork lengths of fall-run fish by water year. We evaluated these means by two statistical methods. To compare between the YBY and the lower Sacramento River, we completed a t-test between each location in each water year. To compare all water years, we ran all samples within a specific location through an analysis of variance (ANOVA) test. To compare what years were contributing to the ANOVA statistic, we did further analysis by running a post-hoc Tukey test.

RESULTS

Concordance between LAD and genetic methods for inferring run type varied by run type and habitat. We found higher concordance between LAD and genetic run assignment in fall-run in both habitats and winter-run in the LSR (Figure 2).

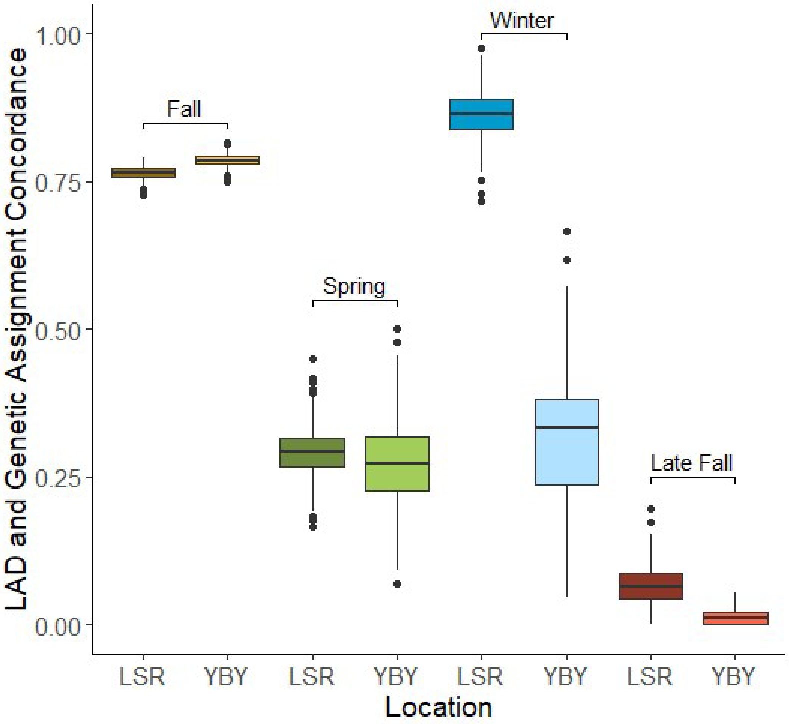

Figure 2 Results from a bootstrap analysis of length-at-date (LAD) classification mismatches, organized by genetic run classification and location. A value closer to 1.0 indicates higher concordance between genetic and LAD classification. LSR = lower Sacramento River and YBY = Yolo Bypass.

Table 2 Summary of fish sampled per location and run, and results from the bootstrap analysis depicted in Figure 2, comparing concordance between genetic and length-at-date (LAD) classification methods. A value closer to 1.0 in the bootstrap mean column indicates higher concordance between genetic and length-at-date (LAD) classification. YBY = Yolo Bypass and LSR = lower Sacramento River. Sample numbers of fish classified to run in each system (YBY vs. LSR) and each method of classification are also reported.

Sample numbers				
Run	**LAD n**	**Genetic n**	**Boot mean**	**95% CI**
Fall				
YBY	1827	1890	0.76	± 0.02
LSR	1573	1811	0.76	± 0.02
Late Fall				
YBY	0	96	0	
LSR	16	97	0	
Spring				
YBY	453	58	0.2	± 0.1
LSR	476	120	0.2	± 0.1
Winter				
YBY	36	29	0.31	± 0.2
LSR	178	81	0.85	± 0.04
Unknown	0	530	—	—

Concordance between assignment methods was very low for spring and late fall-runs in both habitats, and winter-run in the YBY. During all years of sampling, we classified no juvenile Chinook as late-fall by the LAD method in the YBY. In the Sacramento River, we classified a very small number as late-fall. However, our genetic assignments show in both systems, there was a non-negligible amount of genetically late- fall fish. To ascertain which misclassifications were contributing the most to the lack of concordance between genetic and LAD in these statistics, we compared both methods of classification across all years by plotting fork length vs. date of capture (Figure 3). Strikingly, we found that the majority of spring-run misclassifications were genetically fall-run individuals. Most of the genetic fall-run fish above a certain size are reflected in the LAD classifications in the spring graph, leading to spring-run juveniles being massively overestimated. Alternatively, many genetic late-fall-run fish were classified as fall, leading to those juveniles being largely underestimated.

