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Effects of Extreme Hydrologic Regimes on Juvenile Chinook Salmon Prey Resources and Diet Composition in a Large River Floodplain

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Abstract
Climate and hydrologic variability are defining characteristics of California rivers. Recently, the region experienced an unprecedented drought, and the probability of similarly warm, dry conditions is predicted to increase. In addition to warming air and water temperatures, climate change projections predict increased flooding and sea level rise, likely aggravating the water resource issues that already challenge the western United States. Water managers balance many public interests, including the conservation of native fishes, such as the Chinook Salmon *Oncorhynchus tshawytscha*. Given projected changes in climate and hydrology, there is an urgent need to understand how salmon respond to these conditions. In this study, we examined how young salmon responded to extreme drought (2012–2015) versus flood (1998–1999) conditions in the Yolo Bypass, a floodplain–tidal slough complex of the Sacramento River, California. We found that the diets of juvenile Chinook Salmon were dominated by aquatic–riparian insects during flooding and were dominated by zooplankton during the drought. Although juvenile salmon that were caught during the drought seemed to have eaten a higher number of prey items on average, they also had higher metabolic costs. Therefore, it is likely that juvenile salmon must augment their foraging behavior to offset higher temperatures and prey shifts. Finally, preferentially consumed, calorically valuable prey (i.e., larger zooplankton and aquatic–riparian insects) have become rare due to habitat degradation and biological invasions, and resource managers must consider re-establishing productive off-channel habitats, such as riparian corridors, floodplains, and wetlands.

Like many other migratory fishes, juvenile Chinook Salmon *Oncorhynchus tshawytscha* rear across a complex series of habitats, including upper river reaches, riparian corridors, floodplains, tidal wetlands, and open bays (Healey 1991). The relative contribution of each of these to fitness and survival is a key focus of Chinook Salmon research and management, since environmental effects on early life history can impact salmon production (Reimers 1971; Miller et al. 2010; Thorson et al. 2014; Sturrock et al. 2015). This topic is of special interest because historical habitats along migratory corridors for many Chinook Salmon populations have been lost or severely altered. In

particular, floodplains and tidal wetlands have become among the most imperiled habitats in North America (Nichols et al. 1986; Blaber et al. 2000; Vasconcelos et al. 2007). Fisheries managers concerned with the future of salmon production must also understand how the quality and availability of these altered habitats can change under climate extremes, which are likely to increase due to climate change (Dettinger et al. 2015).

Habitat alteration is of great concern at the southern end of the Chinook Salmon's range—the San Francisco Estuary (SFE) and its watershed (Figure 1). More than 95% of tidal freshwater wetlands have been lost in the Sacramento–San Joaquin Delta (hereafter, the Delta), a complex network of channels formed by the confluence of the Sacramento and San Joaquin rivers. These tributaries have become heavily channelized and cut off from their historical flood basins, with over 1,700 km of levees and approximately 80% of the channels hardened by shoreline armoring (Suddeth et al. 2010). Although much of the tidal freshwater Delta has experienced extreme habitat loss, some features of the region retain aspects of the historical landscape (Whipple et al. 2012). In particular, a dominant feature of the upper SFE is the 23,876-ha (59,000-acre) Yolo Bypass (Figure 1), the largest remnant floodplain in the Delta (Sommer et al. 2001a). The Yolo Bypass is part of the historical flood basin of the Sacramento River, a partially leveed basin that was
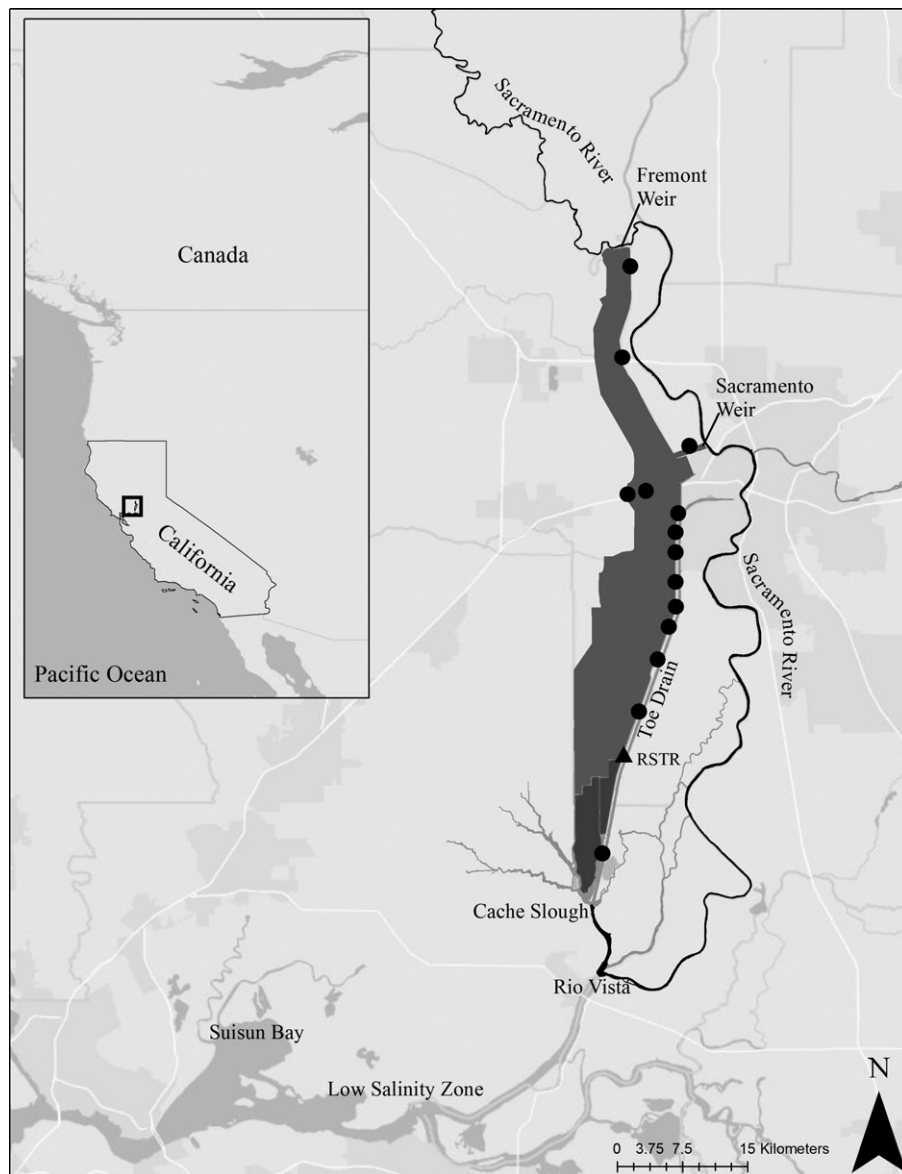

