Environ Biol Fish
DOI 10.1007/s10641-017-0631-0

Rearing and migration of juvenile Chinook salmon (*Oncorhynchus tshawytscha*) in a large river floodplain

Lynn Takata · **Ted R. Sommer** · **J. Louise Conrad** ·
Brian M. Schreier

Received: 4 November 2016 / Accepted: 12 June 2017

Abstract Off-channel habitat has become increasingly recognized as key for migratory fishes such as juvenile Chinook salmon (*Oncorhynchus tshawytscha*). Hence, floodplain habitat has been identified as critical for the continued persistence of California's Central Valley salmon, particularly the Yolo Bypass, the primary floodplain of the Sacramento River. To provide insight into factors supporting juvenile salmon use of this 240 km^2, partially leveed floodplain, we examined inter- and intra-annual relationships between environmental correlates and residency time, apparent growth, emigration, migratory phenotype, and survival over more than a decade for natural-origin ("wild") fish and experimentally-released hatchery fish. Flood duration was positively associated with hatchery juveniles residing longer and achieving larger size. Wild juveniles grew larger and emigrated later with cumulative temperature experience (accumulated thermal units) and warmer average annual temperatures during flood years. Within years, both wild and hatchery salmon departed the floodplain as flood waters receded. Parr-sized juveniles dominated outmigrant composition, though fry and smolt-sized juveniles were also consistently observed. Survival to the ocean fishery was not significantly different between hatchery fish that reared in the Yolo Bypass versus those that reared in the main stem Sacramento River. Our study indicates improved frequency and duration of connectivity between the Sacramento River and the Yolo Bypass could increase off-channel rearing opportunities that expand the life history diversity portfolio for Central Valley Chinook salmon.

Keywords Juvenile Chinook · Restoration · Floodplain · Habitat use

Introduction

Central Valley Chinook salmon in California's Sacramento-San Joaquin Delta (Delta) have declined precipitously in recent decades (Yoshiyama et al. 2000), and their long-term persistence is uncertain (Katz et al. 2013). Two of the four Central Valley runs are listed under the federal Endangered Species Act. The Fall-run population, the most numerous of the four, has shown considerable instability, underscored by the sudden collapse and closure of the U.S. West Coast fishery in 2008 (Lindley et al. 2009). There are many causes of salmon decline, but the loss of wetland and floodplain rearing habitat is amongst the most important stressors (NMFS 2014). Frequent and widespread flooding was once an integral part of the Delta, but the construction of dams and levees along with other activities that "reclaimed" lowlands for agriculture and development eliminated 97% of historic wetlands (Whipple et al. 2012). This dramatic landscape transformation has decimated juvenile salmon rearing habitat, resulting in reduced life history diversity (Lindley et al. 2009; Waples

---

L. Takata (✉) · T. R. Sommer · J. Louise Conrad ·
B. M. Schreier
California Department of Water Resources, 3500 Industrial Blvd,
West Sacramento, CA 95691, USA
e-mail: Lynn.Takata@water.ca.gov

et al. 2009) and an eroded ability to buffer against variable conditions (Carlson and Satterthwaite 2011).

In an effort to support struggling Central Valley salmonid populations, substantial restoration projects are planned to create, reconnect, and augment floodplain habitats in the Delta. Growth benefits of off-channel floodplain rearing have been documented (Sommer et al. 2001a; Jeffres et al. 2008; Limm and Marchetti 2009) and some basic information is known about fish use of floodplain habitat (Sommer et al. 2005). However, more comprehensive information is needed to help guide restoration design, particularly with respect to how fish respond to the dynamic physical and hydrological conditions of the floodplain environment. Towards this goal, we examined over a decade of data on juvenile Chinook salmon survival, growth, residency, and emigration patterns in the Yolo Bypass – the largest remaining off-channel floodplain in California.

The Yolo Bypass is a 240 km^2 partially-leveed floodplain that inundates in years with high flow during the winter or spring (Fig. 1). Originally designed to protect the urban areas of Sacramento by directing floodwaters around the city, the Bypass occupies a portion of the historic Central Valley flood basin in the northern Delta (Whipple et al. 2012). When the Sacramento River reaches a stage of 9.2 m, it spills over Fremont Weir, a concrete sill located at the northern end of the floodplain. Localized flooding can also occur from four smaller tributaries to the west, Knights Landing Ridge Cut, Cache Creek, Willow Slough, and Putah Creek, creating flooded habitat in the absence of overtopping at Fremont Weir. Prolonged connectivity with the Sacramento River, however, can lead to complete inundation of the Yolo Bypass, doubling the wetted surface area of the entire Delta, and providing an expansive shallow water habitat for floodplain-adapted fishes (Sommer et al. 2001b, 2005). Overtopping at Fremont Weir also allows migrating juvenile salmon direct access from the Sacramento River into Yolo Bypass, where they are one of the most frequently captured native species in the floodplain (Sommer et al. 2004a; Feyrer et al. 2006). Fish can also enter the Yolo Bypass through a tidal slough complex at the base of the floodplain, though primarily during non-flood conditions.

In this study, we examined long-term patterns in juvenile Chinook salmon habitat use in the Yolo Bypass. Specifically, we focused on relationships between environmental and biological covariates and demographics of juvenile salmon habitat use in the floodplain. We addressed the following questions: 1) How do environmental factors (flow, water temperature, accumulated thermal units, or flood duration) affect inter-annual fish growth and use of the Yolo Bypass floodplain (e.g. residence time, growth, size, and timing at emigration)?, 2) Which environmental covariates influence the relative annual abundance of juvenile Chinook salmon utilizing the Yolo Bypass?, 3) What is the relative contribution of different migratory phenotypes (e.g. fry, parr, and smolts) from the floodplain?, 4) Do juvenile Chinook salmon rearing on the floodplain have enhanced survival compared to fish rearing in the adjacent Sacramento River?, and 5) What are environmental triggers of emigration from the Yolo Bypass?

Methods

Fish data

Juvenile Chinook salmon were captured each winter and spring using a 2.6 m diameter rotary screw trap (RSTR) located near the base of the Yolo Bypass floodplain from 1999 to 2011 (Fig. 1) (Sommer et al. 2005). The trap was typically operated 5–7 days per week January through June. The sampling location was strategically located near the downstream end of the Toe Drain, a perennial tidal channel which empties the Bypass along its eastern edge following flooding events. To compare survival between juvenile salmon rearing in the Yolo Bypass and the Sacramento River, we conducted paired releases of approximately 50,000 to 100,000 hatchery-origin fall-run Chinook salmon from the Feather River Fish Hatchery. Releases were conducted at the northern end of the Yolo Bypass in the Toe Drain and at an adjacent location in the mainstem Sacramento River (Fig. 1) (Sommer et al. 2001a, 2005). One or two release events were conducted in February each year during 1999–2009 (Table 1). During very large flood events, the Toe Drain release location was not accessible and Yolo Bypass releases were carried out at the Fremont Weir, approximately 10 km to the north (Fig. 1)(Table 1). All fish in the paired releases received an adipose fin clip and a coded-wire-tag (CWT) with a code specific to the release location. Hereafter, we refer to these release events as “CWT releases”.

We also examined within and among year patterns of habitat use by juvenile Chinook salmon from CWT releases as well as those of unmarked individuals