We found a significant difference in run proportion between years in both the YBY and LSR sites (YBY: X-squared = 128.58, df = 18, p-value

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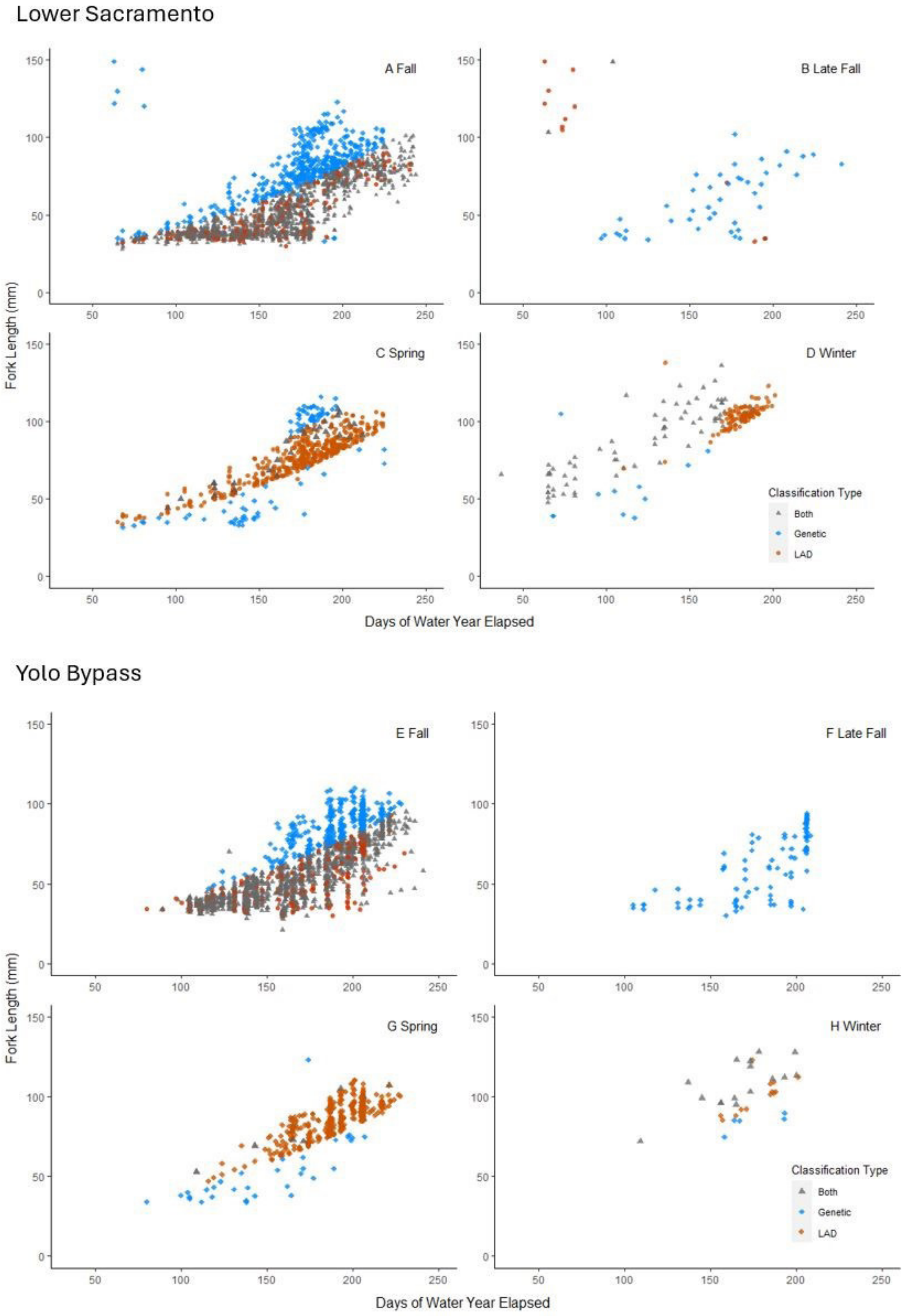