FIGURE 1. Map of the northern San Francisco Estuary, Sacramento River, and Yolo Bypass floodplain extent (gray shading) and the locations of sampling sites (black symbols).

retained to direct floodwaters away from urban centers, such as Sacramento. The Yolo Bypass floods from the Sacramento River and smaller tributaries in more than 50% of years, generating large areas of shallow-water fish habitat (Sommer et al. 2005). Floodwaters drain from the Yolo Bypass back into the Sacramento River in the northern Delta at Rio Vista (Figure 1), with a residence time generally less than 10 d (Sommer et al. 2004).

The Yolo Bypass is a valuable rearing location for juvenile Chinook Salmon during flood years, when migrating fish can enter the system from the Sacramento River (Sommer et al. 2001a, 2001b, 2005; Goertler et al., in press). Key benefits of this habitat during flood periods include increased rearing area, enhanced prey resources, improved feeding success, higher growth rates, and increased size diversity relative to the adjacent Sacramento River. The Yolo Bypass is also used by young Chinook Salmon in drier, non-flood years, when they are still able to access its lower tidal sloughs and open-water habitat by swimming upstream from the lower Sacramento River (McLain and Castillo 2009; Goertler et al. 2016a). This may be an important adaptation allowing the species to locate suitable rearing habitat during dry periods, which commonly occur in California's variable climate (Dettinger et al. 2015). However, little is known about how the Yolo Bypass' key food web benefits to juvenile salmon are altered during dry periods. Climate change model projections indicate that the SFE and its watershed will experience increased temperatures and greater variability in precipitation (Dettinger et al. 2015), so the ability of Chinook Salmon to persist will depend heavily on their use of diverse environments along migration corridors.

Given projected changes to regional temperatures and outflow patterns (Cloern et al. 2011), there is an urgent need to understand how young Chinook Salmon utilize different habitats, particularly under extreme environmental conditions. This issue has become especially timely given California's recent and unprecedented drought during 2012–2016 (Griffin and Anchukaitis 2014; Diffenbaugh et al. 2015; Robeson 2015), a period in stark contrast to the unusually sustained wet period that occurred during 1995–2000. Hence, Chinook Salmon populations may already be experiencing episodes of the environmental variability projected to be commonplace in the future. Understanding how juvenile salmon adapt to different hydrologic regimes will be critical for adaptively managing restoration and conservation activities in response to climate change. The responses of young Chinook Salmon to recent extreme hydrologic conditions could provide insight into (1) the effects of climate-induced increases in water temperature and flow variability within the SFE and (2) the role of dynamic habitats, such as floodplains and tidal sloughs.

Our objective was to examine how juvenile salmon responded to extreme drought (2012–2015) versus flood (1998–1999) years in the Yolo Bypass. We focused on juvenile Chinook Salmon prey resources and feeding because these metrics are important indicators of habitat quality and rearing success (Sogard 1994; Brodeur et al. 2007; Armstrong et al. 2008; Beauchamp 2009). Our specific hypotheses were that (1) the prey community would vary with flood and drought conditions; (2) fish diets would vary substantially between flood years and drought years; and (3) the environmental variation in temperature between the two periods would have implications for fish metabolism.

METHODS

Field sampling.— Sample collection for all invertebrate and fish sampling was conducted by the California Department of Water Resources (CDWR) as part of the fish monitoring program that has occurred over the last 20 years (Supplement S.1). Aquatic conditions within the Yolo Bypass were characterized by a temperature probe at the rotary screw trap (RSTR; Figure 1) and CDWR's "Dayflow" calculations for the Yolo Bypass (Figure 2; CDWR 2016). The 2012–2015 drought was defined by the Palmer drought severity index, a measure of relative wetness or dryness over more than 1,200 years.

Invertebrates were sampled at the RSTR (Figure 1) on an ebb tide with a conical plankton net (1999–2015) and rectangular drift net (1998–2015) monthly, with the exception of inundation and draining periods, when invertebrate sampling was conducted weekly (Sommer et al. 2001a, 2004; ERP 2015). The plankton net had 153-μm mesh, was 0.50 m in diameter, and was 2 m in length. The drift net had 500-μm mesh, had dimensions of 0.46 × 0.3 m at the mouth, was 0.91 m long, and was harnessed to a floated stainless-steel frame. After collection in the plankton net, a 1-mL subsample was extracted, identified, and counted under a stereomicroscope. In 2015, the 1-mL zooplankton subsample was further sieved through a 153-μm sieve before identification, and it is likely that larger copepods (anything greater than 153 μm) were excluded from these samples. All drift invertebrate samples were rinsed through a 0.5-mm sieve before identification. All of the material remaining within the sieve was processed for identification. Aquatic insects and other taxa were counted and identified to the family level. Terrestrial insects and other taxa were counted and identified to the order level. The number per cubic meter for each taxon of plankton and for each aquatic and terrestrial organism taken in the aquatic drift net was then calculated (Supplement S.1).