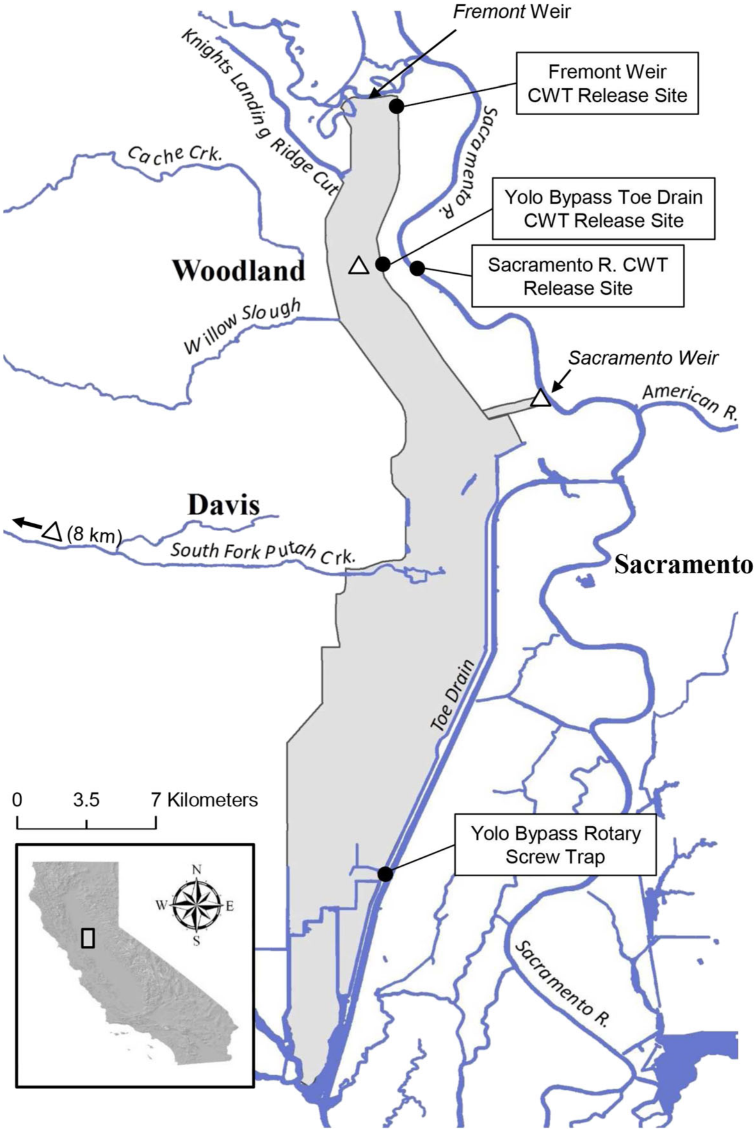


Fig. 1 Map of the Yolo Bypass floodplain, with coded wire tag (CWT) release sites and the rotary screw trap indicated (*circles*). Triangles denote inflow stations used to compute the Yolo Bypass component of DAYFLOW. Putah Creek inflow measurements were taken approximately 8 km to the west of the map extent

captured at the RSTR. Though not all hatchery-produced salmon in the California Central Valley are marked, most unmarked fish in our samples were of natural origin. During our study years, the vast majority of unmarked hatchery fish were released downstream of Fremont Weir or were released after overtopping had ceased (California Hatchery Scientific Review Group 2012; Huber and Carlson 2015). We therefore refer to fish with intact adipose fins as "wild" in this study, but acknowledge that a there is some chance a small portion may be unmarked fish of hatchery origin. We included only unmarked juvenile Chinook salmon in analyses involving "wild" fish. We also only included data from years when the Sacramento River flowed into the Yolo Bypass via Fremont Weir at some point from January through April, giving wild fish the opportunity to enter and rear within the Bypass. These years were 1999, 2000, 2002, 2003, 2004, 2006, 2010, and 2011. Analyses involving CWT fish growth and habitat use in the Yolo Bypass included years when releases were recovered in the RSTR (Table 1, Table 2). Data from 2006 was excluded because CWT recaptures were very low.

Environmental covariates

Environmental parameters were collected concurrently with fish sampling or were obtained for coincident time periods. Daily water temperature (°C) was collected

Table 1 Annual temporal and size information for juvenile salmon included in analyses

Year	CWT	Wild	Release Date (CWT) or First Overtopping Date (Wild)	Yolo Bypass					Sacramento River	
				# Released	Mean Release FL (mm)	Mean Capture FL (mm) (SD) at RSTR	# Captured at RSTR	50th Percentile Capture Date	# Released	Mean Release FL (mm)
1999	x		2/11[a]	103,471	61	85.0 (8.5)	41	4/7	103,882	52
		x	2/9	–	–	65.9 (16.4)	6494	4/7	–	–
2000	x		2/4	53,406	56	82.8 (7.6)	26	2/23	N.A.	N.A.
	x		2/22[a]	54,552	57	74.9 (2.8)	19	3/24	52,886	56
		x	2/14	–	–	68.1 (12.7)	1941	3/24	–	–
2001	x		2/15	47,291	59	58.6 (9.1)	32	2/23	46,523	59
	x		2/27	48,259	59	67.3 (8.9)	21	3/7	49,251	59
2002	x		2/5	49,666	59	69.0 (7.5)	21	3/2	50,946	54
	x		2/21	49,653	59	66.8 (6.8)	21	3/2	50,410	59
		x	1/4	–	–	63.2 (16.2)	164	3/2	–	–
2003	x		2/5	53,133	57	70.9 (12.3)	32	2/28	51,964	57
	x		2/20	51,386	60	66.4 (7.7)	73	2/26	51,388	60
		x	1/1	–	–	73.2 (12.7)	430	3/5	–	–
2004	x		2/11	50,225	47	81.3 (5.5)	3	3/19	50,738	47
	x		2/24[a]	50,213	54	73.3 (5.6)	7	3/19	47,934	54
		x	1/2	–	–	69.9 (15.5)	1561	3/22	–	–
2005	x		2/4	54,365	56	64.6 (7.5)	14	2/22	52,619	56
	x		2/17	51,106	52	60.3 (8.1)	34	2/22	54,324	55
2006		x	1/1	–	–	75.2 (15.6)	3814	5/9	–	–
2007	x		2/6	52,287	57	75.2 (18.5)	5	3/4	51,518	56
2008	x		2/7	54,844	51	76.7 (10.3)	21	3/5	52,855	55
	x		2/21	55,537	60	70.8 (8.0)	17	3/4	53,524	61
2009	x		2/10	51,805	64	73.5 (7.5)	20	2/20	51,560	64
2010		x	1/23	–	–	76.3 (12.4)	19	3/30	–	–
2011		x	1/1	–	–	70.1 (8.9)	192	4/28	–	–

Mean release size for coded wire tag (CWT) fish was provided by the hatchery without variance estimates. “RSTR” is the abbreviation for the rotary screw trap

[a] denotes Yolo Bypass releases conducted at Fremont Weir. The “N.A.” entry for the 2/4/2000 Sacramento River CWT release is due to a tagging error that prohibited identification in the ocean fishery. For wild fish, “date of first overtopping” is the first day of the calendar year when the Sacramento River overflowed Fremont Weir, allowing juvenile salmon access to the Yolo Bypass floodplain

during fish collections at the RSTR in the Toe Drain, and accumulated thermal units (ATUs, °C) were calculated as sum of daily mean temperature (Sykes et al. 2009). We obtained daily Yolo Bypass flows from the California Department of Water Resources DAYFLOW program (http://www.water.ca.gov/dayflow/), which computes daily outflow for the whole Sacramento San-Joaquin Delta (California Department of Water Resources 2014). The Yolo Bypass component of DAYFLOW is based on the combination of flows in the Yolo Bypass at Woodland, CA, the overspill at the Sacramento Weir, and inflow from the South Fork of Putah Creek (Fig. 1). Given the importance of the inundation duration to floodplain adapted fishes (Agostinho et al. 2004), we also calculated flood duration (days) and included it as a covariate in our analyses. We calculated duration of flooding as the number of days that mean Yolo Bypass flows met or exceeded 4000 cfs, as this corresponds to periods when water flows over the banks of the Toe Drain (Sommer et al. 2001b), producing flooded habitat available to fish.

Table 2 Analytical methods and independent variables used to examine inter-annual (among year) and intra-annual (biweekly) juvenile Chinook habitat use patterns. Strongly collinear variables were excluded

Response Variable	Fish	Covariates	Years	Analytical Method
Inter-annual				
Residence time (days: capture date – release date)	CWT	T, Fld	1999–2005, 2007–2009	Multiple Regression
Total growth (mm: capture FL – mean release FL)	CWT	T, Fld	1999–2005, 2007–2009	Multiple Regression
Growth rate (mm/day: total growth/residence time)	CWT	T, Fld	1999–2005, 2007–2009	Multiple Regression
Size at emigration (mm)	CWT	T, Fld	1999–2005, 2007–2009	Multiple Regression
	Wild	T, ATU, Fld	1999, 2000, 2002–2004, 2006, 2010, 2011	
Emigration timing (day of year)	CWT	T, Fld	1999–2005, 2007–2009	Multiple Regression
	Wild	T, ATU, Fld	1999, 2000, 2002–2004, 2006, 2010, 2011	
Relative abundance (CPUE)	Wild	T, ATU, Fld, Esc	1999, 2000, 2002–2004, 2006, 2010, 2011	Multiple Regression
Migratory phenotype	Wild	N.A.	1999, 2000, 2002–2004, 2006, 2010, 2011	Hierarchical Clustering, Similarity Profile Test
Survival (estimated ocean fishery catch/number released)	CWT	N.A.	1999–2005	Paired Sample t-Test
Intra-annual				
Emigration (CPUE)	Wild	ATU, Flo	1999, 2000, 2002–2004, 2006, 2010, 2011	Generalized Linear Model
Emigration timing (day of year)	Wild	Flo, Fld	1999, 2000, 2002–2004, 2006, 2010, 2011	Qualitative Graphical
	CWT	Flo, Fld	1999–2005, 2007–2009	

Abbreviations for independent variables were: water temperature (T), accumulated thermal units (ATU), flooding duration (Fld), flow (Flo), and spawner escapement (Esc). FL = Fork length

Analytical methods

How do environmental factors affect inter-annual fish growth and use of the Yolo Bypass floodplain?

