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RESEARCH

# Sacramento River Predator Diet Analysis: A Comparative Study

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## ABSTRACT

This study examined diets of two predatory fish species, the native Sacramento Pikeminnow (*Ptychocheilus grandis*) and the introduced Striped Bass (*Morone saxatilis*), in the Sacramento River, California, USA. Both species have been implicated in native species declines through predation, eliciting our investigation of their diets in the Sacramento River. Sampling occurred between March and November 2017, and was conducted via hook and line on a 35-km reach near Chico, California. Habitat types sampled include engineered structures (water diversions and beam bridges), rip-rapped channel edges, and natural riverbank. Stomach contents were collected via gastric lavage and later processed using visual, gravimetric, and genetic techniques. Diets of Sacramento Pikeminnow and Striped Bass were highly

similar as determined through index of relative importance and PERMANOVA modeling. Water temperature was the only variable that significantly affected diet composition. Results reflect similar dietary niches for both species in the Sacramento River.

## KEY WORDS

Sacramento Pikeminnow, predation, Striped Bass, introduced species, California, fisheries, water diversion, Chinook Salmon

## INTRODUCTION

Because predation is a challenge with which nearly all organisms must contend, it is often considered in the management of vulnerable populations of fishes (Zimmerman and Ward 1999; Link 2002). In the Sacramento River, California, this challenge may be amplified for populations of juvenile Chinook Salmon by climate change, a complex water diversion system, hatchery domestication effects, lack of juvenile rearing habitat, and non-native predatory fish species (Brown and Moyle 1981; NOAA Fisheries 2018). Factors such as climate change and habitat loss have served to limit the natural production potential of Chinook Salmon (*Oncorhynchus tshawytscha*)

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in the Sacramento River, while domestication of hatchery-reared fish and watershed engineering increase the vulnerability of juvenile Chinook Salmon to predation by both native and non-native predators (NOAA Fisheries 2018).

Of the four Chinook Salmon runs native to the Sacramento River, winter-run are listed as endangered, spring-run are listed as threatened, and both Central Valley fall-run and late fall-run have been identified as California species of special concern (Moyle et al. 2015; NOAA Fisheries 2018). In addition, Green Sturgeon (*Acipenser medirostris*) and Steelhead (*Oncorhynchus mykiss*), both species native to the Sacramento River, are also listed as threatened under the federal Endangered Species Act. Prior studies have investigated the potential for population-scale effects of predation by non-native species on prey populations, including listed Chinook Salmon, through population modeling (Lindley and Mohr 2003), bioenergetic modeling (Loboschewsky et al. 2012), and telemetry survival studies (Cavallo et al. 2013) within the Sacramento River and adjacent watersheds. While these studies identify predation as a tangible “top-down” control of prey populations, population-scale effects are often difficult to quantify in the highly dynamic and heterogeneous Sacramento River system.

The middle Sacramento River contains two abundant piscivorous fish species: Sacramento Pikeminnow (*Ptychocheilus grandis*) and Striped Bass (*Morone saxatilis*). In the Sacramento River and other California watersheds, both predators consume vulnerable native species, including juvenile Chinook Salmon and Steelhead (Stevens 1966; Thomas 1967; Brown and Moyle 1981; Brown and Moyle 1997; Nakamoto and Harvey 2003; Sabal et al. 2016). Sacramento Pikeminnow are native to the Sacramento River drainage; Striped Bass were introduced in 1879 as a recreational and commercial species (Moyle 2002). Both Sacramento

Pikeminnow and Striped Bass are common in the Sacramento River, despite overall population declines throughout the watershed (Stevens et al. 1985; Kohlhorst 1999; Moyle 2002; Brown and Moyle 2005).