Juvenile Chinook Salmon were sampled by beach seine and RSTR (Sommer et al. 2001a, 2005). Beach seine sites were sampled monthly with a single haul from an 8.3- × 1.3-m pole seine (0.333-cm² mesh). The seine sites included one perennial pond, nine sites along the perennial
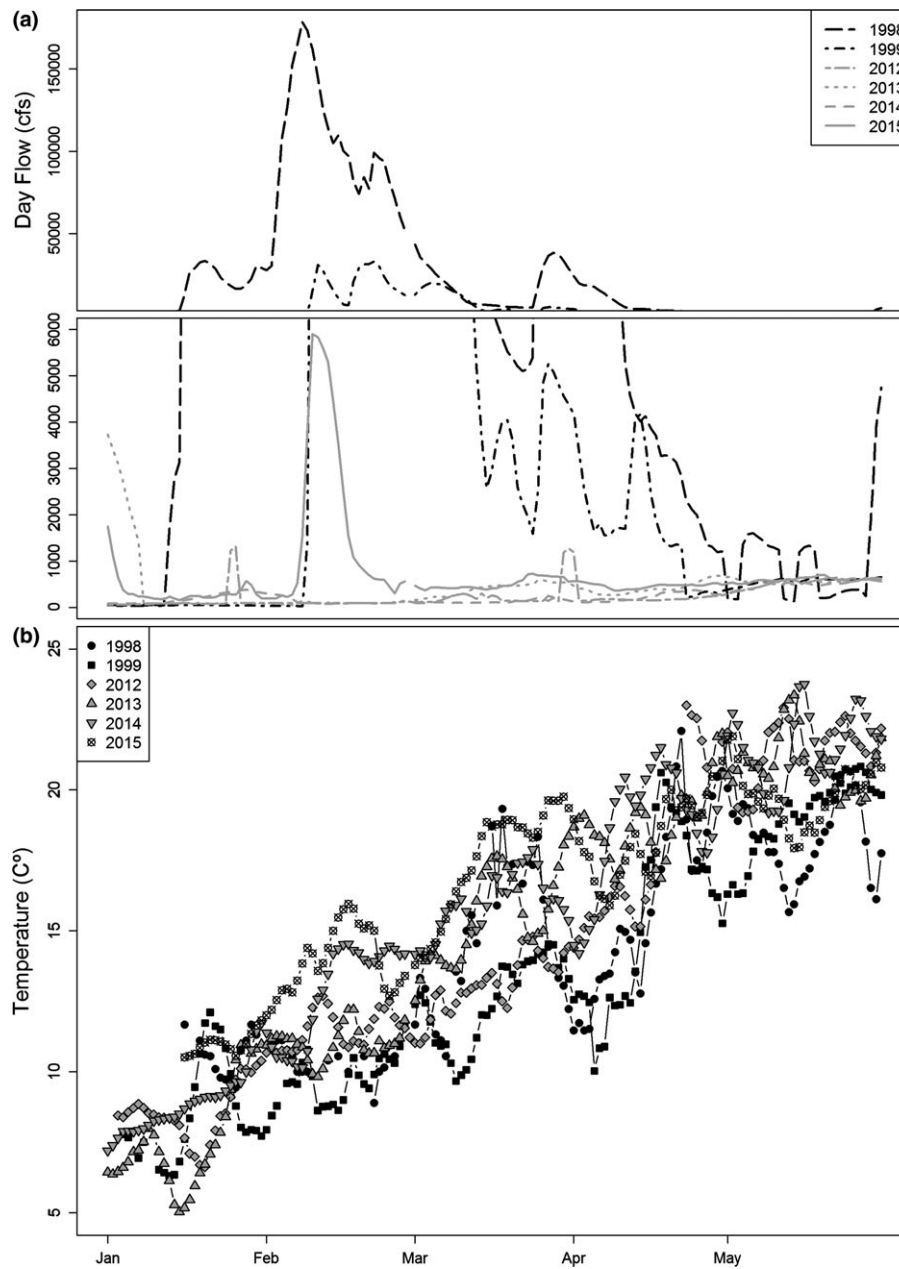
FIGURE 2. **(A)** Flow (cubic feet per second [cfs]; 1 cfs = 0.0283 m³/s) and **(B)** temperature (°C) in the Yolo Bypass from January to May for each year in this study. Drought years (2012–2015) are depicted in gray, while years during which the Yolo Bypass flooded (1998–1999) are depicted in black. The flow figure excludes mid-range day flow values to highlight the contrast between flow levels in the drought and flood years.

channel (e.g., Toe Drain), and four high-flow sites to capture floodplain inundation periods (Figure 1). A 2.6-m-diameter screw trap was installed near the lower end of the Toe Drain (Figure 1). The RSTR was fished daily but generally was not operated on weekends except during substantial flooding. Fish were identified to species, counted, and measured for FL (nearest mm) for up to 50 individuals of each species. In 2012–2015, a subset of juvenile Chinook Salmon was lethally sampled for diet analysis (*n* = 240; Supplement S.2). Diet results from Sommer

et al. (2001b) were used to examine conditions in 1998 and 1999.

Sample processing for diet composition.— Juvenile Chinook Salmon that were lethally sampled during 2012–2015 were weighed, and their stomachs were dissected. The stomach contents were then sorted, separating all unidentifiable matter from recognizable prey organisms. Prey identification was made to the lowest taxonomic level possible given the digestive state. All organisms were also sorted into life history stages if the diagnostic characters

were identifiable. After prey were sorted into groups and identified, they were counted and blotted dry, and each group was weighed (to the nearest 0.0001 g).

Effect of hydrologic conditions on diet composition.— For direct comparison to the results reported by Sommer et al. (2001b), we calculated the index of relative importance (IRI) for juvenile Chinook Salmon lethally sampled in February and March 2012–2015. The taxonomic groups were binned into the four groups used by Sommer et al. (2001b) plus a fifth "nondescript" category for any prey matter that was too digested to be categorized (Table 1). Percent numeric (%N) and gravimetric (%G) contribution, frequency of occurrence (%F), and IRI (IRI = %F[%N + %G]) were estimated for each prey category by month and year (Pinkas et al. 1970). Here, we compare diets from February and March of 1998–1999 and 2012–2015, but due to insufficient data, we were unable to examine continuous changes in juvenile Chinook Salmon diet across the 18-year period.

