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Ecology of
FRESHWATER FISH

Seasonal floodplain-tidal slough complex supports size variation for juvenile Chinook salmon (*Oncorhynchus tshawytscha*)

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Abstract

Population diversity is a mechanism for resilience and has been identified as a critical issue for fisheries management, but restoration ecologists lack evidence for specific habitat features or processes that promote phenotypic diversity. Since habitat complexity may affect population diversity, it is important to understand how population diversity is partitioned across landscapes and among populations. In this study, we examined life history diversity based on size distributions of juvenile Central Valley Chinook salmon (*Oncorhynchus tshawytscha*) within the Yolo Bypass, a remnant transitional habitat from floodplain to tidal sloughs in the upper San Francisco Estuary (SFE). We used a generalized least squares model with an autoregressive (AR1) correlation structure to describe the distribution of variation in fish size from 1998 to 2014, and tested the effect of two possible drivers of the observed variation: (i) environmental/seasonal drivers within the Yolo Bypass, and (ii) the juvenile Chinook source population within the Sacramento River and northern SFE. We found that the duration of floodplain inundation, water temperature variation, season, and sampling effort influenced the observed time-specific size distribution of juvenile Chinook salmon in the Yolo Bypass. Given the lack of seasonally inundated habitat and low thermal heterogeneity in the adjacent Sacramento River, these drivers of juvenile size diversification are primarily available to salmon utilizing the Yolo Bypass. Therefore, enhancement of river floodplain-tidal slough complexes and inundation regimes may support the resilience of imperiled Central Valley Chinook salmon.

KEYWORDS
California Central Valley Chinook salmon, habitat complexity, hydrologic disturbance, phenotypic diversity, resource management, seasonal floodplain inundation

1 | INTRODUCTION

Population diversity has emerged as an important mechanism for resilience in changing environments (Hilborn, Quinn, Schindler, & Rogers, 2003). For Pacific salmon (*Oncorhynchus* spp.), the link between increased spatial variation in habitat use and decreased interannual variation in production is apparent for both juvenile (Thorson, Scheuerell, Buhle, & Copeland, 2014) and adult (Schindler et al., 2010) life stages.

These studies suggest that some aspects of population diversity are dependent upon the maintenance of a range of habitats (Carlson & Satterthwaite, 2011; Jonsson, 1988; Moore, McClure, Rogers, & Schindler, 2010; Schindler et al., 2010). The application of this concept has become increasingly important as we become confronted with potentially irreversible and cascading effects of climate change and other stressors (Battin et al., 2007). Further, hydrology is one of the major disturbance regimes thought to shape habitat conditions

for salmon: connectivity, sediment supply, hydrologic regime, thermal regime, riparian vegetation, and nutrient regimes (Waples, Beechie, & Pess, 2009). Therefore, a central issue in salmon conservation is understanding how populations respond to altered hydrology, and the impacts of unnatural disturbance regimes, and reduced habitat complexity (Fausch, Torgersen, Baxter, & Li, 2002; Lytle & Poff, 2004).

The consequences of altered aquatic ecosystems on population diversity and resilience are largely unknown. However, it is likely that salmon populations in homogenized habitats have decreased portfolio performance and may have compromised productivity (Moore et al., 2010). Despite these concerns, reestablishing the natural hydrography is not feasible given the urban and agricultural demands for water, development along waterways and substantial lowland infrastructure vulnerable to flooding. In the pursuit of compromise between human resource use and fish and wildlife needs, habitat restoration in available spawning and rearing habitats below dams has been a suggested solution for increased diversity and resilience in urbanized riverscapes. For example, wetland restoration on the Salmon River, Oregon, expanded juvenile Chinook salmon (*Oncorhynchus tshawytscha*) life history variation by allowing greater expression of estuarine resident behaviors (Bottom, Jones, Cornwell, Gray, & Simenstad, 2005). Understanding what environmental processes and habitat features promote juvenile life history diversity is a key information gap needed to inform restoration and conservation activities.

In this study, we examined the potential effects of habitat on aspects of Chinook salmon life history diversity based on sampling from a floodplain-tidal slough complex located in the upper San Francisco Estuary (SFE), California. Like many west-coast estuaries, the SFE has been altered by urban and agricultural development. Approximately 95% of the estuary's wetlands have been diked, channelization is pervasive, and the biological community and water quality have been changed by exotic species introductions, sediment inputs from mining, and pollution from agricultural and urban chemicals (Kimmerer, 2004; Nichols, Cloern, Luoma, & Peterson, 1986). The hydrography has been altered by upstream dams, which reduce the magnitude of both winter precipitation pulses and spring snow melt pulses when filling reservoirs (Brown & Bauer, 2010; Kimmerer, 2004). In addition to reservoir storage, 35%-65% of tributary inflow is diverted by large water diversions (the State Water Project and the Central Velley Project), as well as thousands of smaller agricultural pumps and siphons (Kimmerer, 2004). The extreme changes in the historical landscape have also been associated with a major long-term decline in salmon resources (Gustafson et al., 2007; Nehlsen, Williams, & Lichatowich, 1991). California Central Valley (CCV) Chinook salmon winter run and spring run are of particular concern as they are listed under the Endangered Species Act (ESA) as endangered and threatened, respectively (Good, Waples, & Adams, 2005). In addition to reduced numbers of returning adult salmon, juvenile survival through the river and estuary is frequently poor (Michel et al., 2015). Therefore, habitat restoration has become a major focus for salmon management in California.

Nevertheless, the SFE retains a substantial area of seasonal off-channel habitat in the Yolo Bypass, the primary floodplain of the Sacramento River. This floodplain wetland system has been shown to be a very productive rearing area for juvenile Chinook salmon during flooding (Henery, Sommer, & Goldman, 2010; Sommer, Harrell, & Nobriga, 2005; Sommer, Nobriga, Harrell, Batham, & Kimmerer, 2001; Sommer, Harrell et al., 2001). Similar benefits of off-channel habitat to juvenile Chinook salmon have been described for other California floodplains (Jeffres, Opperman, & Moyle, 2008), as well as other fishes (Feyrer, Sommer, & Harrell, 2006; Sommer, Baxter, & Feyrer, 2007; Sommer, Baxter, & Herbold, 1997). The benefits of the Yolo Bypass to salmon and other species are reasonably intuitive as it is one of the last remnants of the historically dominant transition from river floodplain to tidal slough. This region was historically a flood basin, with an estimated 360,000 acres of tidal and nontidal freshwater marshes, riparian forests, willow thickets, and seasonally inundated meadows (Whipple, Grossinger, Rankin, Stanford, & Askevold, 2012). Although the floodplain has been substantially altered by flood control activities and agriculture, the Yolo Bypass retains many historical features including tidal sloughs, seasonal floodplain, grasslands, and perennial ponds (SFEI 2014; Sommer et al., 2005). Like many freshwater tidal wetlands, the Yolo Bypass is hydraulically dynamic and is strongly influenced by tides during low discharge periods and dominated by fluvial river dynamics during flood events. This river floodplain-tidal slough complex is, therefore, much more hydrodynamically variable than the adjacent mainstem Sacramento River channel, which is channelized by riprapped banks. Consequently, the Yolo Bypass may offer a juvenile salmon rearing location that responds to natural hydrologic variability and maintains habitat complexity between the river and estuary.