Flow, water temperature, ATU, and duration of flooding for each year were averaged over rearing periods when the majority of juvenile Chinook salmon would have resided in the Yolo Bypass. For CWT juveniles, we constrained the environmental variables to the period between the date of fish release to the date when the 50th percentile of the total seasonal catch was captured at the RSTR (Table 1; del Rosario et al. 2013). For wild juveniles, we presumed floodplain rearing began on the date that the Sacramento River overflowed Fremont Weir, allowing migrating salmon access to the Yolo Bypass floodplain. Covariates for wild fish were thus constrained from the first overtopping event of the calendar year to the date when the 50th percentile of the total seasonal catch was captured at the RSTR (Table 1).

We used multiple linear regression analysis to examine relationships between environmental covariates and residence time, daily apparent growth rate (mm/d), apparent total growth over the entire period of residency (mm), size at emigration, and emigration timing against suites of independent environmental and biological variables hypothesized to influence those demographics (Table 2). Prior to inclusion into models, we calculated the Pearson's correlation coefficient (r) between all variables to identify multicollinearity. If multiple variables exhibited r values likely to distort model predictions ($r > |0.7|$, Dormann et al. 2013), the variable of highest biological relevance to the response variable in question was included and the other(s) excluded. Candidate variables were added to the regression model in a stepwise fashion until remaining variables did not improve model fit at $\alpha = 0.05$ or less. We log-transformed environmental covariates to address non-normality (Anderson-Darling test, $p < 0.05$) and variance heterogeneity.

We performed these multiple regressions separately for CWT fish and wild juveniles captured in the RSTR near the exit of the floodplain. Juvenile Chinook salmon captured with missing adipose fins, indicating the presence of a coded wire tag, were collected, measured, and euthanized. Tags were later removed and read to verify fish origin. Apparent growth and residence time analyses utilized data from CWT releases only, because values for mean initial fish length and date of release were known a priori. We included both CWT and wild juvenile Chinook salmon in emigration timing and size at emigration analyses (Table 2).

Which environmental covariates influence the relative abundance of juvenile Chinook salmon utilizing the Yolo Bypass?

We related inter-annual abundance of wild juvenile salmon captured at the RSTR to environmental covariates and the number of spawning adults for each year. We standardized the annual catch of wild fish by the number of hours the trap was fished, making catch per hour (CPUE) the response variable in analyses. In addition to using the same environmental covariates calculated in analyses of growth and habitat use metrics, we included escapement of the Sacramento River spawning cohort to evaluate whether the adult spawning population affected abundance of juveniles rearing in the floodplain. Escapement data was obtained from the GrandTab dataset managed by the California Department of Fish and Wildlife (Azat 2015). GrandTab is a long-term compilation of Chinook salmon escapement estimates from surveys conducted throughout the Sacramento-San Joaquin basin. Though different methods were used across time and space, GrandTab is the only continuous historical dataset available for California Chinook salmon escapement estimates (Albertson et al. 2013), and it is the primary source used by fishery management agencies (Carlson and Satterthwaite 2011). Only estimates of in-river spawning adults in the Sacramento River main stem and its main tributaries were included in our analysis, and hatchery returns were excluded. We used multiple linear regression to evaluate relationships between predictors and annual CPUE. Strongly collinear independent variables were identified and excluded as described for growth and habitat use analyses above (Tables 2 and 3).

What is the relative contribution of migratory phenotypes from the floodplain?

To evaluate the relative contribution of juvenile phenotypes migrating from the floodplain to the downstream Delta, we categorized unmarked juvenile Chinook salmon captured at the RSTR based on Miller et al. (2010) during the years when the Sacramento River flooded the Yolo Bypass. Juvenile phenotype (fry, parr, smolt) was assigned based on fork length: ≤55 mm, 55–75 mm, and >75 mm, respectively. We compared phenotype composition amongst years through multivariate hierarchical agglomerative clustering and group-average linking, using the Primer 6 program (Clarke and Gorley 2006). Because annual catch varied, we standardized data by total annual catch before performing a cluster analysis on Bray-Curtis similarities. We tested if some year-groups exhibited similar and distinct phenotypic composition using the Primer 6 Similarity Profile (SIMPROF) routine, which compares cluster results with a randomly generated null distribution (Clarke et al. 2008).

Table 3 Mean, range and standard deviation (SD) for independent variables included in quantitative inter-annual (yearly) and intra-annual (biweekly) analyses of coded wire tag (CWT) and wild juvenile Chinook salmon. Variables in intra-annual analyses were averaged over periods when the majority of Chinook salmon resided in the Yolo Bypass floodplain. Variables excluded due to strong collinearity are not depicted

Independent Variables	Coded Wire Tag Releases			Wild		
	$\bar{x}$	Range	SD	$\bar{x}$	Range	SD
Inter-annual Comparisons						
Flooding Duration (days)	7.4	0–40	13	38	15–100	25
Water Temperature (°C)	–	–	–	11.9	10.3–14.0	1.05
Accumulated Thermal Units	274.2	77.75–645.4	152.6	854.0	482.8–1572	410.0
Escapement	–	–	–	273,063	32,674–641,711	200,471
Intra-annual Comparisons (Wild Only)						
Accumulated Thermal Units	–	–	–	1131	11.89–2821	818.3
Flow (CFS)	–	–	–	5247	50.36–76,936	12,222

Do juvenile Chinook salmon rearing on the Yolo Bypass floodplain have enhanced survival compared to fish rearing in the adjacent Sacramento River?

We evaluated inter-annual survival through estimated recoveries of the paired Yolo Bypass and Sacramento River CWT releases in the ocean fishery where most fish are harvested at ages 2 and 3. Regional coordination and management of tagging and recovery data for United States west coast CWT releases is conducted by the Regional Mark Processing Center (RMPC), operated by the Pacific States Fishery Commission. Total estimated catch for CWT release groups is calculated from the total number of fish tagged and an expansion factor based on the proportion of catch sampled each year. These values are then summed for a given tag code across all port and time strata sampled, to yield total estimated catch (Nandor et al. 2010; Johnson 2004). To estimate survival, we calculated a recovery fraction as the estimated number of fish recovered in the ocean fishery, divided by the total number released for each system. Recovery fractions were compared using a paired T-test to determine if overall survival differed between the Yolo Bypass and Sacramento River releases. We assumed that ocean fishing effort was the same for fish from releases conducted on the same date (Newman and Brandes 2010).

What are environmental triggers of emigration from the Yolo Bypass floodplain?