Variation in individual diets, prey availability, and selectivity during flood and drought.— Percent numeric contribution was calculated for each zooplankton and invertebrate drift sample collected during February and March 1998–1999 and 2012–2015. Percent numeric contribution was also calculated for each diet sample collected and analyzed during the 2012–2015 juvenile Chinook Salmon lethal sampling and the diet analysis data available from the Sommer et al. (2001b) study ($n = 159$; Supplement S.2). Nonmetric multidimensional scaling (NMDS) was conducted on the Bray–Curtis dissimilarity matrix of the log-transformed %N data sets at the taxonomic level of order by using the program R (R Development Core Team 2011) and library "vegan" version 2.2-0 (Oksanen et al. 2014). A scree plot was used to determine the most appropriate ordination in NMDS. Empty stomachs were excluded from this analysis (Supplement S.3). Selectivity was determined using Ivlev's electivity index (Ivlev 1961) by prey order. Ivlev's index estimates prey selectivity with a ratio of the relative abundance of the prey in the gut and relative abundance of the prey in the environment, producing a value between −1 (prey occurs in the environmental sample but not in the stomach sample) and +1 (prey occurs in the stomach sample but not in the environmental sample).

Maintenance metabolism.— For all juvenile Chinook Salmon used in the diet analysis, we calculated maintenance metabolism (J_M) via the method of Fiechter et al. (2015),

$$J_M = j_m \cdot e^{dT} \cdot W,$$

where j_m is the mass-specific maintenance costs at 0°C (0.003; B. T. Martin, National Marine Fisheries Service, personal communication), d is the temperature coefficient for biomass assimilation (0.068; Stewart and Ibarra 1991),

T is temperature at the time of capture, and W is the individual fish body mass. In some cases, during 2012–2014 ($n = 189$), juvenile Chinook Salmon were not weighed until after the removal of a fin clip for genetic analysis and/or after being stored in the freezer or in ethanol. Therefore, in 2014, lethally sampled juvenile Chinook Salmon were weighed immediately and after being fin clipped and then frozen ($n = 94$) to aid in extrapolating a more accurate weight for the 2012–2014 individuals ($R^2 = 0.9927$). During 1998 and 1999, there were also instances in which no weight was taken ($n = 72$), and FL (mm) was used to estimate weight ($R^2 = 0.957$). Individuals captured in 2015 ($n = 38$) were weighed directly.

RESULTS

Effect of Hydrologic Conditions on Prey Availability

The NMDS results from prey resource samples at the taxonomic level of order revealed a relationship between flooding periods with Diptera and drought periods with Cladocera and Cyclopoida (Figure 3A). The most distinguishable differences between flood and dry periods (e.g., vectors with the highest statistical significance [$P < 0.001$]) were for Diptera, Cladocera, and Cyclopoida. The NMDS also revealed an association between dry periods and terrestrial invertebrates belonging to the orders Hymenoptera, Coleoptera, Aranae, Hemiptera, and Collembola ($P < 0.01$; Figure 3A). Aquatic invertebrates in the orders Plecoptera and Haplotaxida appeared to be associated with periods of flooding ($P < 0.01$).

When taxonomic resolution finer than order level was available, chironomids were the dominant family of Diptera observed in the prey resources data (1998–1999: 93%; 2012–2015: 96%). For cladocerans, *Daphnia* was the most represented group during wet years (1998–1999; 23%), while the genus *Chydorus* dominated samples during dry periods (2012–2015; 37%). Of the terrestrial invertebrates observed in the prey resources data, only the order Coleoptera had further taxonomic resolution; the aquatic Dytiscidae was the dominant family observed within this order during both wet (1998–1999; 79%) and dry (2012–2015; 90%) periods.

Variation in Diet Composition and Selectivity During Flood and Drought

There was a clear difference in IRI results from Sommer et al. (2001b) in diets sampled during flood years (1998 and 1999) with our analysis from drought years (2012–2015; Table 2). Dipterans were the dominant prey in 1998 and 1999 (Sommer et al. 2001b), and zooplankton were the dominant prey in 2012–2015 (Table 2). The average IRI value for Diptera in February and March 1998–1999 was nearly 10 times the average IRI value for

TABLE 1. Prey taxa identified from juvenile Chinook Salmon stomachs (based on the categories from Sommer et al. 2001b) and used for calculating the index of relative importance (life histories [LH]: L = larva, A = adult, E = emergent, P = pupa, N = nymph).

Diptera		Zooplankton		Aquatic		Terrestrial		Nondescript	
Prey taxon	LH	Prey taxon	LH	Prey taxon	LH	Prey taxon	LH	Prey taxon	LH
Brachycera	A, P	*Bosmina longirostris*		*Americorophium*		Acari		Algae	
Calliphoridae	L, A	Calanoida		*Americorophium spinicorne*		Aphididae	A	Animal matter	
Cecidomyiidae	A	*Ceriodaphnia*		*Americorophium stimpsoni*		Aranae		Coleoptera	A
Ceratopogonidae	A, P	*Chydorus*		Coenagrionidae		Auchenorrhyncha	N	Inorganic matter	
Chironomidae	L, A, E, P	Cladocera		Corixidae		Carabidae	L, A	Insecta	A, L
Diptera	A, P	Copepoda		Corophiidae	N	Chalcidoidea	A	Plant matter	
Dolichopodidae	A	Cyclopoida	P, E	*Crangonyx*	N, A	Cicadellidae	A	Unidentified	
Empididae	A	*Daphnia*	E	Ephemeroptera		Collembola			
Ephydridae	A	Daphniidae		*Eurycercus*		Curculionidae	A		
Nematocera	L, A	Mysidacea		Foraminifera	A	Delphacidae	A		
Phoridae	A			Gammaridea		Entomobryidae			
Psychodidae	A			*Gammarus daiberi*		Flatidae	A		
Sciaridae	A			Harpacticoida		Formicidae	A		
Syrphidae	A			*Hyalella*		Hemiptera	A		
Tipulidae	A			Nematoda		Hydroptilidae	A		
				Odonata		Hymenoptera	A		
				Oligochaeta		Hypogastruridae			
				Osteichthyes	N	Hypogastruridae/ Onychiuridae			
				Ostracoda		Ichneumonidae	A		
				Scapholeberis		Isotomidae			
				Simocephalus		Lepidoptera	L, A		
				Trichoptera		Mymaridae	A		
						Plecoptera	A		
					L	Proctotrupidae	A		
						Psocoptera	A		
						Psyllidae	A, N		
						Raphidioptera	A		
						Scelionidae	A		
						Siphonaptera			
						Sminthuridae			
						Staphylinidae	A		
						Thripidae	A		
						Thysanoptera	A		
						Trichoptera	A		