We hypothesize that aspects of juvenile salmon life history diversity may be enhanced by remnant complex habitats in the Yolo Bypass. For the purposes of our analysis, we examined variation in fish size (fork length) and the timing of fish occurrence (e.g., presence at a particular time and location) as metrics of life history diversity. Although there are multiple potential metrics of life history diversity including genetics (Gustafson et al., 2007; Waples, Teel, Myers, & Marshall, 2004; Waples et al., 2001) and patterns in the timing of ocean or estuarine entry (Beechie, Buhle, Ruckelshaus, Fullerton, & Holsinger, 2006; Dawley et al., 1986; Healey, 1982; Walsworth, Schindler, Griffiths, & Zimmerman, 2015), both fish size and occurrence are thought to be important indicators of variation (Miller, Gray, & Merz, 2010; Sturrock et al., 2015) and fish success (Duffy & Beauchamp, 2011; Woodson et al., 2013). Several studies support the link between size diversity and life history diversity, such as distinct size ranges for anadromous and resident individuals (Gross, 1987), or differential sizes associated with natal drainage basin (Roni & Quinn, 1995), migration, residency, and microhabitat use (Healey, 1991; Jonsson, 1988; McGrath, Scott, & Rieman, 2008). To address our hypothesis, and test what may be driving any effect, our objective was to quantify the variation in size and occurrence in the Yolo Bypass, and test the effects of physical conditions within the Yolo Bypass (discharge, water temperature, turbidity, season, and floodplain inundation), and biological factors (adult escapement, juvenile variation in adjacent and upstream habitats, hatchery releases, and food availability).

2 | MATERIALS AND METHODS

2.1 | Study system

In California's Central Valley, adult salmon spawn in the Sacramento and San Joaquin Rivers (and their tributaries). These two rivers join in a freshwater delta (the Delta) and exit toward the ocean through a series of large bays (Suisun, San Pablo and San Francisco Bay). CCV Chinook Salmon are commonly described by four runs, which signify the season in which adults return to the freshwater system from which they emerged, to spawn: winter, spring, fall, and late fall (Yoshiyama, Fisher, & Moyle, 1998). Historically, the range of salmon encompassed a drainage area roughly two-thirds the state of California (Whipple et al., 2012). Currently, impassable dams reduce available upstream habitat to approximately 5% of the historically available river mileage (Reynolds, Mills, Benthin, & Low, 1993). Declines in the California and Oregon salmon fisheries have given rise to artificial spawning and rearing of juveniles in hatcheries to improve growth and survival in the first year of life. Millions of hatchery-reared CCV Chinook are released

each year, and hatcheries have increased the size of juvenile Chinook at release since the 1980s (Huber & Carlson, 2015). The Central Valley is at the southern end of the Chinook species' range in western North America and can be characterized as a Mediterranean climate, with an average annual precipitation of 330-508 mm (Whipple et al., 2012).

The Yolo Bypass is a partially leveed floodplain basin that has been adapted to support flood management in the region. It comprises 24,000 ha of floodplain that is also managed for wildlife and agriculture (Figure 1). The Yolo Bypass was built as a water conveyance system to avoid flooding in the Sacramento metropolitan area, and therefore is meant to drain more quickly than a natural floodplain. Inundation is possible from several sources: (i) the primary input is the Fremont Weir in the north, which conveys flood water from the Sacramento River and Feather River, (ii) the Sacramento Weir in the east can also convey flood water from the Sacramento River and American River, and (iii) small westside streams, such as Knight's Landing Ridge Cut, Cache Creek, and Putah Creek flow into the Yolo Bypass (Sommer, Harrell, & Swift, 2008; Sommer et al., 2005). During dry periods, the aquatic
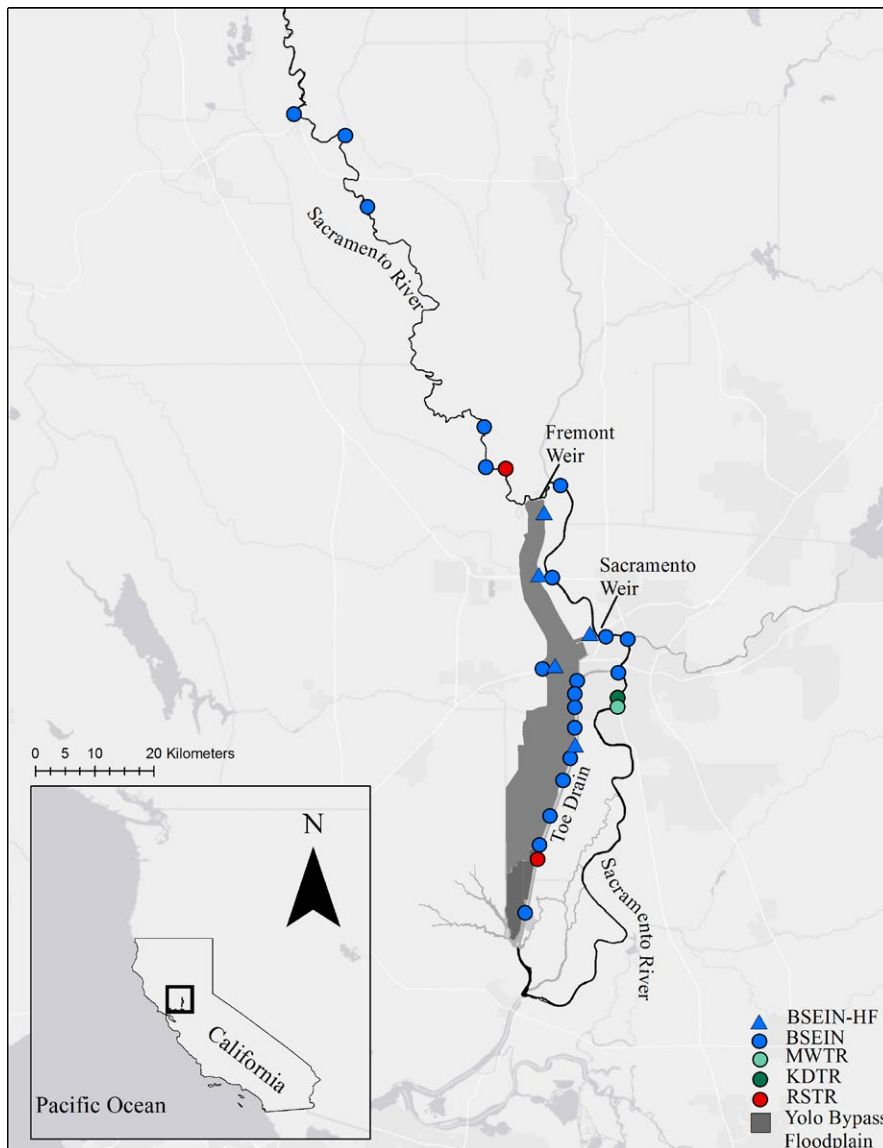
FIGURE 1 Map of the lower sacramento river and northern Delta. The Yolo Bypass floodplain extent is highlighted in dark gray. Each sampling site is identified by a point with the color and symbol denoting the gear used