Figure 3 Comparison of the distribution of run-timing based on classification method across the years 2013–2019. In each plot, the *blue-* and *grey-colored dots* represent the genetic identification, while the *orange points* show the length-at-date (LAD) misidentified fish. In order, starting with the sites on the lower Sacramento River (LSR) we show the (**A**) fall run, (**B**) spring run, (**C**) late-fall and winter runs; followed by the (**E**) fall run, (**F**) spring run, (**G**) late-fall run, and (**H**) winter run in the Yolo Bypass. Many of the larger fall-run fish are erroneously classified as spring-run fish in both systems.

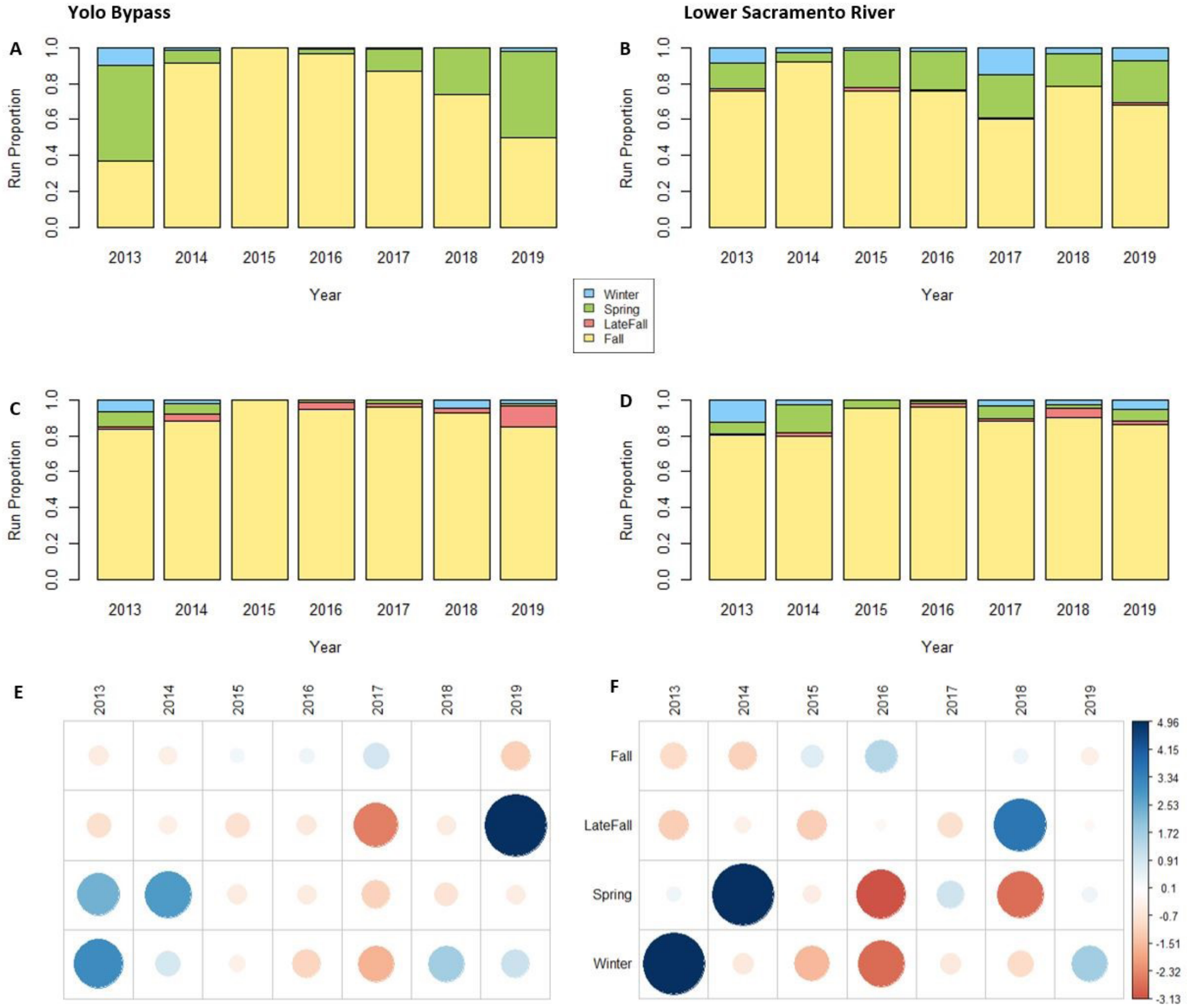

Figure 4 Length-at-date (LAD) and genetic run proportions within the Yolo Bypass and Sacramento River. Overall LAD proportion of each run within year in the (**A**) YBY and (**B**) the lower Sacramento River (LSR) mainstem. Overall genetic proportion of each run within year in the (**C**) YBY and (**D**) the LSR mainstem. Residuals from a chi-square test for independence in the (**E**) YBY and (**F**) lower Sacramento River (LSR) mainstem indicating how significant the difference in that particular cell is compared to all other cells. *Larger dots* indicate a higher contribution to the chi-square statistic, while *blue dots* indicate a positive contribution, and *red dots* indicate a negative contribution.

< 2.2e-16; Sacramento River: X-squared = 103.86, df = 18, p-value = 4.316e-14). When we calculated the residuals, it was clear that some proportions were contributing more to the chi-square statistic than others (Figure 4). In the years 2013 and 2014, our results showed more spring- and winter-run fish in the YBY than expected when compared to the proportion of other runs. In addition, our results also showed more spring- and winter-run fish in the YBY than expected compared to the proportions of winter and spring across years in 2013 and 2014. Both these relationships contributed positively to the chi square statistic. These results were similar to those in the LSR, where only the winter-run proportion was higher than expected in 2013, and spring was similarly higher in 2014. Particularly in the later years of the drought (2015–2016), there was a dearth of ESA-listed runs (spring and winter) when compared to fall-run. Interestingly, we saw an increase in late-fall-run proportions in the years 2018 in the Sacramento River and 2019 in the YBY (Figure 5).

