DECEMBER 2018

SAN FRANCISCO ESTUARY & WATERSHED SCIENCE

Sponsored by the Delta Science Program and the UC Davis John Muir Institute of the Environment

RESEARCH

Non-Native Fish Predator Density and Molecular-Based Diet Estimates Suggest Differing Effects of Predator Species on Juvenile Salmon in the San Joaquin River, California

Cyril J. Michel*[1], Joseph M. Smith[2], Nicholas J. Demetras[1], David D. Huff[2], and Sean A. Hayes[3]

Volume 16, Issue 4 | Article 3
https://doi.org/10.15447/sfews.2018v16iss4art3

* Corresponding author email: *cyril.michel@noaa.gov*

1 University of California, Santa Cruz
Institute of Marine Sciences
Affiliated with Southwest Fisheries Science Center
National Marine Fisheries Service
National Oceanic and Atmospheric Administration
Santa Cruz, CA 95060 USA

2 Estuary and Ocean Ecology Program
Northwest Fisheries Science Center
National Oceanic and Atmospheric Administration
Hammond, OR 97121 USA

3 Northeast Fisheries Science Center
National Marine Fisheries Service
National Oceanic and Atmospheric Administration
Woods Hole, MA 02543 USA

ABSTRACT

The Sacramento–San Joaquin Delta is a major survival bottleneck for imperiled California salmonid populations, partially because a multitude of non-native fish predators have proliferated there throughout the 20th century. Understanding the diets of salmonid predators is critical to understanding their individual effects, role in the food web, and the implications for potential management actions. We collected the stomach contents of Striped Bass *Morone saxatilis*, Largemouth Bass *Micropterus salmoides*, Channel Catfish *Ictalurus punctatus* and White Catfish *Ameiurus catus* sampled from three 1-km reaches in the lower San Joaquin River in 2014 and 2015 during the peak juvenile salmon out-migration period. Using a genetic barcoding technique, we tested each stomach ($n = 582$) for the presence of juvenile Chinook Salmon *Oncorhynchus tshawytscha* and other prey items. Channel Catfish had significantly higher frequency of Chinook Salmon in their stomachs (27.8% of tested Channel Catfish contained Chinook Salmon DNA), compared to the other three predators (2.8% to 4.8%). However, non-native fish species occurred at greater frequencies than salmon in the diets of all four predator species. Using depletion estimation from electrofishing, we were able to generate population densities for Striped Bass and Largemouth Bass in our reaches. Largemouth Bass were evenly distributed throughout all three reaches, at a mean density of approximately 333 (± 195 SE) per km of river. Striped Bass were patchily distributed, ranging from 21 to 1,227 per km. Extrapolating the frequency of salmon detected in stomachs to the predator abundance estimates, we estimate that the population of Largemouth Bass we sampled consumed between 3 and 5 Chinook Salmon per day per 1-km study reach (consumption rate of 0.011 salmon per predator per day), whereas the Striped Bass population consumed between 0 and 24 Chinook Salmon per day (0.019 salmon per predator per day).

KEY WORDS

Predation, non-native species, juvenile salmon, Sacramento–San Joaquin Delta, Striped Bass, Largemouth Bass, Channel Catfish

INTRODUCTION

Understanding predator–prey relationships is essential for understanding the ecology and population dynamics of organisms (Lamberti and Resh 1983; Lindström et al. 1994; Krebs et al. 2001). Predators can dramatically affect prey populations, and have ecosystem-level effects (Estes et al. 2011). Non-native predators can disproportionately affect native prey populations, in part because native prey populations have not evolved behaviors and life-history strategies to minimize their vulnerability to the new predators, often referred to as prey naïveté (Cox and Lima 2006; Salo et al. 2007; Sih et al. 2010). Freshwater ecosystems are particularly sensitive to invasions by non-native predators, which can be attributed to the accentuated naïveté of the prey species from the allopatric insularity of freshwater systems compared to continental terrestrial or marine ecosystems (Cox and Lima 2006). It is particularly problematic for native species when a freshwater ecosystem is subjected to extreme numbers of predator invasions. The Sacramento–San Joaquin Delta (part of California's Central Valley watershed) has more non-native fish species than native species (Brown and Michniuk 2007), and is part of what is considered to be the most invaded estuary in the world, the San Francisco Estuary (Cohen and Carlton 1998).

Central Valley rivers are home to Steelhead, *Oncorhynchus mykiss,* and four distinct runs of Chinook Salmon, *O. tshawytscha*. Before the European settlement of California, these runs were estimated to be some of the largest in North America (Yoshiyama et al. 1998). However, since then, these populations have declined to the point that two of the four Central Valley runs of Chinook Salmon and the only run of Steelhead are listed under the United States Endangered Species Act of 1973 (US Congress 1973). Many anthropogenic stressors that affect different life stages have contributed to these drastic declines, including—but not limited to—loss of spawning and rearing habitat from dams (Yoshiyama et al. 2001), loss of floodplain rearing habitat to diking (Whipple et al. 2012), and reduced survival and spawning success of many life stages as a result of poor water quality, caused, in part, by the water export infrastructure (Baker et al. 1995; Mosser et al. 2013: Martin et al. 2017). However, one poorly understood potential stressor is the predation upon juvenile salmon by non-native fish species.

All anadromous juvenile salmonids in the Central Valley migrate through the Sacramento–San Joaquin Delta—the freshwater portion of the San Francisco Bay Estuary (the estuary)—and, as such, it is at the nexus of predation issues. There is high mortality of juvenile Chinook Salmon in this region as measured by telemetry studies (Perry et al. 2010; Buchanan et al. 2013). These studies assumed that the proximate cause of this mortality was predation. However, the ultimate cause of predation-related mortality may be the habitat and environmental variables that have given predators advantages, disadvantaged prey, or increased the encounter rate between the two. Importantly, the ultimate causes of predation may affect the efficacy of different predator species differently.

To date, most studies investigating the effects of different non-native predator species on ESA-listed fish species in the Central Valley have concentrated on a single predator species: the Striped Bass *Morone saxatilis* (Lindley and Mohr 2003; Nobriga and Feyrer 2008; Sabal et al. 2016). However, Largemouth Bass *Micropterus salmoides* and other predator species have been increasing in numbers (Conrad et al. 2016). Understanding their relative effects on salmonids, and the structure of the Delta food web of which they are a part, can help inform and prioritize management actions that either directly target those particular predator species—or their preferred habitats and conditions—to benefit imperiled fish species. One particular management action actively being considered in the Central Valley is predator removals. Removing top predators from a food web can lead to drastic ecological perturbations (Zavaleta et al. 2001), and therefore requires intensive study before implementation, including investigations into the diets of the predators beyond just the imperiled prey items.

We hypothesize that some non-native fish predators may be having an under-appreciated role in the

predation of native fishes compared to the well-studied Striped Bass. To begin to address this theory, we focused on three questions. First, what are the abundances of the different non-native fish predator species within three study reaches on the lower San Joaquin River? Second, how frequently do these predator species consume native salmonids and other fish prey species? Third, how can we extrapolate these findings to estimate total salmonids consumed per study reach per predator species? Finally, we provide a framework for discerning population-level effects of different predator species on San Joaquin Delta salmonid populations.

METHODS

Study System

Historically, juvenile Central Valley salmon had few native piscine predators. The only significant native piscine predator of salmon is the Sacramento Pikeminnow *Ptychocheilus grandis* (Brown and Moyle 1981). However, since the late 1800s, hundreds of intentional and accidental introductions have occurred. This has led to a suite of new predator species that juvenile salmon have to elude when emigrating to the ocean. These include Striped Bass, Largemouth Bass, Smallmouth Bass *Micropterus dolomieu*, Spotted Bass *Micropterus punctulatus*, White Catfish *Ameiurus catus*, Channel Catfish *Ictalurus punctatus*, Green Sunfish *Lepomis cyanellus*, Warmouth *Lepomis gulosus*, White Crappie *Pomoxis annularis*, and Black Crappie *Pomoxis nigromaculatus* (Grossman 2016).

Our study took place in the lower San Joaquin River, which, along with the Sacramento River, is one of the two main rivers that drain California's Central Valley, and that combined support the largest Chinook Salmon runs in the state. Historically, the San Joaquin River watershed was home to large runs of spring-run and fall-run Chinook Salmon as well as Steelhead. As a result of the widespread construction of dams in the watershed in the mid-20th century, the spring-run were extirpated from the system while fall-run Chinook Salmon and Steelhead returns diminished (Yoshiyama et al. 1998; McEwan 2001; Williams 2006). The few Chinook Salmon and Steelhead that remain in the San Joaquin River watershed return primarily to three tributaries: the Stanislaus, Tuolumne, and Merced rivers. These three rivers flow into the lower stretches of the San Joaquin River, after which the San Joaquin River flows north another 30 river kilometers before joining the Sacramento–San Joaquin Delta, a complex network of tidally influenced freshwater channels. It is in this tidally influenced transitional area that mortality of acoustic-tagged out-migrating juvenile Chinook Salmon is greatest (Buchanan et al. 2013), and where we conducted this study during the spring of 2014 and 2015.