habitat in the Yolo Bypass is reduced to a tidal perennial channel along its eastern edge ("Toe Drain" in Figure 1). There are also perennial ponds and seasonally managed wetlands on the floodplain (Feyrer, Sommer, Zeug, O'Leary, & Harrell, 2004). During high flow conditions, downstream migrating young salmon can enter the seasonally flooded Yolo Bypass habitat from the Fremont Weir on the Sacramento River (Figure 1). In both wet and dry conditions, juvenile Chinook salmon can also access the Yolo Bypass through the tidally influenced Cache Slough Complex into the base of the floodplain (Figure 1).

2.2 | Biological sample collection

Juvenile Chinook salmon data were obtained from aquatic monitoring programs in the northern Delta and Sacramento River: (i) the California Department of Water Resources' (DWR) Yolo Bypass Fish Monitoring Program (YBFMP, [Sommer, Harrell et al., 2001; Sommer, Harrell, Kurth et al., 2004; Sommer, Harrell, Solger, Tom, & Kimmerer, 2004]), (ii) USFWS Delta Juvenile Fish Monitoring Program (Dekar et al., 2013), and (iii) the Knight's Landing rotary screw trap (Vincik, Titus, & Snider, 2006) operated by CDFW.

2.3 | Prey resources

Invertebrates were sampled in the tidal perennial channel of the lower Yolo Bypass (at "RSTR" site in Figure 1) on an ebb tide with a conical plankton net and rectangular drift net, monthly with the exception of inundation and draining periods when it was typically sampled weekly (Sommer, Nobriga, et al., 2001; Sommer, Harrell, Solger, et al., 2004). The plankton net was made of 153 μm mesh net, with a 0.5-meter diameter mouth and two meters in length. The drift net was a 500 μm mesh net, measuring 0.46 meters by 0.3 meters at the mouth and 0.91 meters long, attached to a floated stainless steel frame. Plankton net samples had a 1 ml subsample extracted, identified, and counted under a compound microscope. All drift invertebrate samples were rinsed and passed through a 0.5 mm sieve. All the material remaining within the sieve was processed for identification. All aquatic insects and noninsects were counted and identified to the family level. Terrestrial insects and noninsects were counted and identified to the order level. The number per cubic meter (N/m^3) for each taxon was then calculated.

2.4 | Juvenile Chinook Salmon

In the Yolo Bypass, juvenile Chinook salmon were sampled by beach seine and a rotary screw trap from December through June (Sommer, Nobriga, et al., 2001, 2005; Sommer, Harrell, Kurth et al., 2004). Beach seine sites (BSEIN in Figure 1) were sampled monthly with a single haul from an 8.3 meter by 1.3 meter pole seine (1/3 sq. cm stretched mesh). For low flow periods, we sampled nine sites along the Toe Drain; four additional sites were added during high flow periods when there was seasonal floodplain inundation (BSEIN-HF in Figure 1). A 2.6 meter diameter rotary screw trap was operated near the base of the Toe Drain (RSTR in Figure 1). The rotary screw

trap was fished 5-7 days/week depending on hydrology (Sommer, Harrell, Kurth et al., 2004; Sommer et al., 2005). Captured fish were identified to species, counted and measured for fork length (mm) for up to 50 individuals of each species. Effort was calculated for the beach seine (volume, m^3) and rotary screw trap (hours fished). We documented a slight size bias to each gear type (Figure S1), and the slightly larger median fork length in the Yolo Bypass rotary screw trap is generally thought to account for the capture of out-migrating juveniles occupying the center of the channel, while beach seines include a variety of shallow-water habitats and rearing or migratory behaviors.

We also compiled Chinook salmon data from outside the Yolo Bypass to include both trends within the larger Chinook population and the influence of fish from particular runs, origins (e.g., hatchery or wild) and upstream or adjacent locations. Additional data were obtained from USFWS trawl and beach seine sampling in the adjacent tidal Sacramento River and upriver fluvial Sacramento River (Figure 1). Two types of trawling were conducted in the adjacent tidal Sacramento River: (i) a Kodiak trawl (KDTR) was operated between October and March and towed between two boats; (ii) a midwater trawl (MWTR) was towed with one boat between April and September (Dekar et al., 2013). Both trawls were towed at the surface with sampling generally conducted 3 days per week and ten tows per day. USFWS beach seine sampling was conducted at 58 sites across six geographic regions, with two regions used for this study; the lower Sacramento River (sites SR080E, SR071E, SR094E, SR130E, SR144W, SR090W, SR138E, and SR119E) and the north Delta (sites SR062E, SR057E, and SR055E) (Dekar et al., 2013). Sampling consisted of one seine haul per sampling day, usually conducted three times per week, but could be up to daily depending on management objectives and river conditions. In addition to beach seining, we also obtained data from the CDFW rotary screw trap at Knight's Landing on the Sacramento River (Figure 1). At Knight's Landing a variable number and size of rotary screw traps were used. In some cases, two 2.4 meter diameter and one 1.5 meter diameter rotary screw trap were used, and in other periods two 2.4-meter diameter rotary screw traps were used or a single trap of either size (Vincik et al., 2006). Sacramento River hatchery release data were assembled from several sources: Huber and Carlson (2015), Feather River Fish Hatchery (Anna Kastner, unpublished), Coleman National Fish Hatchery (Kevin Offill, unpublished), and Livingston Stone National Fish Hatchery (Kevin Offill, unpublished). Finally, adult escapement data were provided by the CDFW CCV Chinook Population Report (Azat, 2014).