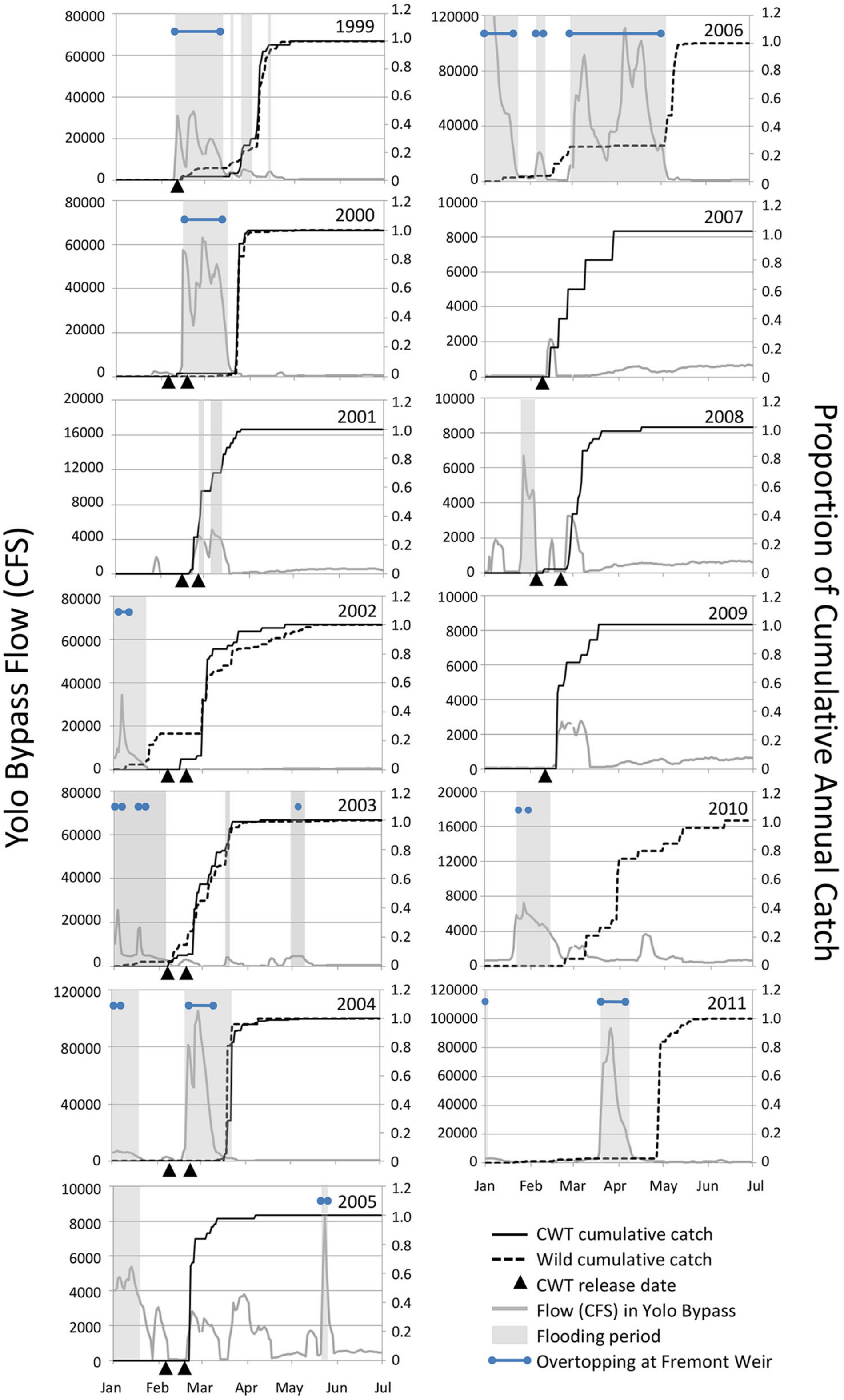
For the analysis of intra-annual juvenile Chinook salmon emigration patterns, we averaged independent variables over bimonthly (twice a month) periods to address temporal autocorrelation. Variables were Yolo Bypass flow (CFS), water temperature (°C), and ATU (°C). At the time scale of this analysis, rotary screw trap catches exhibited a high frequency of low and zero counts, so we evaluated relationships using generalized linear modeling specified with a Poisson error distribution (Maunder and Punt 2004) and the glmulti package in R (R Development Core Team 2008; Calcagno and de Mazancourt 2010). We specified effort as an offset term in the model because screw trap operations varied depending on safety conditions. Main effects models were compared using Akaike's Information Criteria adjusted for small sample datasets (AICc) and Akaike weights (w_i). We included only years when the Sacramento River overtopped Fremont Weir, as these were periods when wild juveniles would have access to inundated floodplain habitat. As explained for among-year analyses, we calculated Pearson's correlation coefficient (r) for all covariate pairs and retained only variables of higher biological relevance in instances of high correlation.

We also examined patterns of emigration with respect to flow in the Yolo Bypass through qualitative examination of cumulative catch curves at the RSTR. Both CWT and wild salmon were examined during years when wild juveniles could access the Bypass via overtopping at Fremont Weir. During years without overtopping, only CWT juveniles released in the Bypass were evaluated (Tables 2 and 3).

Results

Hydrographs of the 13 years we examined were highly variable and complex, spanning a range of overtopping dates, flood durations, and flow magnitudes (Fig. 2). The Sacramento River connected to the floodplain via overtopping at Fremont Weir during 9 years (69%), generally during the winter and early spring. Connectivity was longer than 10 consecutive days during six of these events, with the longest continuous overtopping event lasting 65 days in March–May of 2006. In one year, 2005, a brief four day event occurred very late in the season, when the majority of wild juvenile salmon transiting through the Sacramento River were likely downstream of Fremont Weir. There was no connectivity with the Sacramento River in four years, though flooding sourced exclusively from western tributaries to the Yolo Bypass occurred during two of these years. The rearing period of six of the 17 CWT releases coincided with the availability of flooded habitat (Fig. 2).

Several environmental variables exhibited collinearity at both inter- and intra-annual time scales. Among-years, flow was highly correlated with flood duration for both wild ($r = 0.82$) and CWT ($r = 0.75$) juveniles. Because of the importance of flood duration for floodplain adapted fishes (Agostinho et al. 2004), we retained the duration variable and excluded flow from both sets of analyses. For analyses involving only CWT fish, flood duration was also strongly correlated with ATU ($r = 0.80$), and the latter variable was excluded. For the analysis of within-year emigration of wild fish at the bimonthly time scale, water temperature was highly correlated with ATU ($r = 0.94$) (Table 2). Other studies


Yolo Bypass Flow (CFS)
Proportion of Cumulative Annual Catch
1999
2000
2001
2002
2003
2004
2005
2006
2007
2008
2009
2010
2011
0
20000
40000
60000
80000
100000
120000
2000
4000
6000
8000
10000
12000
16000
20000
0.2
0.4
0.6
0.8
1.0
1.2
Jan
Feb
Mar
Apr
May
Jun
Jul
CWT cumulative catch
Wild cumulative catch
CWT release date
Flow (CFS) in Yolo Bypass
Flooding period
Overtopping at Fremont Weir

◀ **Fig. 2** Flow, flooding periods, and Fremont Weir overtopping periods with cumulative catch curves of coded wire tag (CWT) and wild juvenile Chinook salmon collected at the rotary screw trap. Only years with overtopping at Fremont Weir include wild fish curves (*dotted lines*). Catches of CWT fish in 2006 were excluded due to low catch. Note that scales for y-axes vary

have found ATU to be a better predictor of downstream migration in juvenile salmonids, so we excluded temperature (Zydlewski et al. 2005; Sykes et al. 2009).

How do environmental factors affect inter-annual fish growth and use of the Yolo Bypass floodplain?

Flood duration was significantly related to several habitat use demographics for CWT fish in multiple regression models. Apparent total growth, emigration date, size at emigration, and residence time were positively correlated with the duration of flooding ($p < 0.01$ for all variables; $R^2 = 0.4$–0.8) (Fig. 3). The addition of other covariates did not significantly improve model fits. Apparent daily growth rate of CWT juveniles was not significantly related to any predictor variables. For wild fish, average temperature was a significant predictor of size at emigration ($p = 0.022$, $R^2 = 0.61$, Fig. 4a), but flood duration and ATU were not good predictors. Annual emigration timing for wild fish was positively related to ATU but not to other variables ($p = 0.018$, $R^2 = 0.64$, Fig. 4b).

Which environmental covariates influence the relative abundance of juvenile Chinook salmon utilizing the Yolo Bypass?

Annual catch of wild juvenile Chinook salmon at the RSTR ranged widely across Fremont Weir overtopping years, from 19 individuals in 2010 to nearly 6500 in 1999 (Table 1). CPUE of wild fish was significantly related to duration of flooding ($p = 0.020$, $R^2 = 0.62$, Fig. 4c), but not to any of the other independent variables.

What is the relative contribution of migratory phenotypes from the floodplain?

We consistently captured wild juvenile Chinook salmon of all developmental stages exiting the Yolo Bypass floodplain during Fremont Weir overtopping years. With the exception of 2006 and 2010, parr made up the largest proportion of outmigrants (46–70%), and fry compromised the smallest proportion in all years except 2002 (6–13%). In 2002, fry were captured slightly more frequently than smolts (29% vs. 21%). In 2006, parr and smolts were captured in similar proportions (46%), and in 2010 smolts were captured in slightly higher proportions than parr (50% and 44%, respectively)(Fig. 5). Cluster analysis identified 3 year-groups with similar outmigrant composition (90–95% similarity): 2003, 2006 and 2010; 2000, 2004 and 2011; 1999 and 2002. However, these groups were also similar to each other (77%), and the SIMPROF test did not detect significant differences between them ($p = 0.07$).

Do juvenile Chinook salmon rearing on the floodplain have enhanced survival compared to fish rearing in the adjacent Sacramento River?