February and March in 2012–2015. The range of %*F* for Diptera in the two periods was a contributing factor (74–100% for 1998–1999; 44–75% for 2012–2015), as well as much lower %*N* and %*G* composition in 2012–2015 diets. Average IRI values for zooplankton were almost four times higher in 2012–2015 than in 1998–1999. This difference was mainly due to the increased numerical composition of zooplankton in the 2012–2015 diets relative to 1998–1999. Mean IRI values for aquatic prey were more comparable between the two periods in this study: the 1998–1999 IRI was 1.5 times the 2012–2015 IRI. For terrestrial prey, the IRIs in 2012–2015 were 2.5 times the
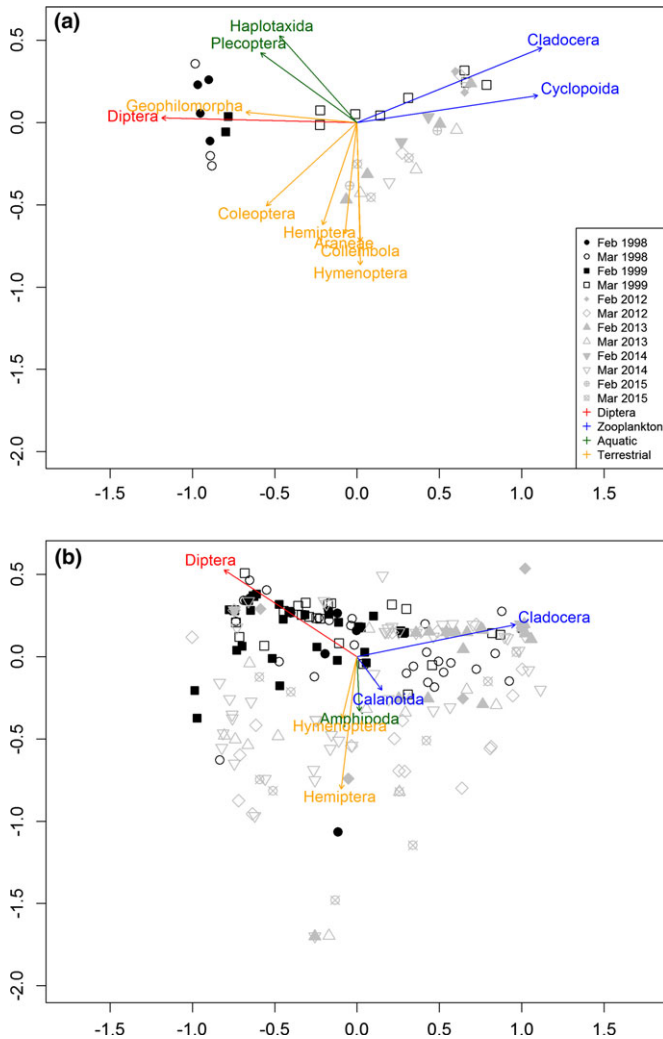
FIGURE 3. Nonmetric multidimensional scaling analysis of the percent numeric composition of invertebrate orders found in **(A)** zooplankton and drift invertebrate sampling (stress = 0.063) and **(B)** stomach samples from individual juvenile Chinook Salmon (stress = 0.083). Drought years (2012–2015) are depicted in gray, while years during which the Yolo Bypass flooded (1998–1999) are depicted in black. Vectors with a P-value less than 0.01 are shown. [Color figure can be viewed at afsjournals.org.]

1998–1999 IRI. Analysis of similarity of the IRI values indicated a statistically significant difference ($P < 0.001$) in prey taxonomic categories among time periods.

Similar to the IRI results, the NMDS plot of the diet data indicated a relationship (1) between flooding periods and Diptera and (2) between drought years and zooplankton and terrestrial invertebrates ($P < 0.001$; Figure 3B). Specifically, the orders Cladocera and Calanoida were associated with drought diets, particularly in February. Terrestrial invertebrate orders Hemiptera and Hymenoptera played a role in distinguishing drought diets, particularly in March. Amphipods were also important in characterizing the drought diet composition in March.

Finally, there was a relatively high diversity of taxa in March flooding diet composition that included Diptera, Cladocera, and Calanoida. In addition to the drought versus flooding differences, the NMDS also indicated separation by month in diet composition when comparisons were made at the order taxonomic level.

Taxonomic resolution finer than the order level was not always available, but when it was, there were some additional distinctions in diet composition among time periods. Similar to the findings of Sommer et al. (2001b), chironomids were the dominant family of Diptera (96%) in the diet during 2012–2015. However, 71% of the chironomids in the 2012–2015 stomach samples were adults, whereas Sommer et al. (2001b) found that larvae (56%) were the dominant chironomid life stage consumed. Adult chironomids are terrestrial insects, while chironomid larvae are an aquatic life history stage. This distinction may be indicative of different foraging behaviors and may have been influenced by the substantial increase in aquatic habitat during flooding. In 2012–2015 diets, *Daphnia* (83%) was the dominant cladoceran genus; within *Daphnia*, *D. pulex*/*D. pulicaria* was most common (87% of those counted and identified to species). *Daphnia* was also the most common cladoceran genus in the Sommer et al. (2001b) study, but species information was not available. Within the terrestrial invertebrates, there were distinctions between the environmental samples and stomach samples. Although drought was associated with terrestrial invertebrates in both cases, the two NMDS plots only had two terrestrial orders in common (Hymenoptera and Hemiptera). In the 2012–2015 diets, all of the hymenopterans and hemipterans were adults. Within Hemiptera, Aphididae (72%) was the dominant family.