We chose these three study reaches as representative of the overall lower San Joaquin River habitat, and as part of the primary migratory corridor of San Joaquin River anadromous salmonids. Juvenile anadromous salmonid that originate from the San Joaquin River watershed would either have to pass through these three reaches during their out-migration, or they could use an alternate route through Old River (Figure 1). During our study periods, a temporary barrier was in place to prevent fish from entering the Old River route, effectively forcing all fish to take the San Joaquin River and transit through our study reaches. The three reaches consisted of 1-km-long river segments and were approximately equidistant. The distance between the furthest upstream and downstream reach spanned 16 kilometers. We named these reaches R1, R2, and R3 in the order from most upstream to most downstream. We chose the R1 site as a result of management concerns about predation on juvenile Chinook Salmon at the head of Old River, whereas we chose R2 and R3 randomly so as to be equidistant from each other and within the bounds of the Delta portion of the lower San Joaquin River before it enters the Stockton Deepwater Shipping Channel (near Stockton, California). All three of these reaches are subject to tidal fluctuations but were upstream of the brackish portions of the estuary. As is typical of the Delta, the river channel in these three reaches is highly modified with constricting steeply sloped riprap levees on both sides, leaving little room for shallow water habitat. The little shallow water habitat that does exist in the 2- to 3-m littoral margin of the river often has long continuous beds of submerged aquatic vegetation, mainly the invasive Brazilian waterweed (*Egeria densa*). Largemouth bass have been known to associate with such waterweed beds in the Delta (Conrad et al. 2016). Overall, little

https://doi.org/10.15447/sfews.2018v16iss4art3

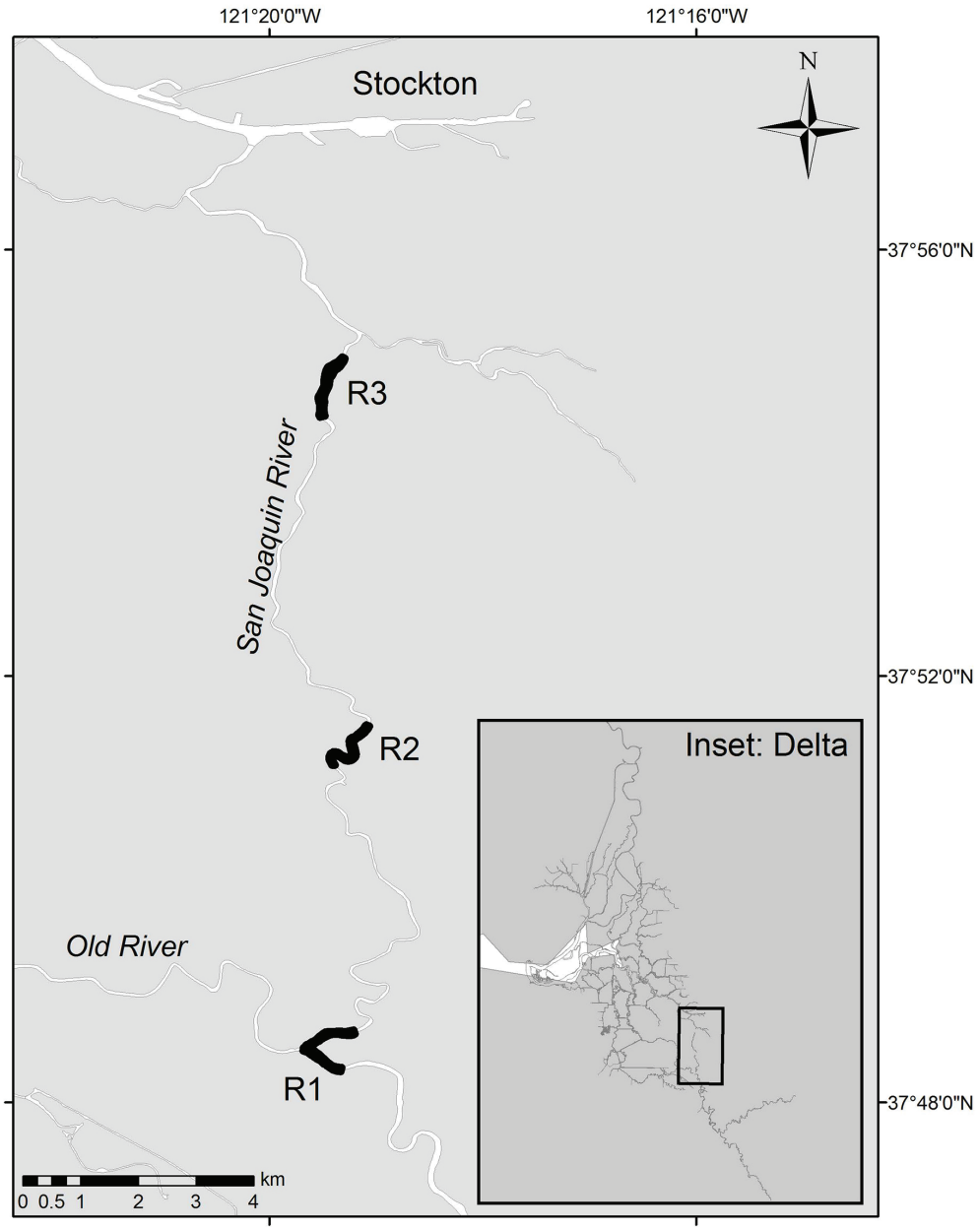

Figure 1 A map of the study region on the lower San Joaquin River, bordered by Mossdale, California, to the south and Stockton, California, to the north. The three study reaches are depicted in bold river outline: R1, R2, and R3.

structure existed in these three reaches, with almost no large woody debris or man-made structures, and fine sediment throughout the river bottom. Besides the very steep littoral margins of the river, the reaches were largely uniform in depth, as is typical for the larger region, averaging approximately 3.8 m deep, with a few deeper scour holes that ranged from 7 to 11 m in depth.

Data Collection

To estimate predator density for both years of the study, we used three Smith–Root boat electrofishers to collect predators within these reaches during consecutive passes on a single day. We used three electrofishing boats simultaneously that worked in tandem from one end of a reach to the other, with one boat driving along each bank of the river, and one boat driving down the central channel of the

river, covering the entire cross-section of the river for the length of the 1-km-long reaches. These three boats would shock the entire reach length repeatedly for three to five successive "passes." During each pass, all fish considered predators were netted, counted, weighed, measured, and kept in aquaria until all electrofishing passes for that day were complete. During each pass, the total time-period that an electrical current was applied to the water was tracked, which allowed us to standardize predator collection per pass for effort. These successive passes allowed us to use multi-pass depletion analysis techniques to estimate abundances (Lockwood and Schneider 2000).

Electrofishing efforts were scheduled to occur during the historical peak out-migration of sub-yearling fall-run Chinook Salmon through these reaches. This peak of out-migration has typically occurred from late April to early May, as reported in the Mossdale Kodiak trawl catch data sets collected near the R1 site by the U.S. Fish and Wildlife Service (USFWS) and the California Department of Fish and Wildlife (CDFW) as part of the Delta Juvenile Fish Monitoring Program from 1994 to 2011 (available from *https://www.fws.gov/lodi/juvenile_fish_monitoring_program/jfmp_index.htm*). Specifically, 2014 electrofishing efforts occurred on May 6, May 8, and May 12. In 2015, they occurred on April 29, April 28, and April 27 in R1, R2, and R3, respectively.

For the purposes of this study, we captured any fish known to be a salmonid predator. However, because all predator species of interest are non-piscivorous during early life stages (Moyle 2002), we set minimum size thresholds for individuals to be considered salmon predators. For the larger-gaped predators, i.e., Striped Bass and Largemouth Bass, this threshold was 150 mm, and for the remaining smaller-gaped predators, namely ictalurids and non-bass centrarchids, the threshold was 200 mm, based on Feyrer et al. (2003) and unpublished predation studies led by the authors in which predators were collected using out-migrating fall-run Chinook Salmon as bait.

Few studies have found direct evidence of predation on juvenile salmon in the Delta (Grossman et al. 2013). Part of the problem is the relatively low ratio of juvenile salmonids to predators in the Delta; they are proverbial needles in the haystack (numerically < 1% of the fish community (Brown and Michniuk 2007). This means that finding salmonids in the diets of predators requires large sample sizes. Most studies' methods consist of visually identifying partially or completely digested stomach contents, which can be a slow and difficult task. Furthermore, fish prey species, especially in the larval or early life stages, become visually unidentifiable in predator stomachs in a very short time-frame (Legler et al. 2010). Molecular laboratory techniques have recently been developed that have shorter processing times and can provide definitive identification of stomach contents even at trace levels. Species-specific genetic analysis (i.e., "genetic barcoding") using highly sensitive, quantitative, polymerase chain reaction (qPCR) has been used to identify the presence of Chinook Salmon, as well as other native species of concern, within a given predator's stomach (Brandl et al. 2015, 2016). This technique does not provide information on the percent of total or total amount of salmonid parts found in stomachs, but can determine over a short-term time period if an individual predator has eaten a salmonid.

For this diet analysis technique, we euthanized a random subset of the predators collected during multi-pass depletion electrofishing efforts from all reaches in both years of the study ($n = 582$). We collected the four most common predator species that we captured in the lower San Joaquin River, all of which were non-native: Largemouth Bass (LMB), Striped Bass (STB), White Catfish (WHC), and Channel Catfish (CHC). We euthanized and processed fish in a sterile environment on a boat designed for processing to prevent cross-contamination of samples. Processing consisted of injecting predator stomachs with 10 mL of 100% ethanol using 33-cm-long disposable pipettes inserted through the fish's esophagus, putting the fish into an individual heavy-duty plastic bag, and then freezing the specimen whole. Between each fish, a new pipette was used and the fish handler's gloves were changed. We removed stomachs and emptied their contents in a sterile laboratory setting.

Stomach content samples were incubated overnight at 56 °C in a proteinase K-buffered ATL (animal tissue lysis) solution. After overnight digestion, DNA was extracted from each solution using QIAGEN

https://doi.org/10.15447/sfews.2018v16iss4art3

DNeasy Blood and Tissue Kit affinity columns following manufacturer's protocols. Extracted DNA from each diet sample was used as a template for each laboratory reaction, with species-specific molecular assays for twelve species (including six special-status species) applied to each sample (Table 1). The molecular assays used for this study were developed previously (Baerwald et al. 2012; Brandl et al. 2015). The assays took the form of a sequence-specific oligonucleotide hybridization (i.e., 5′ exonuclease TaqMan™) interrogated using qPCR. This procedure uses conventional forward and reverse polymerase chain reaction (PCR) primers to amplify a specific region of DNA, but incorporates a fluorescently labeled probe that hybridizes (i.e., targets) to the conserved sequence diagnostic for each species. For each template, we performed qPCR using all assays simultaneously on a 192.24 Gene Expression Integrated Fluidic Circuit (Fluidigm) and BioMark System (Fluidigm) following manufacturer's protocols. We analyzed fluorescent output using the Fluidigm Real-Time PCR analysis v4.0.1 software (*https://www.fluidigm.com*). We did not validate diet contents by direct visual observation because most diet contents are difficult to identify when in an advanced state of digestion.

Data Analysis

We used the multiple pass depletion methods as outlined in Lockwood and Schneider (2000) to estimate abundance and 95% confidence intervals for the different predator species and capture probability for our electrofishing efforts. This method assumes equal effort for each successive pass, so fish counts were standardized by the electrofishing duration. Since these abundance estimates were for 1-km reaches, they could be reported as predator densities per kilometer.