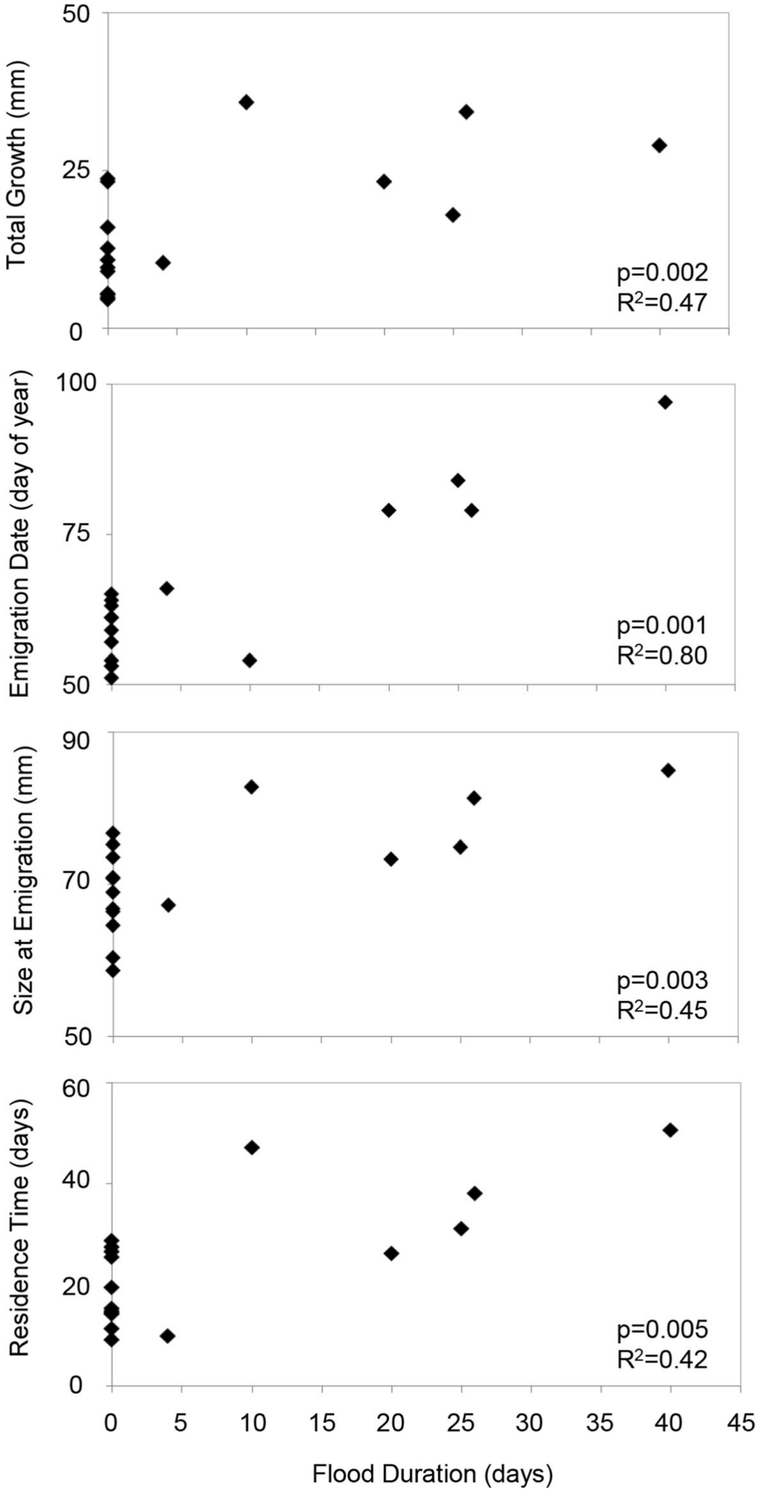
Inter-annual survival of CWT fish to the ocean fishery did not exhibit obvious patterns between rearing systems. Estimated recoveries of paired CWT releases in the ocean fishery ranged between 0.01%–0.15% for Sacramento River release groups and 0.01%–0.13% for Yolo Bypass release groups. Overall survival was not statistically different between release locations (paired t-test, $p = 0.75$) (Fig. 6).

What are the environmental triggers of emigration from the Yolo Bypass?

Generalized linear modelling indicated that neither ATU nor flow predicted intra-annual emigration at the bimonthly time scale. Of the main effects models, the null, intercept-only model received the best (lowest) AICc score, and all remaining models were within 2.5 ΔAICc indicating similar fit. Low model probabilities and coefficients that approached zero in parameterized models indicated that none may be very ecologically relevant (Table 4).

Graphical examination of cumulative catch curves for CWT and wild juvenile Chinook salmon captured at the RSTR indicated that fish delayed emigration from the Bypass while flooded habitat was available and would move out after flood waters receded (Fig. 2). We observed a spike in emigration following floodwater recession for CWT fish in 1999, 2000, and 2004, when releases coincided with flooded periods. In years when

Fig. 3 Coded wire tag (CWT) juvenile Chinook inter-annual growth and habitat use demographics were significantly explained by flood duration at the among-year time scale ($\alpha \leq 0.05$). Each point denotes a CWT release in the Yolo Bypass. Zero values denote CWT releases with rearing periods that did not overlap with flooding (>4000 CFS). Independent variables that did not contribute significantly to regression model fit are not depicted



overtopping at Fremont Weir allowed wild juveniles access to the floodplain, wild fish also appeared to delay emigration until after recession (1999, 2000, 2002, 2003, 2004, 2006, 2010, 2011).

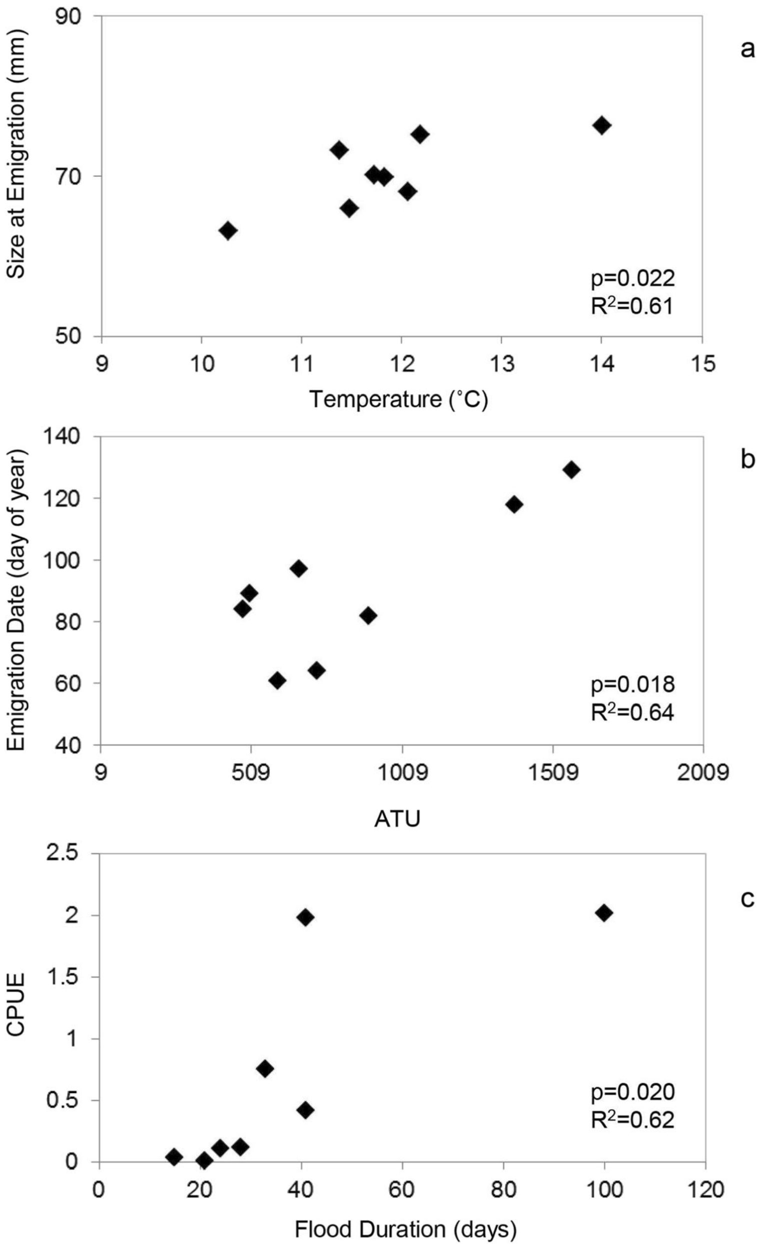


Fig. 4 Inter-annual habitat use and catch demographics for wild juvenile Chinook salmon significantly related to independent covariates. Points denote years when the Sacramento River connected to the Yolo Bypass floodplain via overtopping at Fremont Weir. Non-overtopping years were excluded. Independent variables that did not contribute significantly to regression model fit are not depicted