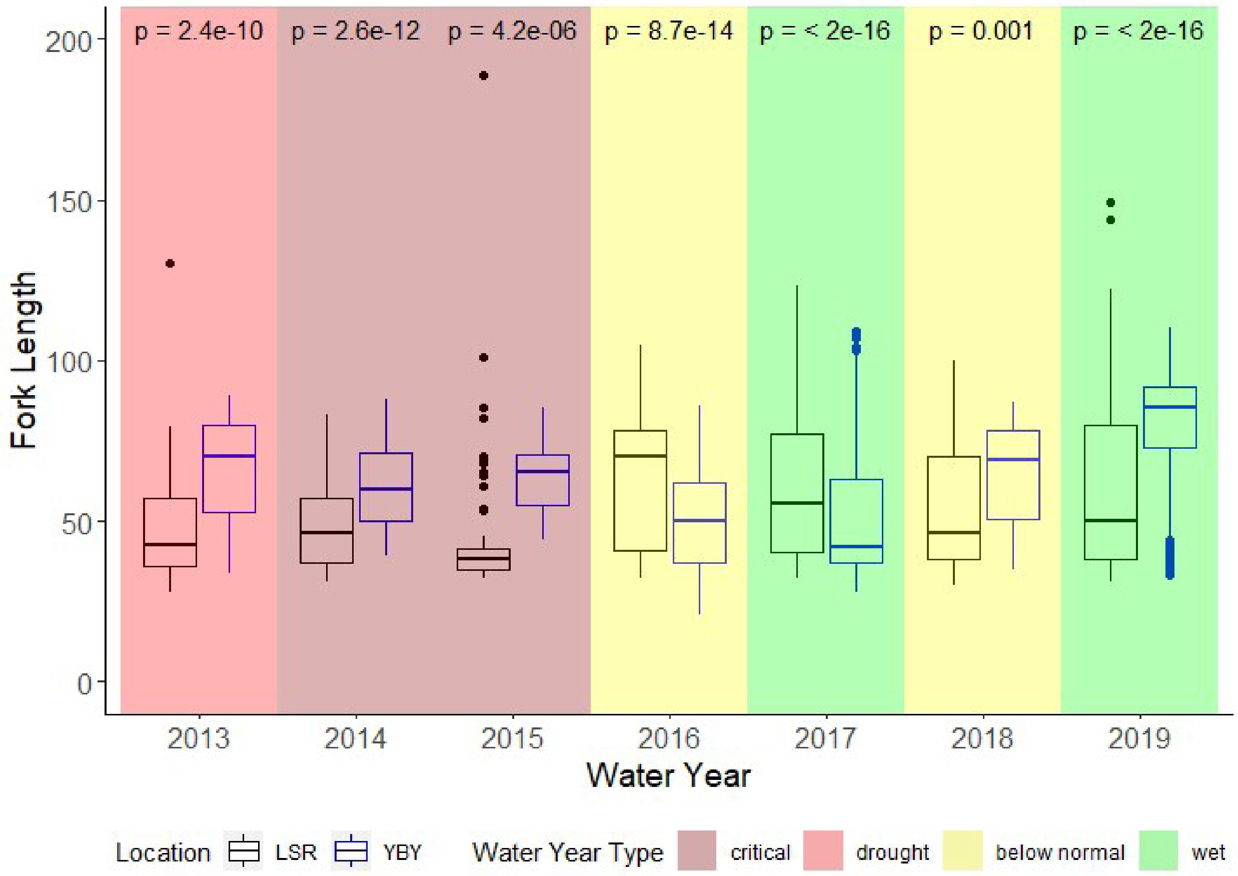

Figure 5 Mean fork length (mm) of genetically assigned fall-run juvenile Chinook Salmon in the lower Sacramento River (LSR) vs. the Yolo Bypass (YBY), organized by water year. Comparisons for all years were statistically significant, as indicated by the p-values.

We found different fork lengths in fall-run between habitat types across all years, with the YBY having significantly larger fall-run fish in every year except 2016 and 2017, where the means were significantly smaller (Table 3). We also found a significant difference among years within habitat type (Table 4). We found that in 2019, fish in both habitats had a larger mean fork length, compared with other years. In the LSR in years classified as Wet or Below Normal, we found fish attained greater size. This same pattern is not reflected in the YBY, where the smallest mean fork lengths were in 2016 and 2017.

To further explore how habitat affects the size distribution of juvenile fall-run Chinook in the YBY, we evaluated the fork lengths of fish over time in the YBY compared to the LSR. When we used the linear regression based on year and location, the slope of fall-run fish log normal fork lengths over time from the YBY were significantly different from that in the LSR in the years 2016 and 2019 with the YBY lengths being significantly smaller in 2016 and significantly larger in 2019 (Table 4, Appendix A). We found that the slopes of fork lengths over time were not significantly different between habitat types for 2013 through 2015 (the three Drought and Critical years), as well as 2017 (Appendix A).

DISCUSSION

Habitat diversity is essential for supporting diverse juvenile salmon populations, particularly as climate change creates large fluctuations in environmental conditions (Beechie et al. 2013; Herbold et al. 2018). The diversity of migration timings, natal homing strategies, and out-

Table 3 Results from the post-hoc Tukey test, comparing fork length of fall-run juveniles within each year in the (**A**) Yolo Bypass (YBY) and the (**B**) lower Sacramento River (LSR). Each Tukey group represents a significantly different mean fork length as it contributes to the overall significant difference in the analysis of variance (ANOVA). Groups with the same letter are similar to each other, while groups with different letters are significantly different from each other.

(A)

Fall-run – Yolo Bypass			
Water year	**Mean fork length**	**Tukey group**	**Water-year type**
2013	67.92857	b	Drought
2014	59.62445	c	Critical
2015	63.8333	bc	Critical
2016	51.78302	d	Below Normal
2017	51.33795	d	Wet
2018	62.82222	bc	Below Normal
2019	77.94915	a	Wet

(B)

Fall-run – lower Sacramento River			
Water year	**Mean fork length**	**Tukey group**	**Water-year type**
2013	49.19048	bc	Drought
2014	49.60440	bc	Critical
2015	46.02941	c	Critical
2016	63.64217	a	Below Normal
2017	65.16715	a	Wet
2018	54.96350	b	Below Normal
2019	62.6407	a	Wet

Table 4 Changes over time in the log normal fork length between habitat types as input in a linear regression. Here we show the results from comparison of slopes of both sampling regions as input in a glm model. The coefficient indicates the level of interaction between the location and sample date, where the Yolo Bypass (YBY) is the point of reference.