Sacramento Pikeminnow and Striped Bass have both been considered as potential contributors via predation to native species decline in the highly modified Sacramento River system (CDFG 1999; Moyle 2002; Lindley and Mohr 2003; Bonham 2011). Pikeminnow species (*Ptychocheilus* spp.) have been shown to consume large amounts of outmigrating salmonids from a range of US West Coast watersheds under hydraulically favorable conditions, and, in response, predator control measures have been implemented with mixed results (Brown and Moyle 1981; Brown and Moyle 1997; Tucker et al. 1998; Friesen and Ward 1999; Zimmerman and Ward 1999; Moyle 2002; Nakamoto and Harvey 2003). Likewise, Striped Bass have also been shown to consume salmonids (Stevens 1966; Tucker et al. 1998), which modeling suggests may have population-scale effects (Lindley and Mohr 2003; Sabal et al. 2016). Within the Sacramento River drainage, the effects of dams and diversions on predation have been a point of concern (Brown and Moyle 1981; Tucker et al. 1998; Sabal et al. 2016). Altered water dynamics near these structures may serve as ambush habitat, making conditions favorable to opportunistic predators such as Striped Bass and Sacramento Pikeminnow. In addition, juvenile Chinook Salmon show a preference for low-water-velocity areas (Hillman et al. 1987), and may be more susceptible to predation when exposed to disorienting flows caused by engineered structures (Brown and Moyle 1981; Tucker et al. 1998; Deng et al. 2010; Sabal et al. 2016).

Striped Bass long avoided management as a predatory species because of their value as a game fish; that changed, however, in the 1990s, when the California Department of Fish and Game (now California Department

of Fish and Wildlife; CDFW) ceased stocking Striped Bass so as not to facilitate predation on listed salmonids (CDFG 1999; Moyle 2002). Several studies investigated diets of Striped Bass in the Sacramento–San Joaquin Delta (Delta); however, there is little recent literature on Striped Bass diets in the middle reaches of the Sacramento River below Shasta Dam (Brown and Moyle 1981; Tucker et al. 1998; Moyle 2002; Nobriga and Feyrer 2007). Likewise, although Nobriga and Feyrer (2007) compared the diets of Sacramento Pikeminnow and Striped Bass concurrently in the Delta, diets for these two species have not been compared in the middle Sacramento River since Tucker et al. (1998) investigated predation around the Red Bluff Diversion Dam (RBDD) in the mid-1990s. The middle Sacramento River is colder and is generally a single channel, as opposed to the Delta's warmer network of channels or open water. It contains a different assemblage of prey species (Moyle 2002), some of which are only seasonally available, potentially affecting predator diets. We investigated the diets of these two species over a year, using visual and genetic techniques to identify prey species. Using these methods, we describe Sacramento Pikeminnow and Striped Bass diets by quantifying: (1) relative importance of prey, (2) overlap of predator diets, and (3) effects of engineered structures on predator diet.

## MATERIALS AND METHODS

### Study Organisms

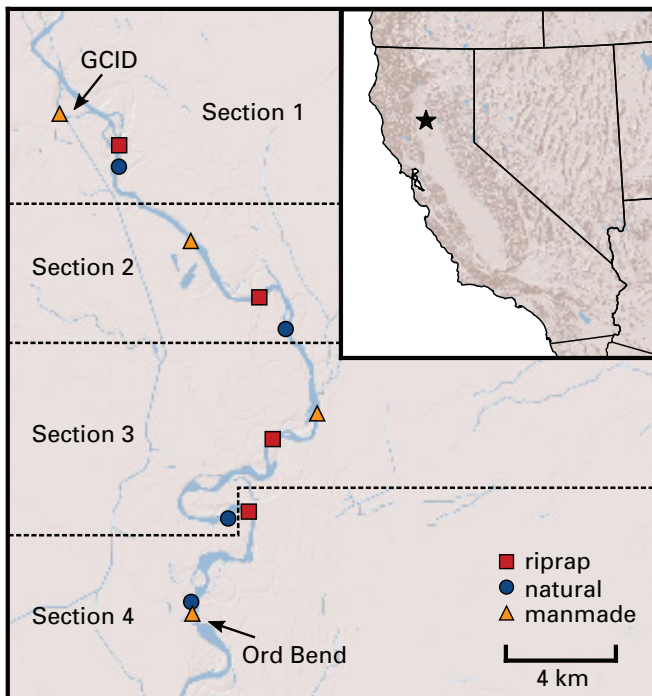
Sacramento Pikeminnow are native to the Sacramento River and are an abundant piscivorous fish within the freshwater portions of the system. They become piscivorous at 10 to 20 cm total length, sexually mature at 3 to 4 years of age, and may exhibit either resident or migratory life-history strategies within the fresh and brackish portions of the system (Moyle 2002; Nobriga et al. 2006).