Prey frequency of occurrence per predator species were pooled across study reaches to increase sample size; in the context of the Sacramento–San Joaquin Delta, our three study sites were relatively close spatially, and morphologically similar. For each predator species, we estimated prey frequency for each year individually and both years combined. To calculate 95% confidence interval limits for prey frequencies, we used the normal approximation to the binomial distribution (Zar 2010). Because of the presence of an individual's own DNA in the diet sample, LMB diets would always test positive for LMB DNA, and STB diets would always test positive for STB DNA. Therefore, using this method, it was impossible to determine if cannibalism in both of those predator species occurred. To determine differences in prey species occurrence per predator species, we used a four-sample chi-square test for equality of proportions per prey species, followed by pairwise two-sample tests, if significant (p-value <0.05). Finally, to determine annual differences in the frequency of salmonids in the diets of the four predator species, we used a two-sample chi-square test for equality of proportions.

We multiplied the predator abundance estimates with the prey proportions (and associated confidence

Table 1 List of the 4 predator species and 12 different prey species tested for in predator diets

Predator species	State and federal special-status prey species	Other prey species
Striped Bass (*Morone saxatilis*; "STB")	Chinook Salmon (*Oncorhynchus tshawytscha*; "CHK")	Largemouth Bass (*Micropterus salmoides*; "LMB")
Largemouth Bass (*Micropterus salmoides*; "LMB")	Green Sturgeon (*Acipenser medirostris*; "GS")	Sacramento Pikeminnow (*Ptychocheilus grandis*; "SASQ")
Channel Catfish (*Ictalurus punctatus*; "CHC")	Steelhead (*Oncorhynchus mykiss*; "RBT")	Striped Bass (*Morone saxatilis*; "STB")
White Catfish (*Ameiurus catus*, "WHC")	Delta Smelt (*Hypomesus transpacificus*; "DSM")	White Sturgeon (*Acipenser transmontanus*; "WST")
	Longfin Smelt (*Spirinchus thaleichthys*; "LFS")	Threadfin Shad (*Dorosoma petenense*; "TFS")
	Sacramento Splittail (*Pogonichthys macrolepidotus*; "SPT")	Mississippi Silverside (*Menidia beryllina*; "MSS")

interval limits) from the qPCR analysis to estimate the total amount of juvenile Chinook Salmon eaten by all STB and LMB within each reach (as well as minimum and maximum amount eaten). We also multiplied the confidence interval limits of abundance estimates with the diet proportions (and confidence intervals) of the qPCR results to get an estimate and approximate limits of the total amount of Chinook Salmon eaten at these abundances. We did not perform this analysis for WHC or CHC because of the weak confidence we had in their abundance estimates.

The qPCR assay can detect the presence of prey items over a window of detectability, which may differ, depending on the predator and prey species of interest. The most relevant estimate for detectability of prey in a predator diet using qPCR is from a laboratory experiment by Brandl et al. (2016), which found that Chinook Salmon prey were 100% detectable in the diets of sub-adult STB (180 to 250 mm fork length) for up to 36 hours, after which detectability declined to near zero at 84 hours. Taking the midpoint of this decline in detectability, 60 hours or 2.5 days, we divided all estimates of Chinook Salmon eaten by 2.5, approximately bringing estimates to a per-day basis. We also used this same detectability time-frame for LMB, for lack of studies that estimated this time-frame for LMB or a similar species.

Assumptions and Limitations

One of the underlying requirements of multi-pass depletion analyses is a closed population, where no fish can enter or leave the reach during electrofishing. However, block nets on such a large navigable waterway were logistically unrealistic, and therefore we were unable to keep predators from coming into or leaving the reach during our sampling efforts. As a result, we recognize that abundance estimates may be less accurate, in particular for the highly mobile STB of the San Joaquin River (Smith et al. 2017). Furthermore, differing environmental conditions (such as water temperature or water depth) between sites and years can affect our ability to catch predators and therefore potentially bias our abundance estimates; caution should therefore be used in drawing conclusions from differences in abundances between reaches or years.

One important assumption was necessary to pursue this analysis: the qPCR assay only provides presence/absence of a prey species, but not total individuals of that prey species found in a predator diet. Given that this analysis focused on out-migrating juvenile Chinook Salmon, and given that they are relatively rare in these reaches compared to other prey species (numerically, only 0.3% of prey-sized fish caught during electrofishing were Chinook Salmon), we assumed that if a diet tested positive for a Chinook Salmon, it contained exactly one individual. Given this assumption, all estimates of total Chinook Salmon eaten are likely conservative, because some predator diets could have contained more than one individual.

An important consideration for this analysis is that water temperatures will influence gut evacuation rates, and ultimately detectability time-frames of prey in predator diets using qPCR techniques. Laboratory experiments performed by Brandl et al. (2016) estimated 36- to 84-hour detectability at a constant water temperature of 18 °C. If water temperatures leading up to the collection of a predator diet were significantly warmer (or cooler) than 18 °C, this would likely shorten the detectability time-frame and therefore bias our Chinook Salmon consumption estimates low (or high). Because prey size and water temperature can influence the rate of consumption, we calculated these for our study reaches and compared them to the values reported in the Brandl et al. study. We collected hourly water temperature recordings from nearby water quality gauges to determine how close temperatures were to the 18 °C used by Brandl et al. (2016). Water temperature data were acquired from the California Department of Water Resources – California Data Exchange Center's temperature gauges (station identification codes SJD, BDT, and SJG). We collected the mean hourly water temperature from the 72 hours preceding the collection of every predator diet. Overall, the average of all individual 72-hour mean water temperatures was 18.0 °C, ranging from 16.7 to 20.5 °C, with 69% of all diets collected having a mean 72-hour temperature experienced within 1.5 degrees of 18 °C. To determine how similar prey size (Chinook Salmon) was in our reaches as compared to the detectability

https://doi.org/10.15447/sfews.2018v16iss4art3

experiment by Brandl et al. (48- to 96-mm fork length in that study), we used the fork length data for 471 juvenile Chinook Salmon captured in the nearby Mossdale Kodiak trawls in the week that preceded the multi-pass electrofishing events in 2014 and 2015. Mean and median Chinook Salmon fork length were 84 and 83 mm, respectively, and values ranged from 64 to 113 mm (with one 165-mm outlier). Overall, water temperatures and prey size in our study closely mimicked those in the Brandl et al. study, supporting the use of the detectability time-frames reported in that study.

The estimates provided by the coupling of the diet proportions with predator abundance estimates are approximate, and some potential sources of bias are worth discussing. This study was scheduled to occur as close as possible to the peak out-migration time of Chinook Salmon. From Chinook Salmon catch per unit effort (CPUE) data from a daily Kodiak trawl that occurred 1 km upstream of our most upstream reach, we know that we were successful in scheduling our multi-pass electrofishing efforts during peak out-migration (Figure 2; data from *https://www.fws.gov/lodi/juvenile_fish_monitoring_program/jfmp_index.htm*). This suggests that the frequency of Chinook Salmon in predator diets that we collected is likely near the maximum for those seasons. However, the 2014 and 2015 water years were considered severe drought years in California, which was likely the cause of some of the lowest relative annual abundance estimates of Chinook salmon for those years from the nearby Kodiak trawl, and also led the only salmon hatchery in the San Joaquin watershed to truck their Chinook Salmon around the lower San Joaquin River and release them downstream of our study reaches (Miller et al. 2017). Therefore, whereas these diet frequencies and the associated reach-specific extrapolations of total Chinook Salmon consumed probably represent estimates that bias high within those seasons, they likely represent estimates that bias low when evaluating a multi-year time-frame. Another important consequence of the trucking of hatchery salmon on the interpretation of our results is that this suggests that our estimates of Chinook Salmon and Steelhead occurrence in predator diets—as well as the resulting estimates of Chinook Salmon consumption by LMB and STB—are largely for natural-origin salmonids.

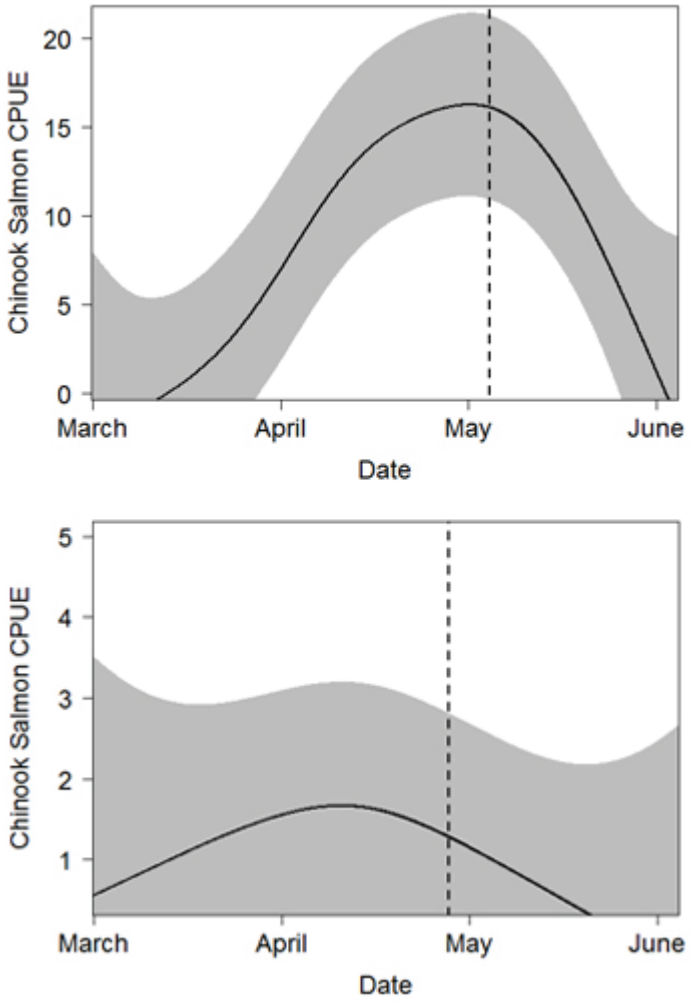

Figure 2 Two plots representing the predictions from a generalized additive model (GAM) for juvenile Chinook Salmon catch per unit effort (CPUE) from empirical data collected from the Mossdale Kodiak Trawl survey just upstream of R1 reach. CPUE is the number of individuals captured per 100,000 m^3 of estimated water volume trawled, pooled by week of sampling (14 weeks total). The *x-axis* represents the date, and the *y-axis* represents the predicted juvenile salmonid CPUE from the GAM. The *top* plot are the predictions for 2014, the *bottom* for 2015. The *solid line* represented the prediction, and the *grey area* represents 95% confidence intervals. The *vertical dotted line* represents the time at which multi-pass electrofishing occurred in that year, during which all predator diets were collected.