Fall-run			
Water year	**Coefficient**	**P value**	**Water-year type**
2013	0.0009	0.363	Drought
2014	0.0006	0.485	Critical
2015	0.0009	0.703	Critical
2016	0.0027	0.0045 [a]	Below Normal
2017	0.0003	0.247	Wet
2018	0.0021	0.439	Below Normal
2019	0.0045	5.30-11 [a]	Wet

a. Indicates a significantly larger slope between locations.

migration tactics provides population buffering under differing environmental conditions, such as differing water levels and temperatures (Hilborn et al. 2003; Greene et al. 2009; Schindler et al. 2010). It is therefore imperative to monitor and manage life-history diversity accurately—and how varying habitat conditions affect that diversity. Our study found that genetics methods would be most effective, and that floodplain habitat in the Central Valley is vital for supporting diverse Chinook Salmon populations. In particular, the diverse habitat provided by the YBY supports all runs, as well as a diversity in fish size.

LAD vs. Genetic Methods

Because monitoring life-history diversity requires accurate classification of this diversity, we first compared classification methods in the system. LAD methods are still being widely used as the main method of classification, so we sought to understand how those compared with genetic methods. We found a large mismatch between the length at date and genetic run assignments, indicating a lack of accuracy in the LAD model. Our work shows that length-at-date metrics overwhelmingly overestimate the occurrence of spring-run, and underestimate fall-, late-fall, and winter-run (Figure 3). This is an important issue because it means that the LAD approach does not present an accurate picture of how many threatened and endangered juvenile fish are in the system. For example, this has contributed to a knowledge gap around the abundance of threatened spring-run in the system (Nelson et al. 2022). For endangered winter-run, the export of water by state and federal pumping operations is directly tied to how many fish are in the system (NOAA Fisheries 2009; Harvey et al. 2014). These management decisions rely heavily on quantifying the exact number of winter-run juvenile fish in the system to mitigate negative effects. Therefore, accurate classification methods are vital to protecting the listed run and sustainable use of