2.5 | Physical data collection

Yolo Bypass flow was based on regional estimates (http://www.water.ca.gov/dayflow/output/). Inundation acres were modeled using TUFLOW software, which is a 1D/2D finite difference numerical model that incorporates GIS mapping and simulates hydrodynamic conditions in floodplains (Bahia, 2015; http://www.tuflow.com/). The duration of inundation was approximated as the number of days in which Yolo Bypass flow was greater than 113.27 m^3/s^1 following an

inundation event from the Sacramento River (e.g., when the stage height of the Sacramento River exceeded the height of the Fremont Weir, 10.2 meters), which occurred nine of the seventeen years observed for this study. Water temperature (°C) was measured at the Yolo Bypass rotary screw trap continuously, but discrete measurements during fish sampling were also used to fill in data gaps when the continuous monitor failed. Water clarity was based on discrete measurements of Secchi depth (cm) at sampling sites.

2.6 | Data analysis

To examine juvenile Chinook size variability in the floodplain/tidal slough complex, we calculated the biweekly coefficient of variation (CV) in fork length (mm) for juvenile Chinook salmon collected in the Yolo Bypass. CV is the standard deviation divided by the mean, a common diversity metric (Sternberg, Gutman, Perevolotsky, Ungar, & Kigel, 2000; Gallardo 2003), and has been used to examine salmon diversity among populations over time (Carlson & Satterthwaite, 2011; Satterthwaite & Carlson, 2015; Schindler et al., 2010). However, an essential caveat to our use of variation in size as a proxy for life history diversity is the unmeasured role of factors outside the Yolo Bypass in driving the baseline size variation in the juvenile salmon population, from which salmon within the Yolo Bypass are drawn at different times of year. Juvenile salmon which enter the Yolo Bypass are born primarily in the Sacramento River and its tributaries, therefore, variation in parental run timing (and subpopulations within fall and spring runs), emergence time, in-river growth, and size-dependent migration and survival may all have impacted the size distribution of juvenile salmon before entering the Yolo Bypass. In addition, within the Yolo Bypass prior to capture individual condition of the juvenile salmon (a reflection of cumulative in-river conditions) may impact growth and size-dependent migration and survival, which may influence how individuals interact with the conditions within the Yolo Bypass and the size distributions present at the time of sampling.

2.7 | Model structure

Statistical modeling was used to evaluate the potential effects of different factors on size variation observed within the Yolo Bypass. Data diagnostics of the juvenile Chinook salmon size variation data were assessed following the methods reported in Zuur, Ieno, and Elphick (2010). Our response variable was the coefficient of variation in juvenile Chinook salmon size captured in the Yolo Bypass, and the main effects were inundation days, discharge, water temperature, operation hr of the rotary screw trap, volume of beach seines, hatchery releases, season (measured as weeks since the previous December 31st), adult escapement and sample size; all of which was summarized over two-week intervals. Secchi depth, prey resources, and the coefficient of variation in juvenile Chinook salmon size captured at the entrance and exit of the Yolo Bypass were also examined as possible covariates, but not included as candidates for selection in the final models due to missing data and collinearity (details provided in Table S1, Data S1

and Figure S1). No outliers were detected, but the residuals showed temporal autocorrelation. The variance inflation factor was less than four for all covariates included in the model, and so collinearity was not accounted for. To account for temporal autocorrelation, we employed a generalized least squares model (GLS) with an autoregressive (AR1) correlation structure, applied using program R (R Development Team, 2011), following methods in Zuur, Ieno, Walker, Saveliev, and Smith (2009). An AR1 correlation structure accounts for temporal autoregressive correlation (e.g., accounting for the previous time step affecting the current observation). Main effects were included as explanatory variables in the GLS, and no interactions were included in the interest of tractability and ease of interpreting results, and in many cases there was no clear mechanistic basis to support a hypothesized interaction. However, we performed a separate analysis exploring the potential for an interaction between inundation and temperature (Data S3) with inundation treated as a categorical variable.

Our GLS models centered around two possible drivers of observed variation in size for juvenile salmon: environmental variables within the Yolo Bypass, and changes to the Sacramento River salmon population. Our covariates characterizing sampling methods (to account for how sampling affects how much diversity is observed) included the time interval in which the data were summarized (e.g., two-week interval), sample size (n) and sampling effort. Our within-Yolo Bypass covariates included environmental variables separately and together, and flow variables only (e.g., discharge and inundation). To describe the Sacramento River juvenile salmon population, we tested the relationship between the number of hatchery fish released in the Sacramento River and the CV in size in the Yolo Bypass. We also examined CV in size for fish caught above (Knight's Landing and USFWS beach seine region one) and adjacent to (USFWS Sacramento trawl and beach seine region seven) the Yolo Bypass; however, we excluded these variables from consideration in the final model (details provided in Data S2). We had hoped to include an estimate of the wild Sacramento juvenile Chinook salmon population size, but reliable abundance estimates do not currently exist at our time scale and for all runs of CCV Chinook salmon. Therefore, we used naturally spawned Sacramento River adult escapement estimates of the parental cohort for each run of CCV Chinook salmon, and the total number of hatchery fish released in the Sacramento River as our metrics for juvenile Chinook salmon population size in the final models. The total number of hatchery fish is a reasonable proxy for population size because it is estimated that naturally spawned juveniles contribute 10% ± 6% to the ocean fishery (Barnett-Johnson, Grimes, Royer, & Donohoe, 2007); however, hatchery releases are unlikely to accurately characterize the timing or size ranges of naturally spawned fish (Huber & Carlson, 2015). In all, twenty-two candidate GLS models were tested: the null model, full model, each covariate separately, four models with environmental factors only, four alternative models, and a population metrics only model (Table 1). The models were compared using Akaike Information Criterion with a correction for sample sizes (AICc) for relative model performance (Burnham & Anderson, 2002), using the package MuMIn (Barton, 2013). The model with the lowest AICc value was considered the best representation of the data. Akaike weight was also calculated

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TABLE 1 A summary of the AICc ranking and Akaike weights of each generalized least squares (GLS) model tested in this study

Model	AICc	ΔAICc	weight
Inundation days + CV in temperature + BSEIN volume + RSTR hours + season	−215.22	0	0.689
Inundation days + season + BSEIN volume + RSTR hours	−212.6	2.6	0.186
Inundation days + CV in temperature + BSEIN volume + RSTR hours	−211.5	3.7	0.107
Inundation days + BSEIN volume + RSTR hours	−207.5	7.7	0.015
Inundation days + CV in temperature + CV in discharge	−204.2	11	0.003
Inundation days + CV in discharge	−201.5	13.7	0.001
Inundation days + season	−200.57	14.7	0
Inundation days + CV in temperature	−200.2	15	0
Inundation days	−195.1	20.1	0
CV in temperature	−190.8	24.4	0
Full	−190.51	24.7	0
BSEIN volume + RSTR hours	−190.5	24.7	0
Season	−190.38	24.8	0
CV in discharge	−187.6	27.6	0
Winter-run escapement	−183.6	31.6	0
Null	−183.1	32.1	0
Spring-run escapement	−181.37	33.9	0
Fall-run escapement	−181.32	33.9	0
Hatchery release	−181.2	34	0
n	−181	34.2	0
Late-fall run escapement	−180.96	34.3	0
Hatchery release + all escapement	−175.16	40.1	0

The models are ranked by most representative to least representative of the coefficient of variation in juvenile Chinook salmon size captured in the Yolo Bypass. The main effects were number of inundation days, coefficient of variation in discharge (CV in discharge), coefficient of variation in water temperature (CV in temperature), operation hr of the rotary screw trap (RSTR hr), volume of beach seines (BSEIN volume), in-river hatchery releases, season (measured as weeks since the previous December 31st), adult escapement by run (winter, spring, fall and late-fall), and sample size (n); all of which was summarized over two-week intervals.