RESULTS

In the 2 years of the study, we captured 3,050 potential juvenile salmon predators during multi-pass electrofishing efforts from the three study reaches. Largemouth Bass (42%) and Striped Bass (40%) were by far the most commonly captured predators in the study reaches, followed by White Catfish, Channel Catfish, and finally various other Centrarchid species (Figure 3). No native salmonid predators were captured during electrofishing efforts. Catch composition of the four main predator species remained similar between years (Table 2). During a subset of the electrofishing efforts, we tallied the catches by location within cross-sectional regions of the river. This revealed that an order of magnitude more predators were captured along the littoral habitat (approximately within 5 meters of the river bank) than in the channel habitat (everything outside of an approximate 5-m margin along the river bank; 1,120 versus 109 predators, respectively), although this large discrepancy is likely in part from electrofishing sampling bias. The catch composition between these two habitats also varied; LMB dominated the littoral habitat, and STB dominated the channel habitat (Figure 4).

We estimated abundances for STB and LMB from multi-pass depletion electrofishing counts in all three reaches in both years (Table 3). Abundances suggest that STB were patchily distributed, whereas LMB were more evenly distributed (Figure 5). Estimated abundance for STB varied widely per reach. In 2014, reach R1 was estimated to have 530.8 (±52.1 SD), R2 had 65.3 (±4.1), and R3 had 118.4 (±45.5). In 2015, reach R1 had 1,226.5 (±137.9 SD), R2 had 21.1 (±1.3), and R3 had 35.3 (±2.6) (Figure 5). LMB density was more consistent. In 2014, reach R1 was estimated to have 275.2 (±147.0 SD), R2 had 344.6 (±55.1), and R3 had 297.3 (±42.3). In 2015, reach R1 had 319.7 (±12.8 SD), reach R2 had 243.4 (±13.7), and R3 had 433.6 (±76.0).

In total, we collected 582 predator diets, comprising 253 LMB diets, 186 STB diets, 107 WHC diets, and 36 CHC diets. Of these, we collected 399 in 2014, and 183 in 2015. Diets were pooled across reaches to increase sample size, comprising 183 diets from R1, 182 from R2, and 217 from R3. Mean fork lengths of the predator species collected were 280 mm (ranging from 160–530 mm) for LMB, 277 mm (154–649 mm) for STB, 262 mm (200–370 mm) for WHC, and 406 mm (208–552 mm) for CHC (Figure 6).

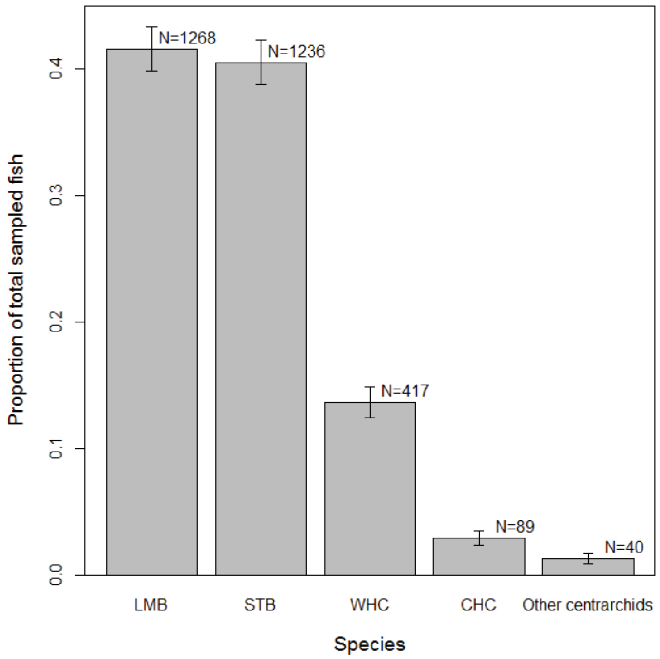

Figure 3 A histogram depicting the species composition during the multi-pass boat electrofishing efforts in 2014 and 2015, with 95% confidence intervals. In total, 3,050 predators were captured.

Table 2 Electrofishing total catch percent proportions by year and by predator species

	STB	LMB	WHC	CHC
Proportion of 2014 catch (%)	43.6	38.8	13.2	4.4
Proportion of 2015 catch (%)	42.3	46.7	9.4	1.6

The results from the qPCR analysis indicated that some prey species were absent or occurred very infrequently in predator diets: Green Sturgeon (0 occurrences), Longfin Smelt (0), White Sturgeon (1), and Sacramento Pikeminnow (2). For the remaining prey items, the overall proportion of diets that contained the different prey items varied by predator species; notably, CHC had the highest proportion of diets that contained prey for every prey species tested (besides the four infrequent prey species listed above). However, the ranking of different prey items that occur in diets was consistent among all four predator species, such that LMB was found in the highest proportion of diets for all species, followed by STB,

https://doi.org/10.15447/sfews.2018v16iss4art3

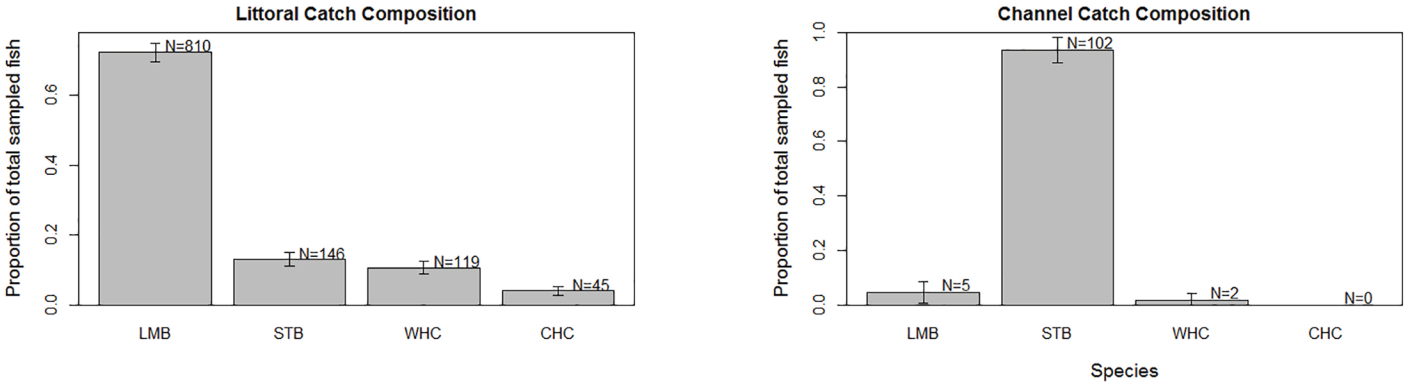

Figure 4 Two histograms depicting the predator species composition for both the littoral and channel zones during supplemental electrofishing efforts, with 95% confidence intervals.

Table 3 Total captures per electrofishing pass of STB and LMB during 1-day multi-pass boat electrofishing, organized per reach and per year. In 2014, electrofishing events consisted of three or four passes; in 2015, electrofishing events consisted of five passes.

Site	Year	Pass 1	Pass 2	Pass 3	Pass 4	Pass 5
			STB			
R1	2014	144	92	64		
R2	2014	15	16	7	4	
R3	2014	10	16	20	5	
R1	2015	173	171	71	83	43
R2	2015	8	5	1	4	0
R3	2015	8	13	4	3	2

Site	Year	Pass 1	Pass 2	Pass 3	Pass 4	Pass 5
			LMB			
R1	2014	20	31	19		
R2	2014	48	31	38	35	
R3	2014	69	48	34	26	
R1	2015	106	62	45	22	8
R2	2015	75	41	33	16	16
R3	2015	39	73	60	13	33

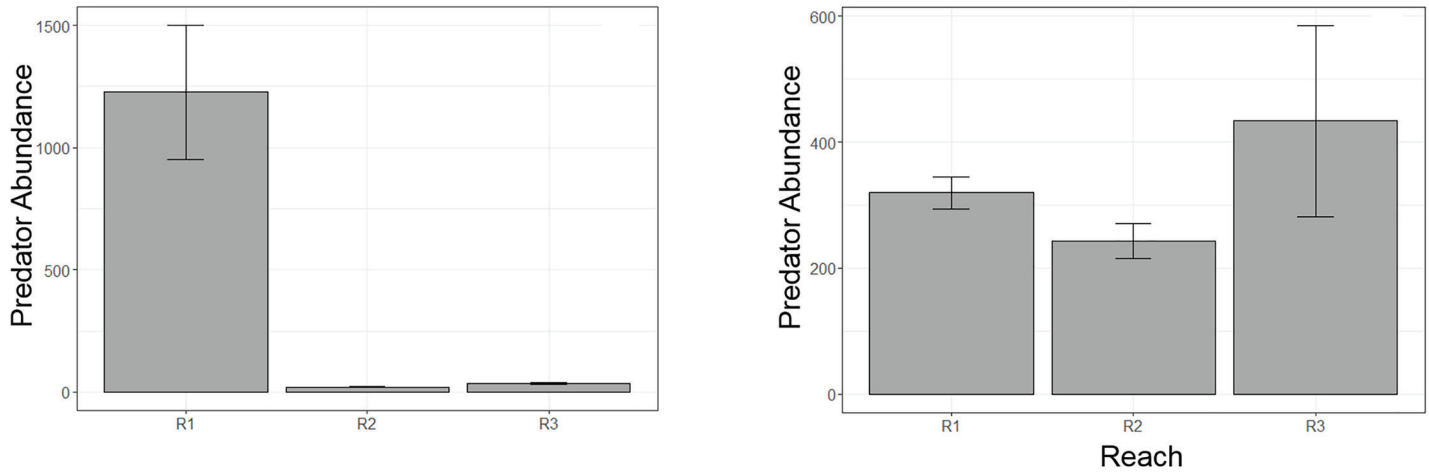

Figure 5 Bar plots representing the predator abundance estimates for STB (*left figure*) and LMB (*right figure*) for all three study reaches for 2015. Abundance estimates in 2014 (not shown) are similar in magnitude and in relation to each other. Abundances were estimated using multi-pass depletion electrofishing efforts. *Error bars* represent 95% confidence intervals.