Piscivory in Striped Bass generally begins at around 15 cm total length (Texas Instruments 1974) as determined by gape limitation; however, piscivory has been shown to have a strong seasonal association in the Delta (Nobriga and Feyrer 2007). Males become sexually mature at 2 years of age; females generally do not mature before 4 years of age (Moyle 2002). Immature individuals may be found throughout the system, while mature individuals exhibit an anadromous life-history strategy, spending much of the year in the San Francisco Estuary (Sacramento–San Joaquin Delta, Suisun Bay and Marsh, San Pablo Bay, San Francisco Bay) and the Pacific Ocean (Thomas 1967; Moyle 2002). Mature Striped Bass generally enter the Sacramento River system in spring to spawn, before returning to downstream habitats (Moyle 2002); however, resident contingents of mature adults exist in their native US East Coast rivers (Morris et al. 2003), and recent studies on California Striped Bass indicate there may be both resident and migratory contingents within the Sacramento River watershed, as well (Le Doux–Bloom 2012; Sabal et al. 2019).

### Study Reach

Fish were collected on the Sacramento River, between Ord Bend boat ramp (river kilometer 296) and Glenn–Colusa Irrigation District diversion facility (GCID; river kilometer 331; [Figure 1](#)). We chose this logistically manageable reach because of the presence of both Striped Bass and Sacramento Pikeminnow, seasonal populations of migratory salmonids, engineered structures, and its diversity of habitat.

We implemented a balanced sampling design, breaking the total sampling reach into four sections of similar length, each of which contained three fixed sampling sites of different habitat types. Habitat types included engineered, rip-rap, and natural locations. Engineered sites were adjacent to engineered structures such as water diversion facilities or beam bridges. Rip-rap sites had



**Figure 1** Location of hook and line sampling sites by site type and section. Map courtesy of Dr. Paolo Segre, Stanford University.

at least one adjacent bank that had been armored with large rock. Natural sites were not near either armored bank or engineered structures. Since the limiting habitat type in our study reach was engineered habitat, the number of rip-rap and natural sites corresponded to the number of engineered sites available. We identified possible rip-rap and natural sites, and randomly selected a subset of four of each site type.

### Sample Collection

We used hook and line sampling methods to collect data from wild Sacramento Pikeminnow and Striped Bass. We selected hook and line sampling because of its low material cost and low risk of listed species bycatch. We generally sampled twice weekly, with one morning shift (starting 45 minutes before sunrise) and one evening shift (starting 5 hours before sunset) to control for diurnal feeding effects (Fraser et al. 1993). We sampled each site for 1.25 hours

per sampling period, with all three habitat types within a section sampled for a total of 3.75 hours. Individual sections were sampled biweekly, and alternated between morning and evening. Before sampling a section, we randomly generated the order in which we visited sites.

Hook and line sampling began in March 2017 and continued through the end of November 2017. High water and unsafe conditions prevented sampling in January and February, as well as part of March and April, and limited crew availability was responsible for lack of sampling in December. We sampled from a 4.9-m jet boat at anchor. Four rods were fished in randomized order, each of which was assigned a unique bait (large sardine piece, small sardine piece, chicken liver, and nightcrawlers) that would not contaminate subsequent diet sample analysis. We selected bait types to attract target species from a range of sizes. When we caught fish, we removed them from the water, measured them for length (fork length; cm) and weight (kg,  $\pm 50$  g), and placed them into an aerated holding tank. We then pumped fish stomachs using non-lethal gastric lavage, a method in which pulses of pressurized water are directed into the esophagus, causing the fish to evacuate its stomach contents (Foster 1977). To retain sample integrity after returning from the field, stomach content samples were collected in a fine mesh bait net (flushed with river water between samples), transferred to sterile Whirl-pak® bags, labeled, stored on ice, and frozen at  $-20$  °C immediately.

We measured water temperature at each site via the transducer from the onboard fish-finder/GPS unit (Garmin® Striker 4), and measured water clarity with a 20.3-cm-diameter white and black Secchi disk. Upon two occasions, when crew failed to record water clarity, it was estimated as the mean of measures taken during the previous and following sampling days.