AICc, Akaike Information Criterion with a correction.

to give the overall weight of evidence for each model; this weight was used to quantify the degree of support or explanatory variable importance (Burnham & Anderson, 2002).

3 | RESULTS

Coefficient of variation in the size of fish collected in the Yolo Bypass ranged between 0.1 and 0.6, and varied over time (Figure 2). Results from the GLS modeling demonstrated that inundation duration, variation in water temperature, season and sampling effort were major drivers of observed size variation within the Yolo Bypass (Tables 1 and 2).

3.1 | Drivers of observed size variation

The CV in fork length of juvenile Chinook salmon caught in the Yolo Bypass was best explained by both environmental conditions in the Yolo Bypass and sampling effort. The GLS with the lowest AICc score included total inundation days, CV in water temperature, season, rotary screw trap operation hr, and beach seine volume (Table 1). The AICc values indicated that the second and third models were also moderately supported, but not the best characterization of the data (e.g. ΔAICc>2). The support for the top three models can be further differentiated by the AIC weights, which are conditional probabilities for model comparison (Burnham & Anderson, 2002). The weight of evidence in favor of the second (best model excluding temperature) and third model (best model excluding season) was a third or less than the support for the best model (Table 1). Finally, a coefficient of determination cannot be computed for GLS models, but when comparing the correlation between the data and values predicted by the best model our "goodness of fit" was 0.23.

Interestingly, models two and three were alternate versions of the best model with or without variation in temperature or season, indicating that these two variables may have a partially shared influence on variation in juvenile Chinook salmon size. The regression coefficients
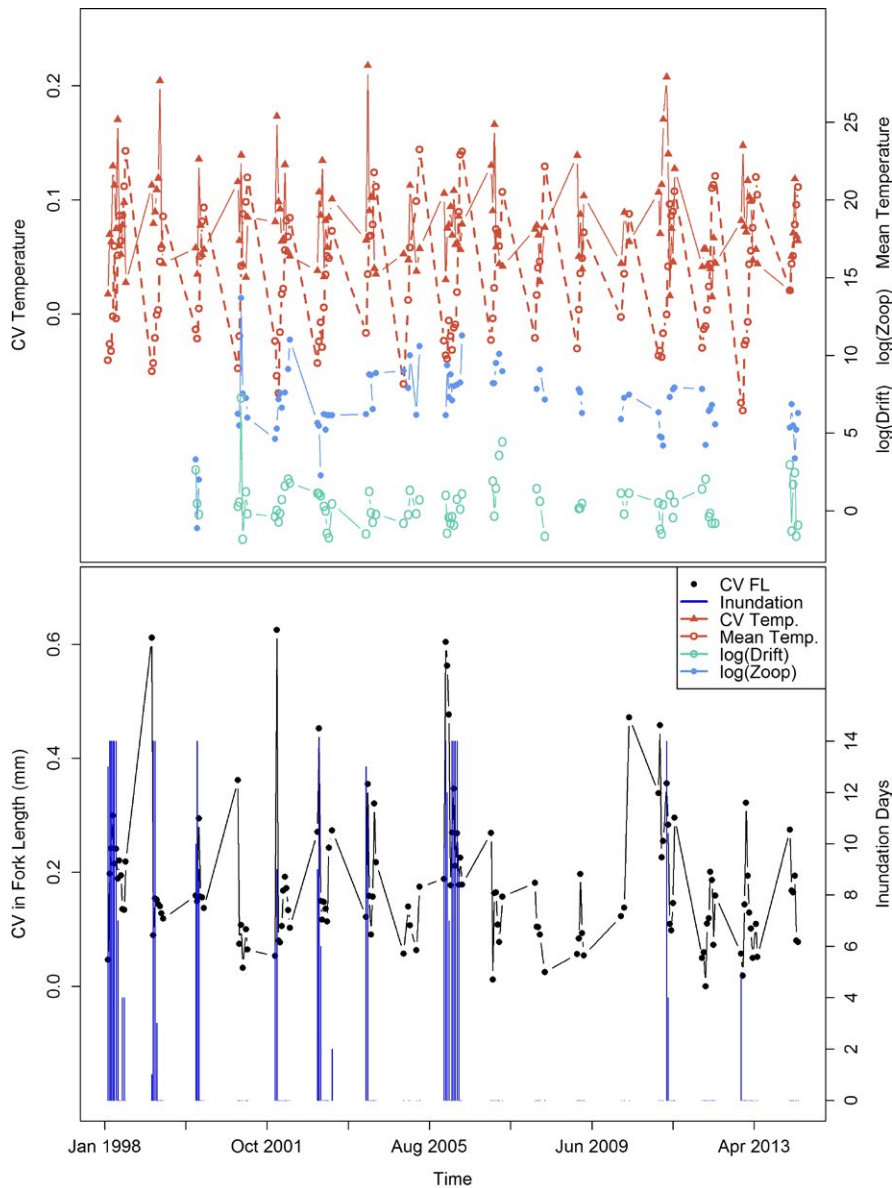
FIGURE 2 CV in fork length, total inundation days, temperature, and prey resources summarized over the time steps used in the GLS. From top, CV in temperature as well as mean temperature, the log of zooplankton catch (N/m^3), and the log of drift invertebrate catch (N/m^3). The bottom graph shows total inundation days and the dependent variable from our GLS models, CV in fork length for juvenile Chinook salmon captured in the Yolo Bypass

TABLE 2 The values and significance of the regression coefficients of the best model

	Value	Std. Error	*t*-value	*p*-value
Intercept	0.133	0.031	4.345	.000*
Inundation days	0.010	0.002	4.044	.000*
CV in temperature	0.482	0.221	2.178	.031*
RSTR hours	0.000	0.000	3.393	.001*
BSEIN volume	−0.000	0.000	−1.876	.063
Season	−0.005	0.002	−2.553	.012*

in the best model show a negative and significant relationship between Season and CV in juvenile Chinook size (Table 2). In contrast, all other significant regression coefficients (the variation in temperature, inundation days, rotary screw trap operation hr, and the intercept) were positive in the best model (Table 2). The only nonsignificant regression

coefficient in the best model, beach seine volume, was not excluded from the final models because CV in fish size was calculated for both sampling methods, and therefore, both estimates of sampling effort were included (Data S3 for more detail).