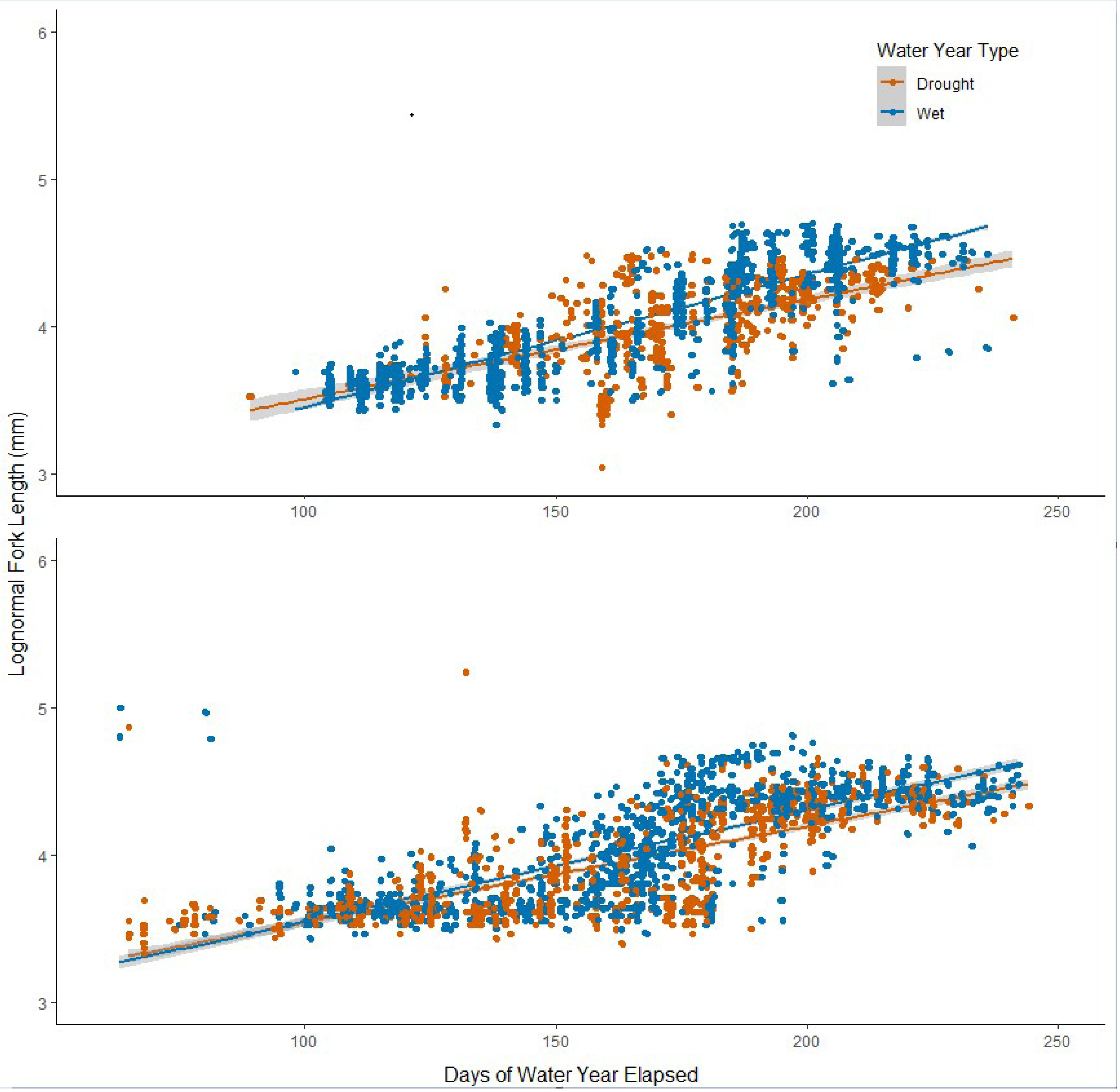

Figure 6 Changes in size of fall-run juvenile Chinook Salmon over time in all years classified as Wet (*blue*) and Drought (*orange*) with 95% confidence intervals (*gray*). Here we show the comparison between (**A**) Wet and Dry years in the Yolo Bypass (YBY) vs. (**B**) wet and dry years in the lower Sacramento River (LSR). In both locations, you can see there is a significant difference between wet and dry years, with the YBY experiencing a larger change in slope across time.

the water resource (Brown et al. 2009; Brown and Bauer 2010).

Chinook Salmon Life-History Diversity

Our data indicates that all four runs and a diversity of sizes are present in the YBY. This is likely because the YBY provides several benefits to juvenile Chinook, including increased food resources and protection from predators (Jeffres et al. 2008; Limm and Marchetti 2009). Unfortunately, during low-water periods, especially years under drought conditions, our work shows the proportion of spring-, late-fall, and winter-run decreased over time, suggesting that life-history diversity is compromised when the YBY is more difficult to access (Figure 4). Spring- and winter-run did not begin to increase proportionally until 2019, when flooding occurred. Proportions of runs other than fall were similarly negatively affected in the LSR. These data indicate that maintaining higher flows helps support life-history diversity in juvenile Chinook Salmon, and the availability of habitat further enhances the system's ability to promote diversity. This is consistent with studies showing that spring-run phenotypes lose habitat with increased drought periods and have decreased survival rates (Notch et al. 2020; Cordoleani et al. 2021, 2024).