Similar to the differences between the prey availability and consumption of terrestrial insects in the NMDS results, prey selectivity results showed a clear preference for a few rare orders, most of which were riparian-produced insects (Supplement S.4). Four orders had overall positive Ivlev electivity values (three of which were also rare in the prey sampling): Diptera, Mysida, Plecoptera, and Trichoptera. The relatively low positive and/or negative selectivity values for Diptera indicate that they had similar relative abundances in both fish and environmental samples. Interestingly, there were many negative Ivlev electivity values, suggesting that generally many of the orders collected for this study were relatively abundant in the environmental samples but were not eaten by juvenile salmon.

Effect of Hydrologic Conditions on Maintenance Metabolism

Juvenile Chinook Salmon that were caught during the drought had higher estimated metabolic costs (Figure 4). The P-values from ANOVA showed that the effects of month, year, and water year type were all significant ($P \leq 0.001$). Furthermore, maintenance metabolism scaled

TABLE 2. Numerical (%N) and gravimetric (%G) percent composition, percent frequency of occurrence (%F), and index of relative importance (IRI) for taxonomic categories in diets of individual juvenile Chinook Salmon for each sample period.

| Group	n	Taxonomic category	%N	%G	%F	IRI
Feb 1998	11	*Diptera*	78.40	86.77	100.00	16,516.95
		Zooplankton	18.52	2.00	63.64	1,305.55
		Aquatic	2.47	11.12	9.09	123.56
		Terrestrial	0.62	0.11	9.09	6.57
Mar 1998	23	Diptera	56.25	73.60	91.30	11,855.92
		Zooplankton	41.45	5.83	86.96	4,111.55
		Aquatic	2.04	20.43	52.17	1,172.39
		Terrestrial	0.26	0.14	8.70	3.44
Feb 1999	29	Diptera	62.81	66.79	96.55	12,513.04
		Zooplankton	25.00	4.15	72.41	2,111.21
		Aquatic	10.43	22.41	31.03	1,019.27
		Terrestrial	1.76	6.65	44.83	376.68
Mar 1999	35	Diptera	65.96	85.06	74.29	11,218.89
		Zooplankton	32.80	9.44	57.14	2,414.06
		Aquatic	1.15	5.49	20.00	132.66
		Terrestrial	0.09	0.01	2.86	0.28
Feb 2012	7	Diptera	8.20	19.28	57.14	1,570.38
		Zooplankton	82.79	58.72	85.71	12,129.30
		Aquatic	2.19	3.14	57.14	304.44
		Terrestrial	6.83	11.59	42.86	789.57
		Nondescript	0.00	7.26	28.57	207.40
Mar 2012	36	Diptera	8.70	12.38	44.44	936.87
		Zooplankton	79.04	44.07	80.56	9,917.13
		Aquatic	4.13	6.91	33.33	368.18
		Terrestrial	8.12	6.91	41.67	626.41
		Nondescript	0.00	29.73	94.44	2,808.02
Feb 2013	17	Diptera	2.93	6.76	64.71	626.69
		Zooplankton	94.83	61.70	94.12	14,732.32
		Aquatic	1.46	1.70	47.06	148.85
		Terrestrial	0.69	0.54	11.76	14.47
		Nondescript	0.09	29.31	94.12	2,766.23
Mar 2013	21	Diptera	11.35	13.99	57.14	1,448.02
		Zooplankton	78.36	45.91	66.67	8,285.08
		Aquatic	6.86	6.26	42.86	562.10
		Terrestrial	3.43	3.78	28.57	206.07
		Nondescript	0.00	30.06	80.95	2,433.05
Feb 2014	4	Diptera	2.94	19.71	75.00	1,698.69
		Zooplankton	95.88	77.37	50.00	8,662.73
		Aquatic	1.18	1.46	25.00	65.91
		Terrestrial	0.00	0.00	0.00	0.00
		Nondescript	0.00	1.46	50.00	72.99
Mar 2014	74	Diptera	15.57	20.15	70.27	2,510.21
		Zooplankton	76.20	30.74	56.76	6,069.67
		Aquatic	4.64	9.72	28.38	407.62
		Terrestrial	3.56	5.62	37.84	347.00
		Nondescript	0.03	33.77	83.78	2,832.02
Mar 2015	17	Diptera	5.94	3.48	53.85	507.21
		Zooplankton	88.82	66.24	30.77	4,771.08
		Aquatic	2.11	12.78	53.85	802.16
		Terrestrial	3.12	2.30	46.15	250.42
		Nondescript	0.00	15.20	84.62	1,285.91
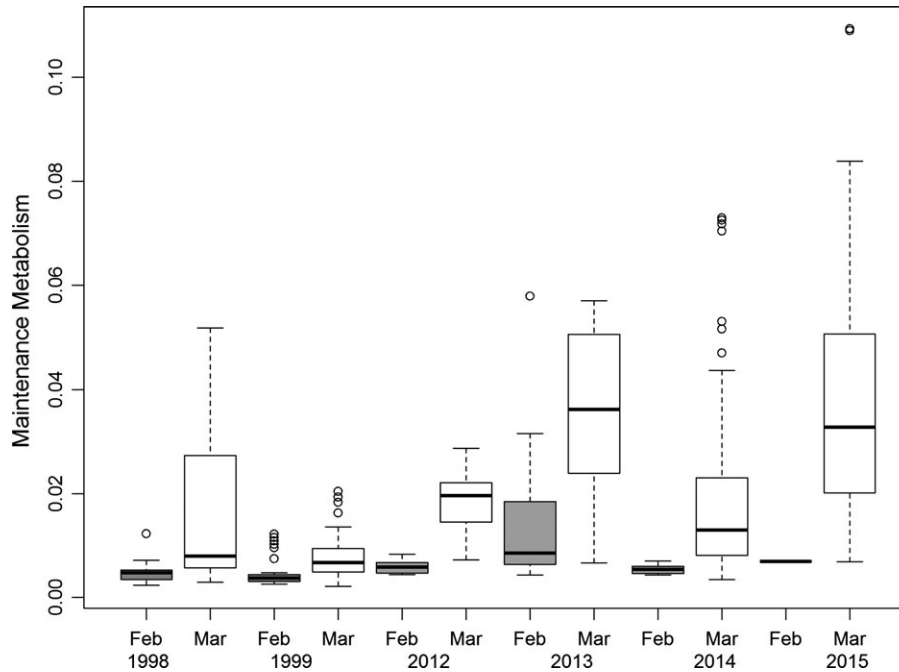
FIGURE 4. Maintenance metabolism (estimated cost of metabolic maintenance) of juvenile Chinook Salmon during each month and year sampled in this study. The horizontal line within each box represents the median, the ends of boxes represent the 25th and 75th percentiles, and the whiskers represent the 10th and 90th percentiles. Open circles indicate outliers.