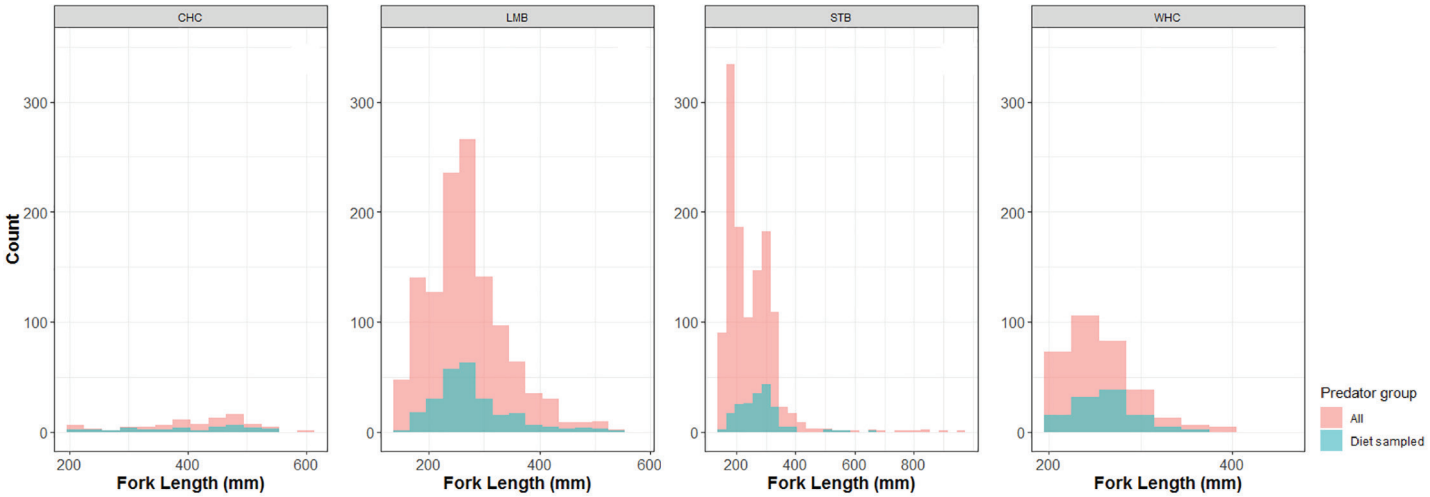

Figure 6 Histograms of fork lengths (mm) by predator species, both for the diet sampled predators (in *blue*), as well as all predators collected during multi-pass depletion electrofishing efforts (in *red*). Left-most plot is for CHC, left-middle plot is for LMB, right-middle plot is for STB, and right-most plot is for WHC. Length data is pooled by year and reach. Histogram bin sizes are 30 mm.

MSS, CHK, and SPT, in approximately that order for all predators (Figure 7). Finally, DSM, RBT, and TFS were found in low frequencies in all four predator species (see Table 1 for species codes). We performed a four-sample chi-square test for equality of proportions for each predator species in combination with all prey species with at least 10 occurrences in all diets combined. Prey species that had unequal proportions in predator diets (p-value <0.01) included SPT (pairwise comparisons indicate a significantly higher occurrence of SPT in CHC versus LMB diets), CHK (pairwise comparisons indicate CHC diets had significantly higher occurrence of CHK than the three other predators), and STB (pairwise comparisons indicate a significantly higher occurrence of STB in CHC versus LMB diets).

Of particular interest in this study is the contribution of salmonids to the diets of different predator species: we found that 27.7% of CHC diets tested positive for Chinook Salmon, followed by 4.8% of STB diets, 4.7% of WHC diets, and 2.8% of LMB diets. For Steelhead, 5.5% of CHC diets and 2.2% of STB diets had Steelhead; no WHC or LMB diets tested positive for Steelhead. Combined, salmonids were present in 33.3% of CHC diets, followed by 7.0% of STB diets, 4.7% of WHC diets, and 2.8% of LMB diets (Figure 8). It should be noted that these diet proportions combined both the 2014 and 2015 results; when looking at the 2 years separately, a two-sample chi-square test for equality of proportions found no evidence for significantly different diet proportions containing salmonids between years for LMB ($x^2=0.26$, df $=1$, p-value $=0.61$), STB ($x^2=3.34$, df $=1$, p-value $=0.07$), and WHC ($x^2=0.05$, df $=1$, p-value $=0.82$). Only CHC had significantly different diet proportions between the 2 years ($x^2=5.06$, df $=1$, p-value $=0.02$): in 2014, the proportion of CHC diets containing salmonids was 45.8% (95% confidence intervals 25.6% to 67.2%); in 2015, it was 8.3% (0.2% to 38.5%).

Based on the frequency of Chinook Salmon detected in stomachs and the predator abundance estimates, our results suggest that all LMB consumed between 3 and 5 juvenile Chinook Salmon per day per 1-km study reach (consumption rate of 0.011 salmon per LMB per day), whereas all STB consumed between 0 and 24 juvenile Chinook Salmon per day per 1-km study reach (Figure 9; 0.019 salmon per STB per day). Overall, estimates of salmon consumed by STB and LMB were similar between reach/year combinations, with the exception of the STB in the R1 reach. In this reach, STB were estimated to consume 10 to 24 juvenile Chinook Salmon depending on the year, primarily because of the large numbers of STB estimated to be in that reach during multi-pass depletion efforts.

https://doi.org/10.15447/sfews.2018v16iss4art3

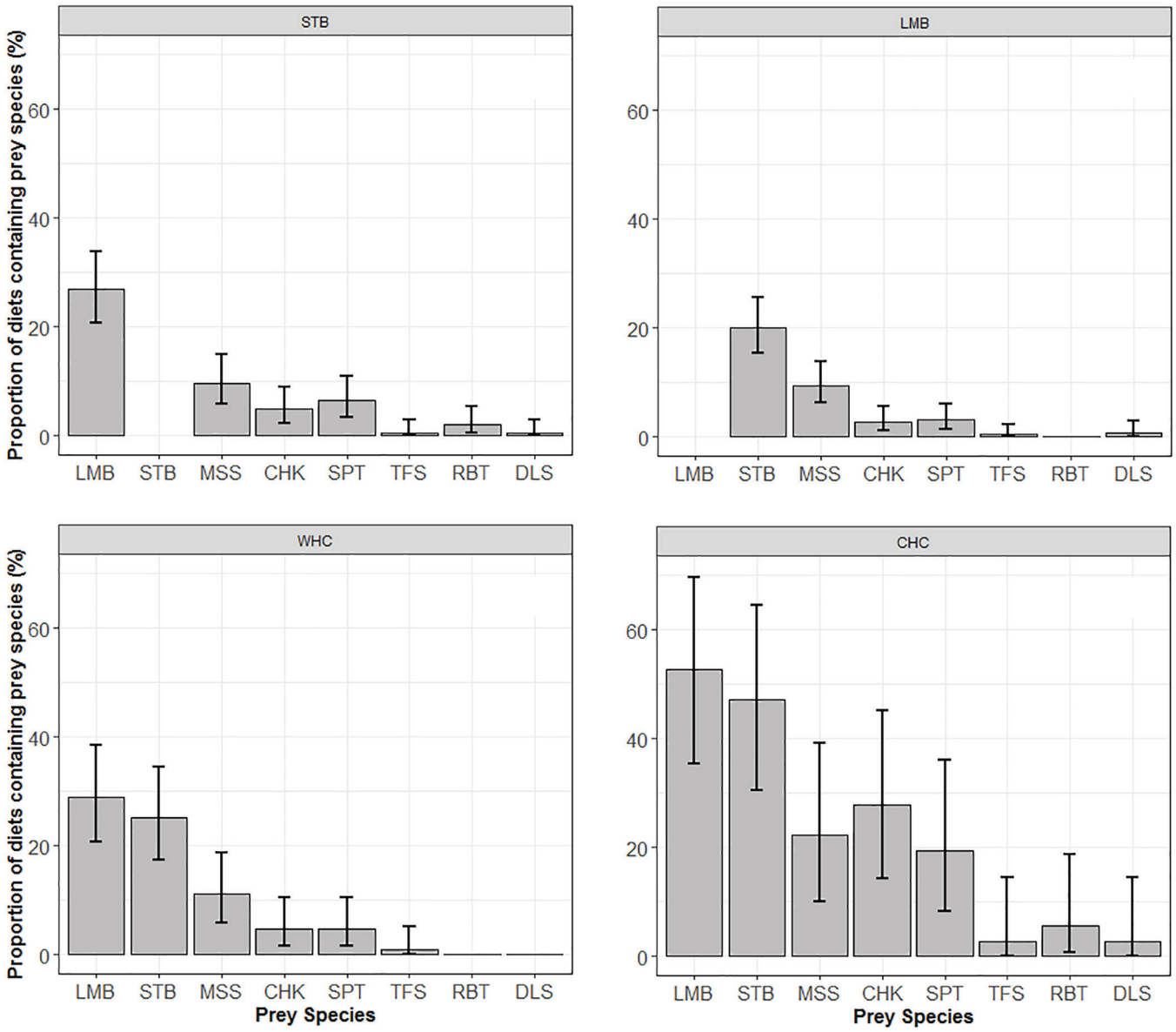

Figure 7 Bar plots representing the percent proportion of diets that contained different prey species. Each of the four plots depicts the results for each of the four predator species; *top-left* is for STB, *top-right* is for LMB, *bottom-right* is for CHC and *bottom-left* is for WHC. In each plot, the *x-axis* has the different prey items listed, with their respective bars depicting the proportion of diets they are found in for that predator. *Error bars* represent 95% confidence intervals. Because of the sensitivity of the qPCR analysis, LMB diets would always test positive for LMB DNA, and STB diets would always test positive for STB DNA, and therefore these bars have been removed from the bar plots.