Previous work has shown the importance of habitat diversity at all life stages for growth and fitness of many Pacific salmon species (Healey 1991). In the Sacramento River, there is evidence that wetland and managed floodplain habitats provide important opportunities for juvenile salmon growth, and different habitats have different food resources that affect growth (Jeffres et al. 2008; Cordoleani et al. 2022). Size and growth in the early life stages is imperative for success in the marine environment, and entering the ocean at a larger size can mean the difference between survival or death, so it is important to maintain habitats that provide opportunities for growth (Beamish and Mahnken 2001; Woodson et al. 2013). We found that there is a significant difference in juvenile fall-run Chinook fork length every year between the YBY and the Sacramento River, as well as across years in both systems during different hydrological conditions (Figure 5). In particular, fall-run juveniles were significantly bigger in the YBY almost every year. Although the variety of gear types and resumption of in-river hatchery releases in 2015 may have affected fish-size data, we do not believe this has greatly affected the results of this study. Despite different gear types, larger fish were still sampled in the YBY. In addition, fluctuating fork length patterns throughout 2016 through 2019 suggest that hatchery-released fish do not drive length patterns. Our research suggests that the YBY is an important habitat for juvenile Chinook that allows growth and refuge, even during drought conditions. Because floodplain conditions have shown to be important for growth—particularly periods of wet conditions or inundation—managing the YBY with an aim of promoting this life- history and run diversity will be imperative for the persistence of these populations.