### Laboratory Analysis

Stomach contents were processed to determine weight (g,  $\pm 0.001$ g), frequency of occurrence, and number of prey within each sample. Stomach content samples were removed from the freezer and allowed to fully thaw at room temperature. Using instruments sterilized in 20% bleach solution, we placed samples onto new polystyrene weigh boats, sorted them, and segregated prey by taxonomic category. Prey categories included fish, crayfish, other macroinvertebrates (primarily terrestrial and aquatic insects), and unknown soft matrix (i.e., visually unidentifiable yet clearly organic stomach content material; what remains after less-digested prey is removed). We used diagnostic parts—such as spinal columns for fish, and head parts for macroinvertebrates—to enumerate individuals.

Next, we weighed the prey group to the nearest thousandth of a gram using an Ohaus® STX223 Scout portable balance, after blotting prey dry with new paper towels. For individual fish that could be clearly identified as such, we removed a sample of tissue ( $\leq 0.25$ g) and transferred it to a new 1.5-mL micro-centrifuge tube, labeled it, and stored it on ice. When individuals could not be clearly differentiated, we homogenized the soft-matrix material with dissecting tools, and took at least one representative grab sample ( $\leq 0.25$ g). Once a processing session was completed, resulting pre-category subsamples were immediately returned to storage at  $-20\text{ }^{\circ}\text{C}$  for later genetic analysis.

### Genetic Analysis

Traditionally, diets of predatory fish have been analyzed by visual prey identification (Stevens 1966; Tucker et al. 1998; Sabal et al. 2016). While this methodology is logistically and economically viable, it best describes only what prey a predator was feeding on immediately before capture. Prey items rapidly deteriorate in the stomach of predators to a point at which they

cannot be easily identified—a process that accelerates with increasing water temperature (Vondracek 1987). Genetic methods, although more costly and labor-intensive than simple visual identification, allowed for a more holistic representation of predator diets (Valdez–Moreno et al. 2012).

We chose quantitative PCR (qPCR) as the primary analysis technique because of its higher throughput than traditional PCR, as well as its ability to quantify sample DNA, allowing for discrimination of true versus contaminant DNA (Rees et al. 2014). Although still a relatively novel method for identifying prey from stomach contents, qPCR has proven successful for this application in a number of studies (Durbin et al. 2011; Hunter et al. 2012; Taguchi et al. 2014; Michel et al. 2018).

We determined a reference list of potential prey species through the lead author's previous CDFW seining and snorkel survey experience, and verified them using Moyle (2002). We referenced previously-designed prey species primers from current literature (Jordan et al. 2010; Baerwald et al. 2012; Brandl et al. 2015), and designed additional primers using Genbank sequence data and the National Center for Biotechnology Information (NCBI) Primer-BLAST tool (Benson et al. 2012; Ye et al. 2012). We tested primer sets for validity against known voucher tissue via PCR and qPCR, and optimized them to determine correct annealing temperatures. Testing and optimizing was done for all primer sets except for River Lamprey (*Lampetra ayresii*) and Western Brook Lamprey (*Lampetra richardsoni*), as the result of an inability to procure tissue; however, this did not meaningfully affect results, because these species were not detected. Although Striped Bass and Sacramento Pikeminnow primers were validated, we excluded these species as potential prey because we were concerned about contamination from predator tissue.

PCR primer sets produced single bands on an agarose gel and consistent melt curves for species-specific products in qPCR in at least duplicate for each prey species considered. Voucher tissue was supplied by the UC Davis Genomic Variation Laboratory, the CDFW Upper Sacramento Watershed Fisheries Project, and the field component from this study. Voucher tissue was either frozen, dried, or stored in ethanol when collected, and DNA was extracted using Qiagen® DNeasy DNA extraction kits. Table 1 contains the prey reference list and associated primers.

The qPCR assays were run using an Eppendorf® EP realplex thermal cycler, in 96-well format. We mixed reagents using 3 uL of undiluted sample DNA, 3 uL of DNase free water, 5 mM of primer pair, and 7.5 uL of Thermo Scientific™ 2X Luminaris Color HiGreen qPCR Master Mix per well. All qPCR runs had at least two negative controls of DNase free water. We ran Brandl et al. (2015) and Baerwald et al. (2012) primers with a qPCR program of 10 minutes at 95 °C, followed by 40 cycles of 15 seconds at 95 °C, and 1 minute at 60 °C. Primers designed for this study and the Jordan et al. (2010) universal fish primer set followed similar programs; however, we changed the annealing step to 45 seconds at 68 °C and 62 °C, respectively. We adjusted the annealing temperatures to maximize the efficiency of primers that had been designed to different specifications.