with temperature and was highest in March 2013 and March 2015. Maintenance metabolism also scaled with fish size, potentially explaining the lower values in 2014, which had a smaller mean fish size than other drought years (mean ± SD FL in March = 70 ± 8 mm in 2012; 76 ± 11 mm in 2013; 55 ± 12 mm in 2014; 68 ± 15 mm in 2015). High values of maintenance metabolism in March 1998 can be explained by a period of high temperature during floodplain drainage (Figure 2). Floodplains are thermally complex (Arscott et al. 2001), and in the Yolo Bypass, water temperature is impacted by inundation duration and the seasonal variation in temperature (Goertler et al., in press).

DISCUSSION

Wildlife and water resource managers face many challenges in forecasting how climate change will affect natural resources and in determining the best practices for balancing California's resource needs. A pressing management concern is how juvenile salmon and their prey will respond to the greater frequency of floods and droughts with climate change and how that may provide insights for sustaining natural resources in the future. Therefore, our objective was to examine how juvenile salmon responded to extreme drought (2012–2015) versus flood (1998–1999) years in the Yolo Bypass. We found that the dominant prey of juvenile Chinook Salmon varied with

varying hydrologic conditions. In contrast to the flooding years documented by Sommer et al. (2001b), the diets of juvenile Chinook Salmon captured during the 2012–2015 drought were dominated by zooplankton (Table 2). Prey availability also varied between the two hydrologic extremes, with Diptera, aquatic invertebrates, and zooplankton being more available during the 1998 and 1999 floods, whereas terrestrial invertebrates and zooplankton were most common during the drought (Figure 3). Therefore, when Diptera became more available (e.g., in flooding years), this taxon became the dominant food type in the diets of juvenile Chinook Salmon, indicating prey switching and possibly diet optimization. Adult insects (e.g., adult dipterans) are calorically more valuable (energy densities of up to 8.92 kJ/g wet mass [wm]; David et al. 2014) than zooplankton (Cladocera: 1.32 kJ/g wm; Calanoida: 4.6 kJ/g wm; Luecke and Brandt 1993; David et al. 2014). Sommer et al. (2001b) found that when juvenile Chinook Salmon in the flooded Yolo Bypass fed mainly on Diptera, they grew faster than juveniles in the adjacent main-stem river, which fed mainly on zooplankton. Although juvenile Chinook Salmon feed extensively on zooplankton (e.g., Columbia River reservoirs [Muir and Emmett 1988], where they can achieve relatively high modeled growth [Koehler et al. 2006]), there may be energetic consequences to the observed changes in prey availability. For example, increased temperatures during the drought (Figure 2) could have impacted fish energy

requirements, and we found that juvenile salmon captured during the drought period had higher metabolic costs than those studied by Sommer et al. (2001b; Figure 4). However, juvenile Chinook Salmon that were captured during the drought were consuming, on average, 60% more individual prey per fish; given that the dominant prey in the flooding periods (chironomids) are two to three times as calorically valuable as the dominant prey during drought periods (*Daphnia*), it is likely that juvenile salmon must eat more of the lower energy prey given higher temperatures during drought years. Our findings support the hypothesis that (1) hydrologic conditions have effects on prey resources (Figure 3), which are then manifested in juvenile salmon diets (Table 2; Figure 3); and (2) salmon may respond behaviorally to changes in their metabolic needs (Figure 4), opportunistically responding to varying environmental extremes. Although California's 2012–2015 drought is considered to be without precedent on the Palmer drought severity index, a measure of relative wetness or dryness over more than 1,200 years (Robeson 2015), juvenile Chinook Salmon were able to adaptively respond to the variability in prey availability, quality, and temperature stress. This adaptive response may be important for future persistence, as the occurrence of drought years and the probability of the co-occurring conditions thought to have created the 2012–2015 drought (warm, dry conditions) have increased and are associated with anthropogenic warming (Diffenbaugh et al. 2015).