DISCUSSION

In the Sacramento–San Joaquin Delta, some studies have focused on how Striped Bass have affected salmonid populations (Lindley and Mohr 2003; Sabal et al. 2016), but little attention has gone toward how other predators and prey species affect salmonid predation, whether through direct or indirect pathways. The Delta today is vastly different from pre-development times, and is now thought to have shifted toward a novel ecosystem that favors non-native, warm-water fish species from eastern North America (Brown and Michniuk 2007; Conrad et al. 2016; Mahardja et al. 2017). In fact, this study captured no native salmonid predators during multi-year boat electrofishing surveys and very

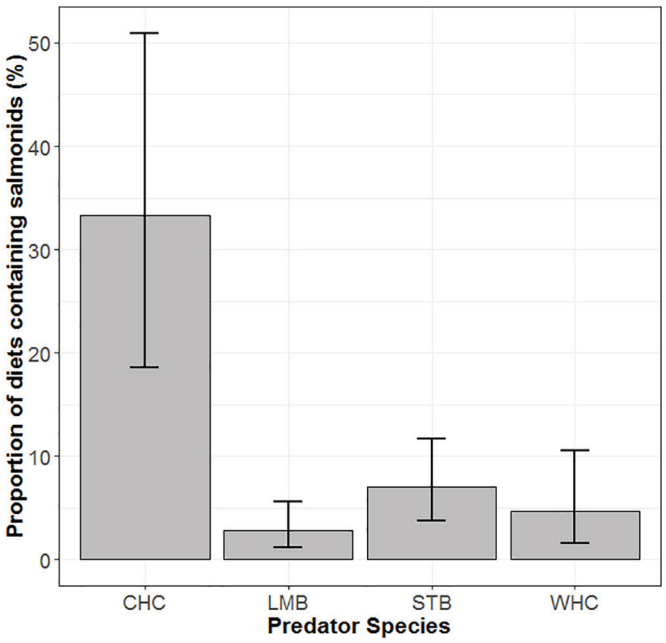

Figure 8 Bar plots representing the percent proportion of predator diets containing salmonids (Chinook Salmon + Steelhead), for both years combined. The four predator species tested are on the *x-axis*. *Error bars* represent 95% confidence intervals.

few native fish. Our study found that although all predator species tested were found to eat salmonids, the predators tested positive more frequently for non-native piscivorous species. They also tested positive for many non-native prey species at higher frequencies, such as the Mississippi Silverside and the Signal Crayfish *Pacifastacus leniusculus* (crayfish were incidentally visually identified in many diets, but not tested for with DNA barcoding). Finally, the effects of different predator species on salmonids seem to differ greatly, as suggested by our finding that CHC diets tested positive for salmonids much more frequently than other predator diets.

This study was successfully able to estimate the STB and LMB population within three 1-km-long reaches in the lower San Joaquin River, a habitat representative of much of the Sacramento–San Joaquin Delta. Largemouth Bass were evenly distributed throughout all three reaches, and were largely found along the littoral margins of the river. Reciprocally, we found STB to be either practically non-existent in our reaches at the time of our electrofishing surveys, or present in large numbers (comprising mostly sub-adult and small adult size-classes), and found in both the littoral and channel portions of the river. This suggests that STB in these size-classes are mostly found in roving aggregations, and whether or not they are found in a study reach during the time of a survey is highly variable. This is consistent with our understanding that STB are highly mobile, migratory, and aggregating fish as sub-adults or small adults (Mather et al. 2010). Overall, these species-specific movement conclusions are further reinforced by the recapture of predators tagged with passive integrated transponder tags (PIT tags) as part of an associated study in the same study reaches (Michel et al., forthcoming). Of the predators PIT tagged during the 2014 multi-pass electrofishing efforts, we recaptured only 0.7% of PIT-tagged STB compared to 8.2% for LMB during 2015 electrofishing efforts.

Abundance estimates for the two catfish species were not available because of low catches. It is difficult to determine if these low catches result from relatively low densities, or sampling bias, but a few key lines of evidence point to the latter hypothesis. First, boat-based electrofishing is known to sample the upper water column most effectively (Bayley and Austen 2002), and catfish are known to be bottom oriented (Moyle 2002). Furthermore, electrofishing studies have shown that, all else being equal, ictalurids are the hardest to capture of the major warm-water North American fish species (Bayley and Austen 2002), likely because of their atypical reaction to electrical currents compared to other fish species (Corcoran 1979). A fish assemblage study in the lower San Joaquin River in 1993 and 1994 used boat electrofishing, gill nets, and hoop nets to assess species composition, and found that although boat electrofishing did capture some catfishes (WHC was the third most commonly caught fish species; CHC was eleventh out of 30 species), ictalurids were the most commonly caught fish for both of the other sampling methods (for gill net, WHC was the first most common, CHC the fifth; for hoop net, WHC was the first, and CHC the second; Feyrer and Healey 2002). This suggests a need for further study of the abundance and distribution of catfish populations in the Delta.

https://doi.org/10.15447/sfews.2018v16iss4art3

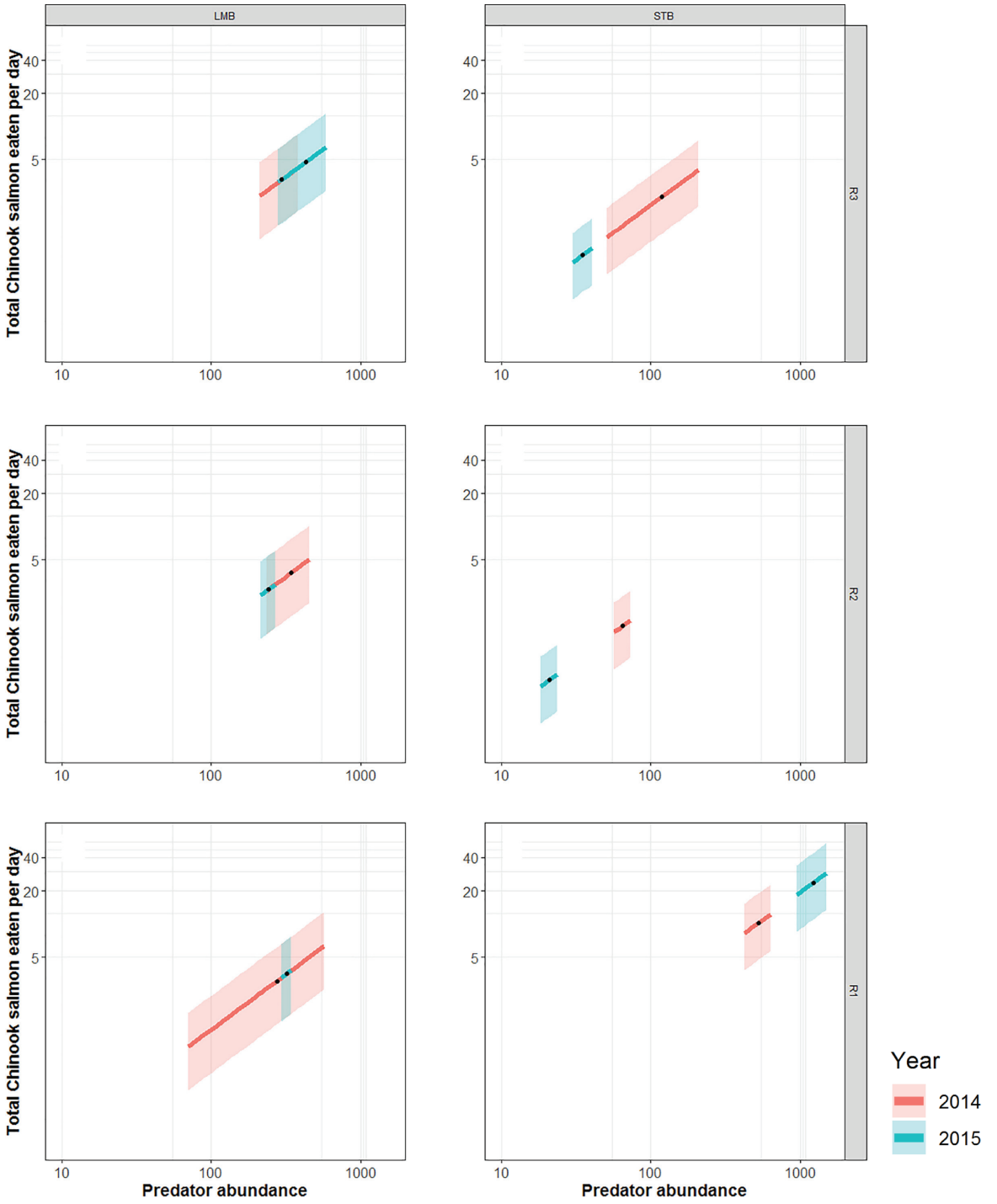

Figure 9 Six plots representing the total juvenile Chinook Salmon predicted to be eaten for each predator (LMB and STB) by reach (R1, R2, R3) combination, per day. Each plot contains an estimate for each year of the study, with the 2014 in red and the 2015 estimate in *blue*. The *black points* represent the best estimate of salmon eaten in that year. The *x-axis* represents the total salmon estimated to be in that reach, with the range of the semi-transparent colored area in the horizontal orientation representing the estimated predators present from the lower to the upper 95% confidence interval. The *y-axis* represents total salmon estimated to have been eaten by the predator in question in that reach, with the range of the semi-transparent colored area in the vertical orientation representing the total salmon eaten from the lower to the upper 95% confidence interval. Both axes are on a log base 10 scale.

Our study found low levels of salmonids appearing in predator diets (2.8% to 7% of diets tested) with the exception of CHC diets. Other studies throughout the Delta have found similarly low frequencies of salmonids in predator diets, with typically less than 5% of STB diets containing salmonids, even during peak out-migration and in regions with higher densities of salmonids (Stevens 1966; Thomas 1967; Nobriga 2007). Only in the rare exception of when a migratory corridor becomes spatially constricted do salmonids become a major component of STB diets in the Delta (such as with fish ladders; Sabal et al. 2016). This does not discount the potential effects of predation on salmonid populations; the size of the different predator populations in the Central Valley are largely unknown, and with 5% or less of the fish predators consuming salmon on a near-daily basis, predators could still be responsible for significant declines in the salmonid populations.