Discussion

There is growing international recognition of the importance of off-channel, floodplain habitat for the conservation of native riverine fishes, particularly in highly altered, highly managed systems (Agostinho et al. 2004; Lanse et al. 2007; King et al. 2008). For salmonids, the benefits of such habitats include more abundant food resources (Sommer et al. 2001a; Eberle and Stanford 2010; Bellmore et al. 2013), increased rearing habitat (Sommer et al. 2005; Cordell et al. 2011), and faster growth rates (Jeffres et al. 2008; Limm and Marchetti 2009). However, floodplains are among the most spatially and temporally variable freshwater habitats on the planet, so fishes rearing in these areas face increased risks such as stranding after floodwaters recede (Sommer et al. 2005). These sorts of risk-reward trade-offs are relatively common among many populations (Stearns 1989). Our observations from the expansive Yolo Bypass floodplain provide insight into how

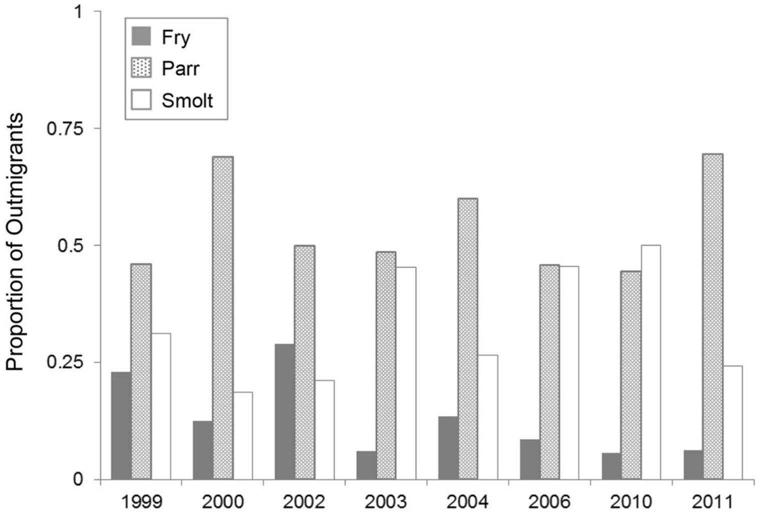


Fig. 5 Migratory phenotypes of wild juvenile Chinook Salmon captured at the rotary screw trap near the exit of the Yolo Bypass during years when the floodplain connected to the Sacramento River via overtopping at Fremont Weir

Chinook salmon may manage this risk in order to maximize benefits. Specifically, our results reveal that the duration of flooding positively affects fish growth and habitat use in the floodplain, without negatively affecting survival. Although our results did not demonstrate survival advantages from the Yolo Bypass, collections of fish emigrating from the floodplain suggest that this seasonal habitat type helps support life history diversity, including larger size at emigration with longer rearing periods as flooding duration increases, which may convey benefits beyond the survival on a cohort by cohort basis.

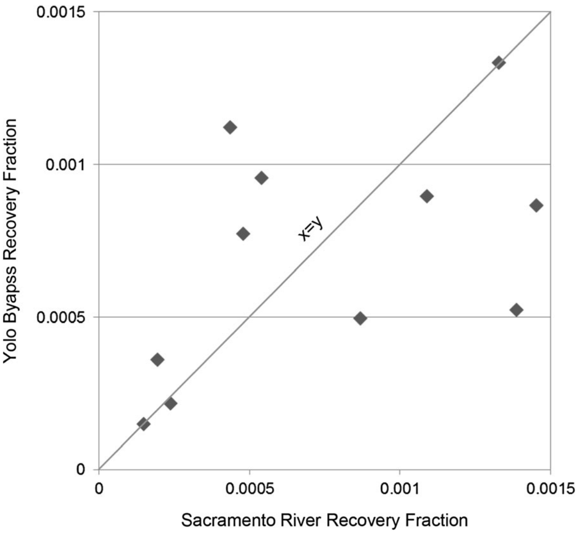


Fig. 6 Recovery fractions for paired coded wire tag releases conducted in the Sacramento River and Yolo Bypass. The fraction is calculated as the estimated number recovered in the ocean fishery divided by the number of fish released. The diagonal 1:1 line indicates where ratios were equivalent for the two systems. Points above the line denote release pairs (conducted on the same date) where Yolo Bypass recoveries exceeded Sacramento River recoveries

Factors affecting habitat use, growth, emigration and abundance Hydrologic regime is recognized as one of the most critical drivers for the functioning of floodplain ecosystems (Junk et al. 1989). Specifically, patterns of connectivity, flooding and recession shape how fish utilize these habitats (Mims and Olden 2012; Gido et al. 2013). In our study, hydrologic regime, specifically the duration of flooding, was the most important driver for juvenile Chinook salmon inter-annual growth and floodplain habitat use at both inter- and intra-annual scales. Among years, fish from our CWT releases spent progressively longer periods rearing on the Yolo Bypass during years with longer periods of flooding, with one release group spending 50.6 days (median) following the start of a 40-day flood event in 1999. Lengthier rearing periods also resulted in CWT fish achieving larger overall size before departing. These results sup-

Table 4 Coefficients, AICc values, ΔAICc values, and model probabilities (w_i) for main effects GLM models of bimonthly CPUE with independent variables of temperature and flow

ATU	Flow	Intercept	AICc	ΔAICc	w_i
—	—	−0.4*	1388.1	–	0.50
−0.0007*	—	0.3*	1389.7	1.6	0.23
—	0.00002*	−0.5*	1390.1	1.9	0.18
−0.0007*	−0.000003*	0.3*	1391.6	2.5	0.09

Variables with p-values less than 0.05 are denoted with * port short-term studies indicating that juvenile Chinook salmon, like other floodplain-adapted species, respond dependably to floodplain hydrology by occupying inundated habitat as long as waters remain high and then departing as floodwaters recede (Sommer et al. 2005; Moyle et al. 2007; Lyon et al. 2010). This general pattern was also apparent on intra-annual time scales, where both hatchery and wild fish consistently delayed emigration during periods while flooded habitat remained available and departed in a pulse when floodwaters receded.

Emigration from freshwater rearing areas have been related to thermal variables for juvenile Chinook salmon (Sykes et al. 2009), and in our study, temperature and ATU appeared to also play a role influencing outmigration from the floodplain. Among-year emigration size and timing of wild juvenile Chinook salmon was positively correlated to annual temperature and ATU, respectively. While our analysis on wild fish did not identify flood duration as a significant covariate for habitat use as we had found for CWT fish, these differences are more likely due to the limited environmental variability captured by our data set rather than fish rearing origin (hatchery vs. wild). Wild juveniles are primarily captured during years when the floodplain connected to the Sacramento River via Fremont Weir and flooded habitat is abundant. CWT releases, in contrast, occurred over a broader range of conditions including several dry years without flooding. However, our study does suggest that given the availability of significant flooded habitat, temperature, and temperature experience are also important correlates for size and timing of emigration for wild juvenile Chinook salmon. The onset of migration in salmonids is a complex interplay between physiological readiness and environmental factors that optimize survival (Sykes et al. 2009). In some studies, fish remain longer in areas with higher growth opportunity (Dodson et al. 2013), and the warmer winter temperatures in the Yolo Bypass are more favorable for feeding and growth than the adjacent Sacramento River (Sommer et al. 2001a). Thus, positive relationships between size at emigration, emigration timing, and thermal variables in our study indicate that growth opportunity may play a role in juvenile emigration under flooded conditions in the Yolo Bypass.

In addition to affecting apparent growth and residence, hydrologic regime also emerged as a key predictor for juvenile Chinook salmon abundance on the floodplain. Our results indicate that the duration of connectivity with the Sacramento River is the most important variable influencing the abundance of wild juvenile Chinook salmon able to access and utilize the Yolo Bypass floodplain for rearing. Relative seasonal catch of wild juveniles was significantly related only to flood duration, indicating that the temporal window during which flooding occurs (e.g. how long Fremont Weir overtops) may govern how many wild fish can gain access to and rear on the floodplain. The strength of the spawning population (i.e. escapement) did not emerge as a significant covariate, a pattern similar to findings for the abundance of Winter Run Chinook salmon in the adjacent Sacramento River (del Rosario et al. 2013).