Additionally, our only available juvenile salmon estimate of a population-level driver, in-river hatchery releases, was not included in the best ranked model and individually ranked nineteenth of twenty-two models (Table 1). Hatchery juveniles may be less likely to enter the Yolo Bypass, which is thought to be perceived by juvenile salmon as shallow-water rearing habitat, generally used by smaller fish (Bottom et al., 2012) than the size of most hatchery fish (Huber & Carlson, 2015). Unfortunately, we were unable to estimate the variation in size for naturally spawned juvenile Sacramento River salmon entering the Yolo Bypass, and therefore do not have an estimate of the size variation produced prior to Delta entry. Estimating an entry abundance or CV in size is complicated by unknown information about how fish enter the Yolo Bypass, size selectivity of the different gears (Data S1),

and the influence of gear efficiency (which is not routinely measured). There are possibly many unincorporated influences of the Sacramento River during parental spawning and early juvenile life that could be dictating what size variability is available to the Yolo Bypass. This is an essential caveat in many salmon studies, which makes specific habitat assessments difficult (e.g. salmon occur across the landscape, which can have cumulative contributions to size variation).

4 | DISCUSSION

The historic Delta commonly experienced shallow seasonal short-term flooding, which has been reduced in area, duration (SFEI 2014), and frequency (Williams, Andrews, Opperman, Bozkurt, & Moyle, 2009). What was once 117,000 ha of shallow seasonal short-term flooding now only exists in the Yolo Bypass and Cosumnes floodplain, totaling approximately 19,000 ha (Whipple et al., 2012). Despite this severe reduction, seasonal inundation is important for juvenile Chinook salmon inhabiting the Yolo Bypass. Recent work by Sturrock et al. (2015) showed that the expression and successful return of varying juvenile Chinook migratory phenotypes were correlated with hydrologic regime. Yet, much of the hydrologic regime in this region is controlled or extensively altered by human activity. Therefore, it is important for both water and fish and wildlife resource managers to understand specifically which hydrologic processes are linked to species resilience. We explored this knowledge gap by exploiting monitoring data within a remnant floodplain-tidal slough complex which still responds to hydrologic disturbance. Our findings are supported by related studies demonstrating that seasonal floodplain inundation in the Yolo Bypass diversifies and expands the available habitat for juvenile Chinook salmon (Sommer et al., 2005), promotes growth through increased productivity, and provides an alternate migratory route (Sommer, Nobriga, et al., 2001).

Here, we present evidence that a seasonal floodplain-tidal slough complex could support life history diversity for juvenile CCV Chinook salmon. The CV in juvenile Chinook salmon length over time within the Yolo Bypass was best explained by inundation duration, variation in water temperature, season, and sampling effort. No model with a single main effect was well supported, suggesting that CV in juvenile salmon length cannot be predicted by a single driver. Both floodplain inundation and thermal heterogeneity have been linked to habitat complexity (Arscott, Tockner, & Ward, 2001; Malard, Mangin, Uehlinger, & Ward, 2001; Tockner, Malard, & Ward, 2000), and habitat complexity is a major driver of salmon diversity in other systems (Bottom et al., 2005; Hilborn et al., 2003; Jones, Cornwell, Bottom, Campbell, & Stein, 2014). Further, the Yolo Bypass has more opportunities for flooding and more water temperature variability than the adjacent Sacramento River (Figure 3), and likely provides habitat complexity for juvenile salmon in the North Delta. Therefore, remnant floodplain-tidal slough complexes, like the Yolo Bypass, may be critical features that promote life history diversity, within the context of the surrounding open water channels that now dominate the Delta and lower rivers. Identifying habitat features linked to increased diversity
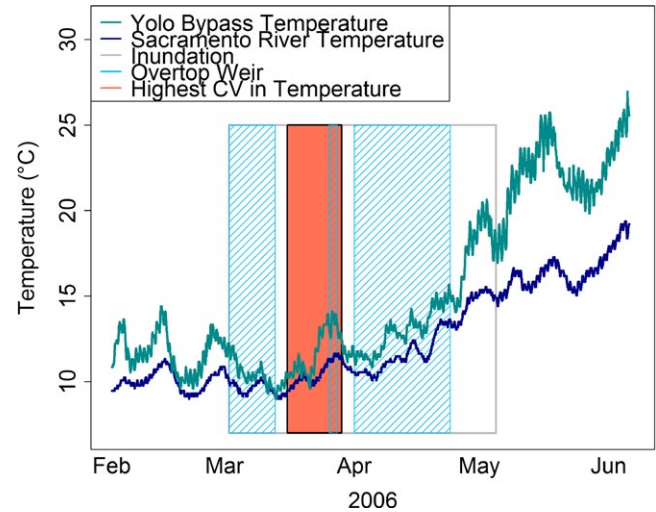
FIGURE 3 Hourly water temperature at Sherwood Harbor on the sacramento river and RSTR site in the Yolo Bypass during the 2006 inundation. Inundation days are shaded in gray, with periods of sacramento river overtopping the Fremont Weir shaded in blue and the highest CV in water temperature period for 2006 shaded in orange

has implications for developing fisheries management strategies to support species resilience. In addition to habitat complexity, inundation increases shallow-water tidal habitats, which may support estuary rearing fry migrants (Bottom et al., 2012) and could offer refuge from high river discharge.

4.1 | Drivers of observed size variation

4.1.1 | Inundation duration

Inundation in the Yolo Bypass creates a complex transition zone between the river floodplain and tidal slough habitat, which likely represents the historically dominant habitat in the North Delta (SFEI 2014). Therefore, inundation brings many advantages for juvenile Chinook salmon, such as increased growth opportunities on the floodplain (Sommer, Nobriga, et al., 2001), an alternative route into the Delta, and an expansion and diversification of rearing habitat. Interestingly, we found the number of inundation days to be the most representative explanatory variable when compared to modeled inundation acreage and discharge. This result suggests that temporal, rather than spatial, expansion of floodplain habitat may provide the greatest benefit to life history diversity of juvenile salmon, at least in the region we studied.