When foraging, animals must weigh the energetic costs of the search, pursuit, capture, and consumption of their prey. Optimal foraging theory suggests that through natural selection, animals forage to maximize fitness, and prey choice is a balance between the energetic value and handling time of prey (Pyke et al. 1977). Furthermore, when diet composition indicates a preference or prey switching, we assume that this is a progression toward an optimal diet by selecting for prey with high profitability (Pyke et al. 1977). In addition to the variation in diet composition due to varying hydrologic conditions, our selectivity results show clear preferences for a few rarer orders regardless of the hydrologic conditions (Supplement S.4). Juvenile salmon appeared to select for riparian-produced insects and large zooplankton; for example, when Ivlev's electivity index results were averaged, Diptera, Mysidacea, Plecoptera, and Trichoptera were estimated to have an overall positive value (Supplement S.4). In drought years, the fish, although mainly planktivorous, were largely ignoring smaller taxa (e.g., cyclopoids) and feeding mainly on cladocerans (*Daphnia* spp.) and, to a lesser degree, calanoids (Figure 3). However, a fundamental constraint on this interpretation is the lack of order-specific capture efficiencies for our zooplankton and drift nets. Size-selective foraging for zooplankton is common (Doble and Eggers 1978; Beauchamp et al. 2004), and our

selectivity analysis suggested that juvenile Chinook Salmon preferred a few orders of calorically valuable prey (e.g., larger zooplankton and aquatic–riparian flying insects), some of which have become rare in much of the modern Delta and were less available during the drought. However, despite the possibly suboptimal conditions during the drought, juvenile Chinook Salmon increased their feeding (number of prey items/stomach) and continued to rear in the Yolo Bypass. Thus, variably inundated floodplains, such as the Yolo Bypass, may provide benefits for juvenile salmon and other planktivorous fish by maintaining a supply of zooplankton and providing access to terrestrial invertebrates during droughts and high-value prey during floods. The importance of off-channel habitats has been demonstrated in several systems (Limm and Marchetti 2009; Hattin et al. 2014; Goertler et al. 2016b), and the Yolo Bypass provides two valuable forms of off-channel habitat: floodplain in wet years and tidal slough in drier years.

Moreover, these climatic effects must be considered in the context of other major ecosystem changes affecting juvenile salmon and their food web. Many habitats used by juvenile salmon throughout the Delta have been lost or severely altered, both by physical restructuring and biological invasions. After the invasion by the Asian clam *Potamocorbula amurensis* in 1987 (Nichols et al. 1990), the summer maximum phytoplankton biomass disappeared in Suisun Bay and the western Delta (Alpine and Cloern 1988), and the size distribution of phytoplankton decreased with the elimination of diatoms (Kimmerer 2005). The abundance of larger zooplankton, such as copepods and mysids, also declined sharply (Kimmerer et al. 1994; Kimmerer and Lougee 2015). Consequences of the Asian clam's invasion along with physicochemical drivers resulted in an ecological "regime shift" that is most pronounced in the SFE's low-salinity zone (see Figure 1; Brown et al. 2016). In addition, introduction of at least 10 non-indigenous zooplankton species in the estuary after the Asian clam invasion resulted in a nearly complete change in species composition that further altered the food web (Brown et al. 2016). These invasions extended to the tidal freshwater estuary, such as the Cache Slough complex and the Yolo Bypass, where several introduced copepod species are now abundant and often dominant (Kimmerer 2004). For planktivorous fishes, such as juvenile Chinook Salmon, the tradeoff may not be negative: studies suggest that the introduced copepod species are nutritionally equivalent to the native species they replaced (Kratina and Winder 2015). However, there is still a question as to whether tidal freshwater habitats without access to riparian areas—in which juvenile Chinook Salmon feed on plankton—are beneficial to the fish. Additionally, chemical contamination, such as changes in pesticide use, could have affected the invertebrate community over our

study period (Smalling et al. 2007; Sommer et al. 2007; Kuivila and Hladik 2008).

Habitat loss, ecological regime shifts, and declines in native prey occurred before our earliest sampling event (February 1998) and are likely contributors to fisheries resource declines throughout the SFE (Baxter et al. 2010). Central Valley winter-run and spring-run Chinook Salmon are listed as endangered and threatened, respectively, under the California Endangered Species Act and the federal Endangered Species Act (Good et al. 2005; CDFW 2016). The upper SFE, including the freshwater tidal Delta, is considered a juvenile Chinook Salmon migration bottleneck, as survival rates through this region are relatively poor (Perry et al. 2010, 2015). Resource managers and conservationists must operate within the context of these stressors on growth and survival of juvenile salmon and must plan for the impacts of the hydrologic extremes that are predicted to increase with climate change. One management action under consideration is the restoration of migratory and rearing habitat designed to provide food web benefits to native fish. Our findings suggest that the interface between aquatic and off-channel habitats (e.g., riparian and floodplain) is important for supporting salmon food webs during both floods and droughts. Juvenile Chinook Salmon (and possibly other fish species) can adaptively respond to the variability in prey quality and temperature stress within dynamic habitats like the Yolo Bypass. Therefore, floodplain–tidal slough complexes may contain important features for responding to rising temperatures and increasingly extreme variation in flow conditions in the estuary. Zooplankton seem to be available regardless of the hydrologic conditions, but the calorically valuable aquatic–riparian insects that juvenile salmon preferentially consume may be particularly important to ameliorate the metabolic stresses of reduced habitat and increased water temperature. Climate change projections specific to the San Francisco Bay–Delta predict warming air and water temperatures (aggravating water supply stress by 10–20%) and increased flooding (flows and frequency; Cloern et al. 2011; Dettinger et al. 2015). Flood management, such as levee setbacks with riparian habitat restoration and managed floodplains (e.g., bypasses), could also aid in reducing flood risks and aquifer recharge to benefit salmon food webs and protect valuable infrastructure (Merenlender and Matella 2013; Matella and Merenlender 2015). Over the last 20 years, riparian habitat restoration has occurred in the upper two-thirds of the Sacramento River (~3% increase between 1988 and 2009), but to the best of our knowledge, the Yolo Bypass represents one of the few riparian corridors bridging the lower Sacramento River and north Delta. Off-channel and freshwater tidal riparian habitats have been severely degraded in salmon streams and rivers, and resource managers adaptively managing for the effects of climate change need to consider re-establishing tidal vegetated habitats, such as riparian corridors, floodplains, and wetlands.

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SUPPORTING INFORMATION

Additional supplemental material may be found online in the supporting information tab for this article.