One unanticipated result from this study is that Channel Catfish diets had the highest frequency of occurrence of all the most commonly occurring prey items than for all other tested predators, including a higher proportion of diets containing Chinook Salmon or Steelhead. We are not aware of any other published literature that describes CHC predation on salmonids in California's Central Valley (see review by Grossman [2016]). If these results are accurate, CHC could be a previously unknown but significant source of salmonid mortality in the Delta. However, some caveats are worth mentioning. Namely, CHC are known to be both detritivorous and piscivorous (Moyle 2002). It is possible that the high proportion of CHC diets containing salmonids results from the consumption of salmonid remains (although WHC are also known detritivores and have a lower proportion of diets that contain salmonids). Another potential reason why prey items appeared more frequently in CHC diets than in other predator diets is the detectability time-frames for prey items in CHC diets compared to other predators using qPCR methods. We know that the half-life of Chinook Salmon detectability in STB diets is 66.2 hours (Brandl et al. 2016), but this information is not available for the other three predators. If for any reason CHC were to have significantly longer detectability time-frames, this could have caused the increased frequency of prey items in CHC diets as seen in this study. This suggests that for future studies similar to this one, paired prey detectability laboratory experiments are critical for the correct interpretation of field results. However, the CHC's propensity for piscivory should not be doubted, as many studies indicate that CHC are piscivorous, especially at larger sizes. One particularly relevant study showed that CHC was one of the most important predators of juvenile salmonids in the John Day Reservoir on the Columbia River, with 19% of the CHC diets sampled containing salmonids (Poe et al. 1991). Another relevant study showed that CHC in the Sacramento–San Joaquin Delta are piscivorous, with 13.3% of sampled CHC over 20 cm having unidentified fish in their diets (Turner 1966). Furthermore, our study was performed in tandem with a Chinook Salmon predation study in the lower San Joaquin River in which live juvenile salmon were tethered in front of cameras to identify the predator species for each predation event (J. Smith et al., forthcoming). During this study, video evidence of CHC eating live salmon was collected.

By coupling the diet analysis with predator abundance estimates, we were able to extrapolate to larger scales in an effort to estimate reach-level effects. We did not attempt to extrapolate these results beyond the scale of the three 1-km study reaches, but given that these three reaches were typical for the lower San Joaquin River, the findings presented here may represent that larger region. Population sizes being equal, we would predict STB to have a larger effect on salmon since they appear more frequently in STB diets than in LMB diets. However, all evidence suggests that the LMB population is quite large and densely distributed throughout the lower San Joaquin River, and even if the per-individual effect of LMB is smaller than STB, the population-level effect of LMB may be comparable if not larger than STB in this region. Another important finding in this study is the approximate habitat segregation between the LMB and STB, notably between the littoral margins and the channel of the river, respectively, which would have an important influence on the susceptibility of a prey species to either of these predators, depending on the prey's habitat preferences.

Some of our most relevant findings to management involve non-salmonid prey items found in predator diets. Predators frequently consumed other non-native

https://doi.org/10.15447/sfews.2018v16iss4art3

predators, and salmonids were a relatively minor prey item for all predators tested. This has important implications when predator removals are discussed. For example, removing large numbers of one predator could release pressure on another predator population (i.e., mesopredator release), by relaxing competitive or predatory relationships (Zavaleta et al. 2001). Our data also suggest that predators consume non-native prey species in much larger numbers than salmonids. High proportions of non-native to native fish in diets and community composition are consistent with other studies (Brown and Michniuk 2007; Nobriga 2007). If predator removals relax pressure on non-native prey species, this may allow these non-native prey fish populations to increase, which can lead to unintended ecological consequences. For example, if predator removals increase the population of non-native Mississippi Silverside, this could have dramatic repercussions for ESA-listed Delta Smelt, since silverside are competitors with adult Delta Smelt and predators of larval Delta Smelt (Bennett 2005; Baerwald et al. 2012). It is difficult to predict the consequences of removing predators on imperiled native fish populations, especially in a complex system comprising multiple non-native predator species that are both competing with and predating upon each other, with non-native prey species dominating the forage base, and with new invasions occurring regularly.

CONCLUSIONS

This study reaffirms that Striped Bass are potentially important predators of salmonids and other native fishes in the lower San Joaquin River, and provides evidence suggesting that other non-native predator species can be similarly important predators of native fishes on a population level. We also found evidence of a food web dominated by non-native fishes at many levels, as also described by Brown and Michniuk (2007) and Mahardja et al. (2017). Salmonids are a small part of this food web, and yet the effects of this alien-dominated ecosystem could significantly affect salmonid populations. A study similar to this one, but with multiple sampling sites that represent the suite of available habitats spread throughout the geographic area of interest—and coupled with abundance estimates of important prey species—could give researchers the ability to not only estimate population-level effects of predators on prey survival, but also determine predation hot-spots mechanistically (i.e., are they because of high predator densities, local environmental variables increasing energetic demands, higher frequency of the target prey item per predator diet, etc.). Furthermore, pairing such a study with predator gut evacuation rate experiments and prey community surveys would further contextualize predator diet composition. Ultimately, this information may be critical to making thoughtful management decisions for the betterment of disappearing native fish populations.

ACKNOWLEDGEMENTS

Funding for this project was provided by the California Department of Water Resources (CDWR), under agreement #4600010100 (CDWR project representative Jacob McQuirk). We would like to thank G. Schumer and S. Blankenship and the GENIDAQS team at Cramer Fish Sciences for processing our diet samples. We would also like to thank B. Martin and E. Danner for their insightful reviews of the manuscript. We are grateful for the help from many technicians and volunteers including (but not limited to): I. Iglesias, B. Burford, M. Sabal, T. Brown, V. Lo, M. Miller, G. Cutter Jr., D. Demer, J. Morinaka, and M. Cane. Material and logistical support was also provided by the National Marine Fisheries Service – Southwest Fisheries Science Center. This study would not have been possible without the generous assistance offered by Marty Gingras and the CDFW Bay–Delta Region staff.

REFERENCES

Baerwald MR, Schreier BM, Schumer G, May B. 2012. Detection of threatened Delta Smelt in the gut contents of the invasive Mississippi Silverside in the San Francisco Estuary using TaqMan assays. Trans Am Fish Soc [Internet]. [cited 2018 September 19]; 141(6):1600–1607. *https://doi.org/10.1080/00028487.2012.717521*

Baker PF, Speed TP, Ligon FK. 1995. Estimating the influence of temperature on the survival of Chinook Salmon smolts (*Oncorhynchus tshawytscha*) migrating through the Sacramento–San Joaquin River Delta of California. Can J Fish Aquat Sci [Internet]. [cited 2018 September 19]; 52(4):855–863. *https://doi.org/10.1139/f95-085*

Bayley PB, Austen DJ. 2002. Capture efficiency of a boat electrofisher. Trans Am Fish Soc [Internet]. [cited 2018 September 19]; 131(3):435–451. *https://doi.org/10.1577/1548-8659(2002)131<0435:Ceoabe>2.0.Co;2*

Bennett WA. 2005. Critical assessment of the Delta Smelt population in the San Francisco Estuary, California. San Franc Estuary Watershed Sci [Internet]. [cited 2018 September 19]; 3(2). *https://doi.org/10.15447/sfews.2005v3iss2art1*

Brandl S, Schumer G, Schreier BM, Conrad JL, May B, Baerwald MR. 2015. Ten real-time PCR assays for detection of fish predation at the community level in the San Francisco Estuary–Delta. Mol Ecol Resour [Internet]. [cited 2018 September 19]; 15(2):278–284. *https://doi.org/10.1111/1755-0998.12305*

Brandl SC, Schreier BM, Conrad JL, May B, Baerwald MR. 2016. Generation of quantitative polymerase chain reaction detectability half-lives and comparison of sampling protocols for genetic diet studies of San Francisco Estuary Fishes. Trans Am Fish Soc [Internet]. [cited 2018 September 19]; 145(3):441–449. *https://doi.org/10.1080/00028487.2015.1131745*

Brown LR, Michniuk D. 2007. Littoral fish assemblages of the alien-dominated Sacramento–San Joaquin Delta, California, 1980–1983 and 2001–2003. Estuar Coast [Internet]. [cited 2018 September 19]; 30(1):186–200. Available from: *https://link.springer.com/article/10.1007/BF02782979*

Brown LR, Moyle PB. 1981. The impact of Squawfish on salmonid populations. North Am J Fish Manage [Internet]. [cited 2018 September 19]; 1(2):104–111. *https://doi.org/10.1577/1548-8659(1981)1<104:TIOSOS>2.0.CO;2*

Buchanan RA, Skalski JR, Brandes PL, Fuller A. 2013. Route use and survival of juvenile Chinook Salmon through the San Joaquin River Delta. North Am J Fish Manage [Internet]. [cited 2018 September 19]; 33(1):216–229. *https://doi.org/10.1080/02755947.2012.728178*

Cohen AN, Carlton JT. 1998. Accelerating invasion rate in a highly invaded estuary. Science [Internet]. [cited 2018 September 19]; 279(5350):555–558. *https://doi.org/10.1126/science.279.5350.555*

Conrad JL, Bibian AJ, Weinersmith KL, De Carion D, Young MJ, Crain P, Hestir EL, Santos MJ, Sih A. 2016. Novel species interactions in a highly modified estuary: association of Largemouth Bass with Brazilian waterweed *Egeria densa*. Transactions of the American Fisheries Society [Internet]. [cited 2018 September 19]; 145(2):249–263. *https://doi.org/10.1080/00028487.2015.1114521*

Corcoran MF. 1979. Electrofishing for catfish: use of low-frequency pulsed direct current. The Progr Fish-Cult [Internet]. [cited 2018 September 19]; 41(4):200–201. *https://doi.org/10.1577/1548-8659(1979)41[200:efc]2.0.co;2*

Cox JG, Lima SL. 2006. Naiveté and an aquatic–terrestrial dichotomy in the effects of introduced predators. Trends Ecol Evol [Internet]. [cited 2018 September 19]; 21(12):674–680. *https://doi.org/10.1016/j.tree.2006.07.011*

Estes JA, Terborgh J, Brashares JS, Power ME, Berger J, Bond WJ, Carpenter SR, Essington TE, Holt RD, Jackson JBC, et al. 2011. Trophic downgrading of planet Earth. Science [Internet]. [cited 2018 September 19]; 333(6040):301–306. *https://doi.org/10.1126/science.1205106*

Feyrer F, Healey MP. 2002. Structure, sampling gear and environmental associations, and historical changes in the fish assemblage of the Southern Sacramento–San Joaquin Delta. California Fish Game [Internet]. [cited 2018 September 19]; 88(3):126–138. Available from: *https://calisphere.org/item/ark:/86086/n26w992t/*

Feyrer F, Herbold B, Matern SA, Moyle PB. 2003. Dietary shifts in a stressed fish assemblage: consequences of a bivalve invasion in the San Francisco Estuary. Enviro Biol Fishes [Internet]. [cited 2018 September 19]; 67(3):277–288. *https://doi.org/10.1023/a:1025839132274*