Inundation duration in particular may be important for both habitat opportunity and habitat capacity because of how juvenile salmon perceive their environment and what is necessary to initiate food web processes (Simenstad & Cordell, 2000). Studies suggest that floodplain inundation produces higher biotic diversity (Junk, Bayley, & Sparks, 1989), increased production (Gladden & Smock, 1990; Halyk & Balon, 1983), increased available habitat (Junk et al., 1989; Sommer, Harrell, et al., 2001), and inputs of terrestrial material into the aquatic

food web (Sommer, Nobriga, et al., 2001; Winemiller & Jepsen, 1998). When flooding occurs it creates a "moving littoral" in the "aquatic/terrestrial transition" resulting in high productivity (Junk et al., 1989). Although high discharge is necessary for inundation to occur, discharge can also be a measure of disturbance for juvenile salmon (Pearsons, Li, & Lamberti, 1992). The distinction between inundation and discharge in our models may relate to the flow pulse/flood pulse concept; short-duration pulsing can flush out organic matter and nutrients, whereas longer-term inundation would initialize floodplain production (Bayley, 1991).

In addition to the food web benefits of the floodplain, an inundated Yolo Bypass increases the connectivity between the upper Sacramento River and the tidal slough complex in the North Delta (Figure 1). The Yolo Bypass is simultaneously a river floodplain, a tidal freshwater slough, and a migratory channel. An individual salmon traveling through the flooded bypass and tidal sloughs to the Delta would likely encounter substantially more shallow-water habitat, tidal and nontidal marsh, wetted riparian habitat, and dendritic channels. The combination of seasonal and tidal inundation provides more natural complex and dynamic habitat which has been linked to life history diversity in other systems (Bottom et al., 2005; Jones et al., 2014). In this scenario, inundation likely represents a useful metric for habitat complexity. In addition to increasing habitat complexity within a flooded Yolo Bypass, inundation also provides an alternative route into the North Delta and in turn may also increase habitat diversity at a landscape scale. This increase in habitat access could further support connectivity, food supply, and nutrient cycling, which could aid in maintaining biodiversity and adaptation potential (Whipple et al., 2012). Thus, the maintenance of habitat connections is likely a critical component of Yolo Bypass inundation. Unnatural disruptions in connectivity can result in a mismatch of environmental cues and migration-timing adaptations, delaying migrants, and in some cases, conferring low survival (Caudill et al., 2007; Marschall, Mather, Parrish, Allison, & McMenemy, 2011; Schaller, Petrosky, & Tinus, 2014). By responding to natural hydrological disturbance (e.g., flooding), Yolo Bypass inundation offers juvenile salmon a dynamic connection to the north Delta during inundation.

4.1.2 | Variation in water temperature and season

Season and variation in water temperature were also identified as being predictors of increased juvenile Chinook salmon life history diversity. CV in temperature can be difficult to interpret ecologically, but our results indicate that high CV in temperature coincided with two notable characteristics: (i) spring months, and (ii) the end of an inundation period. The highest values of CV in temperature by year occurred in March and April for most years: April for 1998, 1999, 2014 and March for 2000, 2001, 2004, 2005, 2006, 2007, 2008, 2010, and 2011. For the other five years, the highest CV occurred in winter; January for 2002 and 2013, February for 2003 and 2009, and December for 2012. For 1998, 2002, 2003, 2004, 2006, 2012, and 2013 (including four of the five winter years), this high CV in temperature period also occurred directly following or in the

last weeks of an inundation period. Therefore, in all but one year, the highest yearly CV in temperature can be explained by these two patterns. Hydrological studies suggest that thermal heterogeneity is an indicator for hydrologic complexity, such as the comparison of a single channel to braided channels, or the complexity of surface and subsurface hydrological connectivity (Tockner et al., 2000). Further, floodplain development has been shown to correlate to thermal heterogeneity (Arscott et al., 2001), because of thermal stratification across the floodplain. This stratification is exacerbated when the floodplain is draining, because water temperatures diverge as water bodies become more hydrologically isolated (Arscott et al., 2001). We see this divergence in temperature during floodplain drainage when comparing water temperature in the Yolo Bypass and Sacramento River (Figure 3). Therefore, CV in temperature appears to be another metric for habitat complexity.

As two aspects of hydrologic complexity, CV in temperature and inundation duration may interact. It is plausible that longer inundation periods would provide more temperature variation or higher discharge flooding would encompass more diverged water bodies and increase temperature variation at drainage. However, there is no clear increase in CV in water temperature during the longest floods in our time series (e.g. 1998 and 2006, Figure 2). We investigated the interaction between inundation and variation in temperature by modeling alternative GLS models (Data S3). These alternative models showed an interaction term to be moderately supported by 2.26 ΔAICc (Data S3). This interaction between temperature variation and inundation presents further evidence that an inundated Yolo Bypass offers habitat complexity.

The Yolo Bypass floodplain may be most thermally and hydrologically complex during drainage, but this cannot be decoupled from the seasonal variation in temperature and seasonal variability in the timing of juvenile salmon outmigration. It is reasonably intuitive that spring periods, when days are getting longer and mean temperatures increasing, could be thermally variable. However, these spring periods also initiate changes in the food web, which interact with how juvenile Chinook salmon experience temperature (e.g., habitat capacity [Simenstad & Cordell, 2000]) (Figure 2). For example, thermal tolerances and optimal temperatures for growth shift with increasing body size and daily ration sizes (Beauchamp, 2009). When expanding the flood pulse concept (Junk et al., 1989) to temperate regions, Tockner et al. (2000) stressed the importance of the timing of floods with temperature because of its effect on decomposition rates and nutrient uptake. Therefore, both the association of high CV in temperature with spring and floodplain draining could influence productivity. However, our data do not demonstrate a clear seasonal pattern in zooplankton or drift invertebrate catch (Figure 2).

In addition to the possible seasonal relationship between variation in temperature and spring, our "Season" variable was influential on juvenile salmon life history diversity. All but one of the highest values for CV in the size of juvenile Chinook salmon was associated with January and February (although also some of the lowest), and the regression coefficient for "Season" was negative (e.g., later in a year size variation for juvenile salmon decreased, Table 2). Additionally, 75% of

these highest values for CV in size in January and February occurred during inundation, suggesting that when inundation occurred earlier in the year there was a higher potential for size variation. It may be that the earlier in the year the salmon accessing the Yolo Bypass consist of a relatively large proportion of winter-run juveniles. Of the six models with population-level drivers, only one model (winter-run escapement) was marginally better than the null model, and none of the models were highly ranked by AICc (Table 1). The importance of winter run may be further evidence for the "Season" affect's relationship with run variation. Winter run are thought to enter the Delta before the other runs, triggered by late-fall and early winter flow pulse events, and in a size range relatively distinct from the offspring of other runs (del Rosario et al., 2013). CCV winter-run Chinook salmon are endemic to the Sacramento River and a source of migration-timing asynchrony for the CCV Chinook population. CCV winter run are also endangered and therefore rare. As a seasonally inundated floodplain, the timing in which the Yolo Bypass floods is complex. CV in temperature may be capturing environmental variables related to productivity (spring warming and a flood pulse) and "Season" may be describing a period in late winter important to migration timing or run variation.