Effects of floodplain rearing on life history diversity and survival There is growing recognition that wide life history diversity is crucial for long-term persistence of salmon populations under variable environmental conditions (Hilborn et al. 2003; Greene et al. 2010; Schindler et al. 2010). Studies examining the life history diversity of Chinook salmon in the Central Valley specifically have demonstrated that life history diversity is essential to maintaining sustainable Chinook salmon populations (Carlson and Satterthwaite 2011). The reconnection of wetland rearing habitats can facilitate this diversity by expanding the geographic and temporal ranges for freshwater rearing, expand variation in migration timing, and increase body size for juvenile Chinook salmon (Bottom et al. 2005). Our study suggests that the Yolo Bypass supports a diversity of migratory phenotypes and could play a role augmenting the juvenile life history portfolio for the larger Central Valley Chinook salmon population. For example, all three migratory phenotypes (fry, parr, smolt) were consistently observed exiting the Yolo Bypass floodplain, with mid-sized parr accounting for the largest proportion of outmigrants in all but one year. Although we did not have data from the parallel reach of the Sacramento River captured with a similar gear type (RSTR), the general pattern in Yolo Bypass appears somewhat different than the adjacent Delta region where unmarked outmigrants are often dominated by fry and smolt-sized juveniles (Miller et al. 2010; USFWS 2016). Thus, the broad array of migratory phenotypes observed on the Yolo Bypass floodplain compared to riverine locations suggests that increasing Yolo Bypass accessibility to juvenile salmonids would support a more robust portfolio of life history types overall, and may contribute to the resilience of the Central Valley Chinook salmon population.

Despite the known growth advantages of floodplain rearing (Sommer et al. 2001a; Jeffres et al. 2008), we did not detect significant differences in survival to the ocean fishery between our paired CWT releases in the Yolo Bypass and Sacramento River. However, our results may have been a consequence of limited power from a relatively small dataset. The closure of the ocean fishery in 2008 restricted our survival analyses to 12 paired releases over seven years (1999–2005), and we likely could not capture a robust range of the environmental variability possible in the floodplain habitat within those limited releases. For example, though flooding was prolonged during some years (e.g., 100 days in 2006), the timing of only five of our CWT releases overlapped with flooded habitat. At the very least, our results indicate that rearing in the Yolo Bypass does not impart disproportionately negative impacts to survival in comparison to rearing in the Sacramento River, as might be expected if risk factors associated with the floodplain such as stranding, low flow, or warm temperatures, were problematic. There is evidence that juvenile Chinook salmon may be capable of negotiating these risks by avoiding areas with high temperatures, and moving out of shallow tidal wetlands and floodplains as waters recede (Sommer et al. 2005; Moyle et al. 2007; Hering et al. 2010).

Management implications Our study adds to a growing body of evidence that off-channel regions are a key component of fish management for species such as salmonids. In California, where nearly all high quality wetland rearing habitat has been eliminated (Whipple et al. 2012), evidence that the Yolo Bypass provides an expansive, highly productive nursery for juvenile Chinook salmon (Sommer et al. 2001a, 2004b) has helped make this region an important component of region-wide habitat restoration efforts to recover threatened and endangered salmon stocks (NMFS 2014).

Our investigation provides insight into specific management actions that could improve floodplain rearing opportunities. Namely, connectivity between the Sacramento River and Yolo Bypass is currently poor, with limited or no flooding in many years. Results from over a decade of Yolo Bypass sampling indicate that increased frequency and duration of floodplain connectivity should be a primary target to increasing rearing opportunities for juvenile Chinook salmon to maximize life history diversity. Such improvements could yield multiple benefits. For example, better connectivity between the Sacramento River and Yolo Bypass can help widen the life history diversity of a stock complex suffering from a narrowing life history portfolio (Carlson and Satterthwaite 2011), declining population (Yoshiyama et al. 2000), and increasingly volatile population dynamics (Lindley et al. 2009). In addition, longer, more frequent flooding events on the Yolo Bypass can increase the quantity of juvenile Central Valley Chinook salmon that rear on the floodplain, offering an alternative route for outmigrants which promotes an increase in size diversity, and variable, possibly delayed, emigration timing. Given that a widened portfolio is critical to buffer against spatial or temporal mismatch as well as against variable sources of mortality (Schindler et al. 2010), the Yolo Bypass has the potential to play a unique and beneficial role supporting a larger species complex at risk in the face of increasing human disturbance and environmental change (Katz et al. 2013).

Acknowledgements Numerous people and organizations have been made this long-term study possible through the years. We thank the California Department of Fish and Wildlife's (CDFW) Ecosystem Restoration Program, and the California Department of Water Resources (DWR) for funding these analyses the ongoing monitoring in the Yolo Bypass floodplain. Thank you to CDFW's Feather River Fish Hatchery staff for providing CWT fish, as well as transport to the Yolo Bypass and Sacramento River. We also thank J. Speegle, K. Reece, B. Harvey, and staff at the US Fish and Wildlife Lodi Office for sharing their data, insight, and helpful comments on this manuscript. Last, but certainly not least, we thank the countless individuals who have tirelessly collected, counted and measured juvenile salmon at the DWR Yolo Bypass rotary screw trap through the years. All applicable international, national, and/or institutional guidelines for the care and use of animals were followed.

References

Agostinho AA, Gomes LC, Verissimo S, Okada EK (2004) Flood regime, dam regulation and fish in the upper Parana River: effects on assemblage attributes, reproduction and recruitment. Rev Fish Biol Fisher 14:11–19

Albertson LK, Koenig KE, Lewis BL, Zeug SC, Harrison LR, Cardinale BJ (2013) How does restored habitat for Chinook salmon *(Oncorhynchus tshawytscha)* in the Merced River in California compare with other Chinook streams? Riv Res Appl 29:469–482. doi:10.1002/rra.1604

Azat J (2015) GrandTab. https://nrmdfgcagov/FileHandlerashx?DocumentID=84381&inline=1. Accessed 10 June 2015

Bellmore RJ, Baxter CV, Martens K, Connolly PJ (2013) The floodplain food web mosaic: a study of its importance to salmon and steelhead with implications for their recovery. Ecol Appl 23:189–207. doi:10.1890/12-0806.1

Bottom DL, Jones KK, Cornwell TJ, Gray A, Simenstad CA (2005) Patterns of Chinook salmon migration and residency in the Salmon River estuary (Oregon). Estuarine, Coastal and Shelf Science 64(1):79–93

Calcagno V, de Mazancourt C (2010) Glmulti: an R package for easy automated model selection with (generalized) linear models. J Stat Softw. doi:10.18637/jss.v034.i12

California Department of Water Resources (2014) Dayflow: An estimate of daily average delta outflow. http://www.watercagov/dayflow. Accessed 12 Jan 2014

California Hatchery Scientific Review Group (2012) California Hatchery Review Report. Prepared for the US Fish and Wildlife Service and Pacific States Marine Fisheries Commission, pp 100

Carlson SM, Satterthwaite WH (2011) Weakened portfolio effect in a collapsed salmon population complex. Can J Fish Aquat Sci 68:1579–1589. doi:10.1139/f2011-084

Clarke KR, Gorley RN (2006) PRIMER v6: User Manual/Tutorial PRIMER-E: Plymouth, United Kingdom, pp 190

Clarke RK, Somerfield PJ, Gorley RN (2008) Testing of null hypotheses in exploratory community analyses: similarity profiles and biota-environment linkage. J Exp Mar Biol Ecol 366:56–69. doi:10.1016/j.jembe.2008.07.009

Cordell JR, Toft JD, Gray A, Guggerone GT, Cooksey M (2011) Functions of restored wetlands for juvenile salmon in an industrialized estuary. Ecol Eng 37:343–353. doi:10.1016/j.ecoleng.2010.11.028

Dodson JJ, Aubin-Horth N, Theriault V, Paez DJ (2013) The evolutionary ecology of alternative migratory tactics in salmonid fishes. Biol Rev 88(3):602–625. doi:10.1111/brv.12019

Dormann CF, Elith J, Bacher S, Buchmann C, Carl G, Carre G, Garcia Marquez JR, Gruber B, Lafourcade B, Leitao PJ, Munkemuller T, McClean C, Osborne PE, Reineking B, Schroder B, Skidmore AK, Zurell D, Lutenbach S (2013) Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. Ecography 36:27–46. doi:10.1111/j.1600-0587.2012.07348

Eberle LC, Stanford JA (2010) Importance and seasonal availability of terrestrial invertebrates as prey for juvenile salmonids in floodplain spring brooks of the Kol River (Kamchatka, Russian Federation). Riv Res Appl 26:682–694. doi:10.1002/rra.1270

Feyrer F, Sommer T, Harrell W (2006) Importance of flood dynamics versus intrinsic physical habitat in structuring fish communities: evidence from two adjacent engineered floodplains on the Sacramento River, California. N Am J Fish Manage 26:408–417. doi:10.1577/M05-113.1

Gido KB, Propst DL, Olden JD, Bestgen KR (2013) Multidecadal responses of native and introduced fishes to natural and altered flow regimes in the American southwest. Can J. Fish Aquat Sci 70:554–564. doi:10.1139/cjfas-2012-0441