Fish tended to be larger in the YBY than in the Sacramento River, although there are two notable exceptions. For example, fish were relatively smaller in two divergent water-year types, 2015 (Extremely Dry) and 2017 (Extremely Wet). This is likely because fish size is an imperfect metric of growth since the target habitats are open to immigration and emigration. This is because fish size in either the YBY or the LSR is a complex function of not only regional growth, but also the influx of new individuals from upstream areas, including, but not limited to in-river hatchery releases. Our analysis did not include data of entry into the sampled habitat to understand relative growth rate, and future studies would benefit from using tagged fish or otolith measurements to better characterize growth patterns. There is ample evidence from tagging methods that growth is consistently faster in the YBY than in the Sacramento River (Sommer et al. 2001b; Katz et al. 2017; Takata et al. 2017)

In addition, our research indicates that during wet conditions the YBY supports smaller fish earlier in the season while sustaining higher growth rates than does the LSR later in the season. This suggests that the YBY proffers benefits for size diversity during wet conditions (Table 4 and

Figure 6). The greatest difference slope of fork length over time between the two locations was during 2019, which had many weir-overtopping events (51 days) compared to years that had fewer (in comparison 2014 had 0 days and 2015 had 3 days) (CDWR). When all data points are combined from Wet and Dry years, there is still a significant pattern of increased growth in the YBY over time (Figure 6). This aligns with other research that has shown that increased rearing opportunities in the YBY lead to increased variation in size and growth rates in juvenile Chinook Salmon (Goertler et al. 2016, 2018a).

MANAGEMENT IMPLICATIONS

The Central Valley is predicted to be one of the areas in the world most affected by drought (Famiglietti 2014). As the climate warms and intensifies, this is predicted to cause longer, more intense, and more frequent droughts in the Central Valley, and more intense flood years (Gershunov et al. 2013; Trenberth et al. 2013; Swain et al. 2016). During more intense drought periods, young juvenile Chinook Salmon may have reduced access to off-channel habitat. Our work shows that diversity of habitats is essential to preserving a diversity of run-types and size distributions in juvenile Chinook Salmon. Consequently, reduced habitat variation could lead to a loss of diversity of juvenile Chinook Salmon, which could weaken the portfolio effect, as well as their long-term stability and resilience. For this reason, managing connectivity between the YBY and the Sacramento River represents a potentially valuable tool to sustain Chinook Salmon populations. For example, an infrastructure change to the Fremont Weir, which separates the YBY and the Sacramento River, is underway that will allow the YBY to be inundated at lower flows (USBR and CDWR 2019). Similarly, several large-scale tidal wetlands projects are being constructed in the lower YBY, which could improve access to the floodplain and habitat quality during dry years and seasons (CDWR 2021; CDWR c2024b).

Another important finding from our study is that the LAD method is relatively inaccurate at identifying the full range of salmon runs. For example, the LAD models overestimate spring-run fish because large fall-run fish in the system are being misclassified as spring-run. This issue is already relatively well-recognized (Harvey et al. 2014; Brandes et al. 2021; Nelson et al. 2022), so genetics is increasingly being added as a monitoring and management tool in the Sacramento watershed and downstream estuary. Hence, we strongly support expanded use of genetic methods to more accurately monitor and manage Chinook Salmon in the system. While genetic methods are increasingly being used to accurately identify the run type of juvenile Chinook salmon at water project operations in the South Delta (CDFW 2024), our analyses indicate that we will gain a broader understanding of how different runs are using available habitat if genetic identification methods could be incorporated into field studies across the Sacramento Valley as well.

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