4.1.3 | Sampling effort

Sampling effort also influenced our observations of size variation in the Yolo Bypass (Tables 1 and 2). However, without explicit testing it is difficult to know how size selectivity and trap efficiency are affected by field conditions and how each method samples the true population. In our final GLS models, we combined catch in the beach seine and rotary screw trap when calculating CV in fish size over time, but there was a slight difference in size selectivity between the gears (Fig. S1). Sampling biases are difficult to generalize as both the rotary screw trap and beach seine sampling must be modified under different velocity and flooding levels because of debris, permitting, and safety issues. Further, the influence of flows and flooding is not straightforward because discharge, tidal inundation, and seasonal short-duration flooding impact the feasibility of any one site, particularly beach seines. Additionally, because sampling is meant to be repeatable both sampling methods are proportionally sampling less when available habitat increases with over-bank flows. Finally, it is possible that screw trap efficiency may be quite low during drought conditions because the rotary screw trap only samples efficiently during an ebb tide.
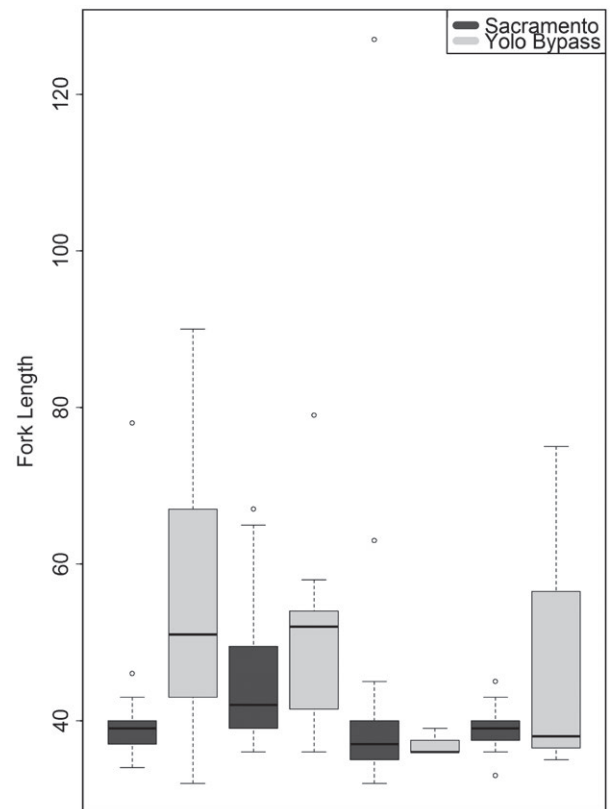
FIGURE 4 Boxplots of the fork lengths of juvenile Chinook salmon caught in beach seines by DWR and USFWS during select inundation events (which represent the best available data). Table includes dates of inundation, periods of weir overtopping, and periods of highest CV in water temperature for the Yolo Bypass. The table also includes the value of CV in water temperature for the Yolo Bypass and Sacramento river over the same period

		1998	2000	2002	2003
Inundation	Date Range	1/16-4/15	2/14-3/17	1/4-1/18	12/31-1/28
	# of Days	90	33	15	29
CV in Temperature	Date Range	4/9-4/22	3/9-3/22	1/10-1/23	2/6-2/19
	Yolo Bypass	0.1704	0.1356	0.1733	0.1345
	Sacramento R.	0.0960	-	0.1137	0.0806
Weir Overtop	Date Range 1st	1/16-3/10	2/14-3/17	1/4-1/10	12/31-1/5
	Date Range 2nd	3/24-4/11	-	-	1/16-1/19

4.2 | Implications for life history diversity

When considering the channelization of the lower Sacramento River, the Yolo Bypass is the primary location exhibiting the environmental characteristics which enhanced life history diversity in our model (e.g., seasonal inundation and thermal heterogeneity), although data were not available to test this directly. The tidal Sacramento River remains in its historical course, but it has been disconnected from branching dendritic channels and dead end sloughs. This channelization has likely reduced inundation potential, residency time of water, and limited habitat complexity (SFEI 2014). The lack of thermal heterogeneity within the Sacramento River compared to the Yolo Bypass, is substantial, particularly in the spring and during inundation periods (Figures 3 and 4). The water temperature of the two migration paths diverge dramatically during floodplain inundation, such as in 2006 (Figure 3), and the narrower water temperature range in the Sacramento River during Yolo Bypass inundation clearly illustrates its lack of inundation potential.

Diversity-stability studies suggest that spatial diversity, in our case an alternative rearing corridor for the mainstem Sacramento River, reduces the risks posed by stochastic events during outmigration. Additionally, diverse rearing habitats used by juvenile Chinook salmon should promote diverse life history strategies, which has been shown in the Salmon River estuary for both Chinook and Coho salmon (*Oncorhynchus kisutch*) (Bottom et al., 2005; Jones et al., 2014). These studies stress the importance of habitat connections between off-channel habitats and estuaries for allowing juvenile salmon the opportunity to express diverse phenotypes (Jones et al., 2014). In the Sacramento River, increased connectivity to the estuary occurs during floodplain inundation, and an asynchrony between the size of juvenile salmon using alternate migratory routes into the Delta can be seen when examining select inundation events (Figure 4).

For example, the median size of juvenile salmon during the 1998 and 2000 inundation events was very different for the two alternative routes (Figure 4). In this example, the median size of juvenile Chinook salmon caught in the Yolo Bypass was much larger than those fish caught in the adjacent Sacramento River. Floodplain inundation throughout the spring may have increased growth benefits, demonstrated by the timing of the highest CV in temperature occurring in spring and during floodplain drainage (Figure 4). Temperature variation was also always lower in the Sacramento River than the Yolo Bypass (Figure 4). However, our interpretation of Figure 4 must be considered within the context of a paucity of information on floodplain entrainment (e.g., without knowledge of the size of juvenile salmon in the source population). Additionally, the range of sizes of juvenile salmon was much broader in the Yolo Bypass during the 1998 and 2003 inundation events than in the adjacent Sacramento River (Figure 4); perhaps more populations accessed the Yolo Bypass due to the earlier inundation timing (e.g. run variation). Conversely, 2002, the shortest inundation event, did not indicate size variation among the two migratory routes (Figure 4). As in the results from GLS model selection, inundation combined with season and temperature to affect juvenile Chinook life history diversity. Finally, restoring floodplain connectivity and channel forming hydrologic regimes may not only enhance aspects of life history diversity but could be a future management strategy for maintaining juvenile CCV Chinook resilience in preparation for the expected flow and temperature changes under future climate change scenarios.

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