Grossman GD. 2016. Predation on fishes in the Sacramento–San Joaquin Delta: current knowledge and future directions. San Franc Estuary Watershed Sci [Internet]. [cited 2018 September 19]; 14(2). Available from: *https://doi.org/10.15447/sfews.2016v14iss2art8*

https://doi.org/10.15447/sfews.2018v16iss4art3

Grossman GD, Essington T, Johnson B, Miller JA, Monsen NE, Pearsons TN. 2013. Effects of fish predation on Salmonids in the Sacramento River–San Joaquin Delta and associated ecosystems. California Department of Fish and Wildlife. Available from: *http://deltacouncil.ca.gov/docs/effects-fish-predation-salmonids-sacramento-river-san-joaquin-delta-and-associated-ecosystems*

Krebs CJ, Boonstra R, Boutin S, Sinclair ARE. 2001. What drives the 10-year cycle of snowshoe hares? BioScience [Internet]. [cited 2018 September 19]; 51(1):25–35. *https://doi.org/10.1641/0006-3568(2001)051[0025:wdtyco]2.0.co;2*

Lamberti GA, Resh VH. 1983. Stream periphyton and insect herbivores: an experimental study of grazing by a caddisfly population. Ecology [Internet]. [cited 2018 September 19]; 64(5):1124–1135. *https://doi.org/10.2307/1937823*

Legler ND, Johnson TB, Heath DD, Ludsin SA. 2010. Water temperature and prey size effects on the rate of digestion of larval and early juvenile fish. Trans Am Fish Soc [Internet]. [cited 2018 September 19]; 139(3):868–875. *https://doi.org/10.1577/T09-212.1*

Lindley ST, Mohr MS. 2003. Modeling the effect of Striped Bass (Morone saxatilis) on the population viability of Sacramento River winter-run Chinook Salmon (*Oncorhynchus tshawytscha*). Fishery Bulletin [Internet]. [cited 2018 September 19]; 101(2):321–331. Available from: *https://spo.nmfs.noaa.gov/content/modeling-effect-striped-bass-morone-saxatilis-population-viability-sacramento-river-winter*

Lindström ER, Andrén H, Angelstam P, Cederlund G, Hörnfeldt B, Jäderberg L, Lemnell P–A, Martinsson B, Sköld K, Swenson JE. 1994. Disease reveals the predator: sarcoptic mange, red fox predation, and prey populations. Ecology [Internet]. [cited 2018 September 19]; 75(4):1042–1049. *https://doi.org/10.2307/1939428*

Lockwood RN, Schneider JC. 2000. Stream fish population estimates by mark-and-recapture and depletion methods. In: Schneider JC, editor. Manual of fisheries survey methods II: with periodic updates. Ann Arbor, MI: Michigan Department of Natural Resources, Fisheries Division.

Mahardja B, Farruggia MJ, Schreier B, Sommer T. 2017. Evidence of a shift in the littoral fish community of the Sacramento–San Joaquin Delta. PLOS ONE [Internet]. [cited 2018 September 19]; 12(1):e0170683. *https://doi.org/10.1371/journal.pone.0170683*

Martin BT, Pike A, John SN, Hamda N, Roberts J, Lindley ST, Danner EM. 2017. Phenomenological vs. biophysical models of thermal stress in aquatic eggs. Ecol Lett [Internet]. [cited 2018 September 19]; 20(1):50–59. *https://doi.org/10.1111/ele.12705*

Mather ME, Finn JT, Pautzke SM, Fox D, Savoy T, Brundage HM, Deegan LA, Muth RM. 2010. Diversity in destinations, routes and timing of small adult and sub-adult Striped Bass *Morone saxatilis* on their southward autumn migration. J Fish Biology [Internet]. [cited 2018 September 19]; 77(10):2326–2337. *https://doi.org/10.1111/j.1095-8649.2010.02811.x*

McEwan DR 2001. Central Valley Steelhead. In: Brown RL, editor. Contributions to the biology of Central Valley salmonids. Volume 1. Fish Bulletin 179. [cited 2018 September 19]; [Sacramento (CA)]: California Department of Fish and Game. p. 1–43. Available from: *https://nrm.dfg.ca.gov/FileHandler.ashx?DocumentID=33115*

Miller TW, Barnard D, Speegle J, Adams J, Johnston C, Day JL, Smith L. 2017. Annual report: juvenile fish monitoring during the 2014 and 2015 field seasons within the San Francisco Estuary, California. [Lodi (CA)]: U.S. Fish and Wildlife Service, Lodi Fish and Wildlife Office. 145 p.

Mosser CM, Thompson LC, Strange JS. 2013. Survival of captured and relocated adult spring-run Chinook Salmon *Oncorhynchus tshawytscha* in a Sacramento River tributary after cessation of migration. Environ Biol Fish [Internet]. [cited 2018 September 19]; 96(2):405–417. *https://doi.org/10.1007/s10641-012-0046-x*

Moyle PB. 2002. Inland fishes of California. [Berkeley (CA)]: University of California Press.

Nobriga M, Feyrer F. 2007. Shallow-water piscivore-prey dynamics in California's Sacramento–San Joaquin Delta. San Franc Estuary Watershed Sci [Internet]. [cited 2018 September 19]; 5(2). *https://doi.org/10.15447/sfews.2007v5iss2art4*

Nobriga M, Feyrer F. 2008. Diet composition in San Francisco Estuary Striped Bass: does trophic adaptability have its limits? Environ Biol Fish [Internet]. [cited 2018 September 19]; 83(4):495–503. *https://doi.org/10.1007/s10641-008-9376-0*

Perry RW, Skalski JR, Brandes PL, Sandstrom PT, Klimley AP, Ammann A, MacFarlane B. 2010. Estimating survival and migration route probabilities of juvenile Chinook Salmon in the Sacramento–San Joaquin River Delta. N Am J Fish Manage [Internet]. [cited 2018 September 19]; 30(1):142–156. *https://doi.org/10.1577/M08-200.1*

Poe TP, Hansel HC, Vigg S, Palmer DE, Prendergast LA. 1991. Feeding of predaceous fishes on out-migrating juvenile salmonids in John Day Reservoir, Columbia River. Trans Am Fish Soc [Internet]. [cited 2018 September 19]; 120(4):405–420. *https://doi.org/10.1577/1548-8659(1991)120<0405:fopfoo>2.3.co;2*

Sabal M, Hayes S, Merz J, Setka J. 2016. Habitat alterations and a nonnative predator, the Striped Bass, increase native Chinook Salmon mortality in the Central Valley, California. N Am J Fish Manage [Internet]. [cited 2018 September 19]; 36(2):309–320. *https://doi.org/10.1080/02755947.2015.1121938*

Salo P, Korpimäki E, Banks PB, Nordström M, Dickman CR. 2007. Alien predators are more dangerous than native predators to prey populations. Proceedings of the Royal Society B: Biological Sciences [Internet]. [cited 2018 September 19]; 274(1615):1237–1243. *https://doi.org/10.1098/rspb.2006.0444*

Sih A, Bolnick DI, Luttbeg B, Orrock JL, Peacor SD, Pintor LM, Preisser E, Rehage JS, Vonesh JR. 2010. Predator–prey naïveté, antipredator behavior, and the ecology of predator invasions. Oikos [Internet]. [cited 2018 September 19]; 119(4):610–621. *https://doi.org/10.1111/j.1600-0706.2009.18039.x*

Smith JM, Michel CJ, Huff DD, Hovel R, Hayes SA, Lindley ST, Quinn TP. 2017. Chapter 2: Determining predator distribution and movement with sonic telemetry. In: Testing the effects of manipulated predator densities and environmental variables on juvenile salmonid survival in the lower San Joaquin River. NOAA–National Marine Fisheries Service Report. p. 147–170. [cited 2018 September 19]. Available from: *https://water.ca.gov/Programs/Bay-Delta/Water-Quality-And-Supply/South-Delta-Temporary-Barriers-Project*

Stevens DE. 1966. Food habits of striped bass, *Roccus saxatilis*, in the Sacramento–San Joaquin Delta. Calif Dep Fish Game Fish Bull [Internet]. [cited 2018 September 19]; 136:68–96.

Thomas JL. 1967. Diet of juvenile and adult striped bass Roccus saxatilis in Sacramento–San Joaquin River system. California Fish and Game [Internet]. [cited 2018 September 19]; 53(1):49–62.

Turner JL. 1966. Distribution and food habits of ictalurid fishes in the Sacramento–San Joaquin Delta. Fisheries Bulletin. [cited 2018 December 16]. Available from: *http://content.cdlib.org/view?docId=kt8h4nb2t8;NAAN=13030&chunk.id=d0e3700*

Whipple AA, Grossinger RM, Rankin D, Stanford B, Askevold RA. 2012. Sacramento–San Joaquin Delta historical ecology investigation: exploring pattern and process. [cited 2018 September 19]. [Richmond (CA)]: San Francisco Estuary Institute–Aquatic Science Center. Available from: *https://www.sfei.org/documents/sacramento-san-joaquin-delta-historical-ecology-investigation-exploring-pattern-and-proces*

Williams JG. 2006. Central Valley Salmon: A Perspective on Chinook and Steelhead in the Central Valley of California. San Franc Estuary Watershed Sci [Internet]. [cited 2018 September 19]; 4(3). *https://doi.org/10.15447/sfews.2006v4iss3art2*

Yoshiyama RM, Fisher FW, Moyle PB. 1998. Historical abundance and decline of Chinook Salmon in the Central Valley region of California. N Am J Fish Manage [Internet]. [cited 2018 September 19]; 18(3):487–521. *https://doi.org/10.1577/1548-8675(1998)018<0487:HAADOC>2.0.CO;2*

Yoshiyama RM, Gerstung ER, Fisher FW, Moyle PB. 2001. Historical and present distribution of chinook salmon in the Central Valley drainage of California. In: Brown RL, editor. Contributions to the biology of Central Valley salmonids. [cited 2018 September 19]. [Sacramento (CA)]: California Department of Fish and Game. p. 71–176. Available from: *https://calisphere.org/item/ark:/86086/n2057dwz/*

Zar JH. 2010. Biostatistical analysis. Upper Saddle River, NJ: Pearson Prentice–Hall.

Zavaleta ES, Hobbs RJ, Mooney HA. 2001. Viewing invasive species removal in a whole-ecosystem context. Trends Ecol Evol [Internet]. [cited 2018 September 19]; 16(8):454–459. *https://doi.org/10.1016/S0169-5347(01)02194-2*

https://doi.org/10.15447/sfews.2018v16iss4art3