Greene CM, Hall JE, Guilbault KR, Quinn TP (2010) Improved viability of populations with diverse life-history portfolios. Biology Letters 6(3):382–386

Hering DK, Bottom DL, Prentice EF, Jones KK, Fleming IA (2010) Tidal movements and residency of subyearling Chinook salmon (*Oncorhynchus tshawytscha*) in an Oregon salt marsh channel. Can J Fish Aquat Sci 67:524–533. doi:10.1139/F10-003

Hilborn R, Quinn TP, Schindler DE, Rogers DE (2003) Biocomplexity and fisheries sustainability. Proceedings of the National Academy of Sciences 100(11):6564–6568

Huber ER, Carlson SM (2015) Temporal trends in hatchery releases of fall-run Chinook salmon in California's Central Valley. San Francisco Estuary and Watershed Science 13(2). doi:10.15447/sfews.2015vol13iss2art3

Jeffres CA, Opperman JJ, Moyle PB (2008) Ephermeral floodplain habitats provide best growth conditions for juvenile Chinook salmon in a California River. Environ Biol Fish 83:449–458. doi:10.1007/s10641-008-9367-1

Johnson JK (2004) Regional overview of coded wire tagging of anadromous salmon and steelhead in northwest America. http://wwwsb.rmpc.org/files/RegionalOverviewProfPaper-30May04.pdf. Accessed 30 June 2016

Junk WJ, Bayley PB, Sparks RE (1989) The flood pulse concept in river-floodplain systems. Can Spec Publ Fish Aquat Sci 106: 110–127

Katz J, Moyle PB, Quinones RM, Israel J, Purdy S (2013) Impending extinction of salmon steelhead and trout (*Salmonidae*) in California. Environ Biol Fish 96(10):1169–1186. doi:10.1007/s10641-012-9974-8

King AJ, Tonkin Z, Mahoney J (2008) Environmental flow enhances native fish spawning and recruitment in the Murray River, Australia. Riv Res Appl 25(10):1205–1218. doi:10.1002/rra.1209

Lanse E, Lek S, Laffaille P (2007) Patterns in fish assemblages in the Loire floodplain: the role of hydrological connectivity and implications for conservation. Biol Conserv 139:258–268. doi:10.1016/j.biocon.2007.07.002

Limm MP, Marchetti MP (2009) Juvenile Chinook salmon (*Oncorhynchus tshawytscha*) growth in off-channel and main-channel habitats on the Sacramento River, CA using otolith increment widths. Environ Biol Fish 85:141–151. doi:10.1007/s10641-009-9473-8

Lindley ST, Grimes CB, Mohr MS, Peterson W, Stein J, Anderson JT, Botsford LW, Bottom DL, Busack CA, Collier TK, Ferguson J, Garza JC, Grover AM, Hankin DG, Kope RG, Lawson PW, Low A, MacFarlane RB, Moore K, Palmer-Zwahlen M, Schwing FB, Smith J, Tracy C, Webb R, Wells BK, Williams TH (2009) What caused the Sacramento River fall Chinook stock collapse? NOAA-TM-NMFS-SWFSC-447, pp 61

Lyon J, Stuart I, Ramsey D, O'Mahony J (2010) The effect of water level on lateral movements of fish between river and off-channel habitats. Mar Freshw Res 61:271–278. doi:10.1071/MF08246

Maunder MS, Punt AE (2004) Standardizing catch and effort data: a review of recent approaches. Fish Res 70:141–159. doi:10.1016/j.fishres.2004.08.002

Miller JA, Gray A, Merz J (2010) Quantifying the contribution of juvenile migratory phenotypes in a population of Chinook salmon *Oncorhynchus tshawytscha*. Mar Ecol Prog Ser 408: 227–240. doi:10.3354/meps08613

Mims CM, Olden JD (2012) Life history theory predicts fish assemblage response to hydrologic regimes. Ecology 91(1): 35–45. doi:10.1890/11-0370.1

Moyle PB, Crain PK, Whitener K (2007) Patterns in the use of a restored California floodplain by native and alien fishes. San Francisco Estuary and Watershed Science 5(3):1–27

Nandor GF, Longwill JR, Webb DL (2010) Overview of the coded wire tag program in the greater Pacific region of North America. In: Wolf K, O'Neal J (eds) Tagging telemetry and marking measures for monitoring fish populations: a compendium of new and recent science for use in informing technique and decision modalities. Pacific States Marine Fisheries Commission Pacific Northwest Aquatic Monitoring Partnership, Portland, pp 5–46

National Marine Fisheries Service (2014) Recovery Plan for the Evolutionarily Significant Units of Sacramento River Winter-run Chinook salmon and Central Valley Spring-run Chinook salmon and the Distinct Population Segment of California Central Valley Steelhead, California. Central Valley Area Office, pp 406

Newman KB, Brandes PL (2010) Hierarchical modeling of juvenile Chinook salmon survival as a function of Sacramento–San Joaquin Delta water exports. N Am J Fish Manage 30(1): 157–169. doi:10.1577/M07-188.1

R Development Core Team (2008) R: A language and environment for statistical computing R Foundation for Statistical Computing. Vienna Austria. http://wwwR-project.org

del Rosario RB, Redler YJ, Newman K, Brandes PL, Sommer RK, Vincik R (2013) Migration patterns of juvenile winter-run-sized Chinook salmon (*Oncorhynchus tshawytscha*) through the Sacramento-San Joaquin Delta. San Francisco Estuary and Watershed Science 11(1):22

Schindler DE, Hilborn R, Chasco B, Boatright CP, Quinn TP, Rodgers LA, Webster MS (2010) Population diversity and the portfolio effect in an exploited species. Nature 465:609–612. doi:10.1038/nature09060

Sommer T, Nobriga ML, Harrell B, Batham W, Kimmerer WJ (2001a) Floodplain rearing of juvenile chinook salmon: evidence of enhanced growth and survival. Can J. Fish Aquat Sci 58:325–333. doi:10.1139/f00-245

Sommer T, Harrell B, Nobriga M, Brown R, Moyle P, Kimmerer W, Schemel L (2001b) California's Yolo Bypass: evidence that flood control can be compatible with fisheries wetlands wildlife and agriculture. Fisheries 26:6–16. doi:10.1577/1548-8446(2001)026<0006:CYB>2.0.CO;2

Sommer TR, Harrell WC, Kurth R, Feyrer F, Zeug SC, O'Leary G (2004a) Ecological patterns of early life stages of fishes in a river-floodplain of the San Francisco estuary. Am Fish S S 39:111–123

Sommer TR, Harrell WC, Mueller-Solger A, Tom B, Kimmerer W (2004b) Effects of flow variation on channel and floodplain biota and habitats of the Sacramento River, California, USA. Aquat Conserv 14:247–261. doi:10.1002/aqc.620

Sommer T, Harrell W, Nobriga M (2005) Habitat use and stranding risk of juvenile Chinook salmon on a seasonal floodplain. N Am J Fish Manage 25:1493–1504. doi:10.1577/M04-208.1

Stearns SC (1989) Trade-offs in life-history evolution. Funct Ecol 3(3):259–268. doi:10.2307/2389364

Sykes GE, Johnson CJ, Shrimpton JM (2009) Temperature and flow effects on migration timing of Chinook salmon smolts. T Am Fish Soc 138:1252–1265. doi:10.1577/T08-180.1

U.S. Fish and Wildlife Service (2016) Delta Junvenile Fish Monitoring Program. https://www.fws.gov/lodi/juvenile_fish_monitoring_program/jfmp_index.htm. Accessed Sept 2016.

Waples R, Beechie T, Pess GR (2009) Evolutionary history habitat disturbance regimes and anthropogenic changes: What do these mean for resilience of Pacific salmon populations? Ecol Soc 14:3

Whipple A, Grossinger A, Rankin RM, Stanford B, Askevold R (2012) Sacramento-San Joaquin Delta historical ecology investigation: Exploring pattern and process. A report of SFEIASCs Historical Ecology Program. San Francisco Estuary Institute-Aquatic Science Center. Richmond

Yoshiyama RM, Gerstung ER, Fisher FW, Moyle PB (2000) Chinook salmon in the California Central Valley: an assessment. Fisheries 25(2):6–20. doi:10.1577/1548-8446

Zydlewski GB, Haro A, McCormick SD (2005) Evidence for cumulative temperature as an initiating and terminating factor in downstream migratory behavior or Atlantic Salmon *(Salmo salar)* smolts. Can J. Fish Aquat Sci 62:68–78. doi:10.1139/f04-179