Once primers had been validated, sample DNA was extracted from tissue using Qiagen® Powerfecal DNA extraction kits. Powerfecal kits are optimized for extracting DNA from low-quality samples high in PCR inhibitors, as is the case with stomach contents. We extracted and tested all sample DNA for DNA concentration and quality using a Thermo Scientific™ NanoDrop One Microvolume UV-Vis Spectrophotometer.

Initially, we tested all samples labeled as soft matrix against the Jordan et al. (2010) universal fish primer set, to determine if samples contained any fish tissue. We excluded from further

analysis samples that did not amplify with the universal fish primer. Soft-matrix samples that did amplify against the universal fish primer set were then tested against a limited assay of species, which included Chinook Salmon, Steelhead, White Sturgeon (*Acipenser transmontanus*), Green Sturgeon, and Pacific Lamprey (*Entosphenus tridentatus*). Soft-matrix samples that tested positively for one or more species were conservatively counted as one individual from each positive amplification.

We tested individual fish from stomach samples against targeted species primers until we reached a positive result. We tested all prey fish, regardless of level of digestion, to confirm visual identifications. Notes on prey morphology taken during sample processing were used to inform primer set selection, targeting the most likely prey items. Occasionally, a single individual sample would amplify for multiple species (potentially as a result of inter- or intra-sample contamination), in which case we selected the species with the lowest cycle threshold value. Samples that amplified at lower cycle thresholds were assumed to contain more prey DNA. We ran a subsample of amplified qPCR products on agarose gels to validate results. Examples of positive, negative, and control amplification curves and melt profiles can be seen in Appendix A, Figure A1.

### Data Analysis

Predator size and spatial-temporal distribution were analyzed using Kruskal-Wallis rank sum test and Dunn's post hoc test of multiple comparisons. We chose these non-parametric tests because of the non-normality of the data. We analyzed predator distribution using site-specific catch per unit effort (CPUE) data as an index of abundance, with CPUE defined as the number of fish captured per hour. Although there are inherent issues with using CPUE as a metric for abundance, the consistency of our sampling efforts does increase the validity of its use (Haggarty and King 2006). We tested temporal distribution by season, with March through May classified as spring, June through August as summer, and September through November as fall.

**Table 1** Prey reference list including mitochondrial reference gene, primer sequences, gene segment length, and accession number

Common Name ( <i>Latin name</i> )	Gene	Primers (5' to 3')	Segment length	Accession number
American Shad <sup>a</sup> ( <i>Alosa sapidissima</i> )	CYTB	FOR – TGCACGCAAACGGGGCATCA REV – CCTCGGCCAATGTGGGCGTAAA	58bp	GU556214.1
Chinook Salmon <sup>d</sup> ( <i>Oncorhynchus tshawytscha</i> )	CYTB	FOR – CCTAAAAATCGCTAATGACGCACTA REV – GGAGTGAGCCAAAAGTTTCATCAG	80bp	KF013235
Delta Smelt <sup>c</sup> ( <i>Hypomesus transpacificus</i> )	CYTB	FOR – AATGGCCAACCTTCGGAAA REV – GARATATTRGAGGGTGCAGG	90bp	HQ667171
Green Sturgeon <sup>d</sup> ( <i>Acipenser medirostris</i> )	COI	FOR – AGGGAAAAAATGGTTAGGTCTACAGA REV – CCCCACTGGCGGGAAA	61bp	KF558288
Hardhead <sup>a</sup> ( <i>Mylopharodon conocephalus</i> )	CYTB	FOR – TGCCGGCGCAACCATCCTACA REV – CGGCCGGGTTGTTTGATCCGGT	62bp	EU747218.1
Longfin Smelt <sup>d</sup> ( <i>Spirinchus thaleichthys</i> )	CYTB	FOR – CTCTGCCGGGACGTCAAT REV – CCCGTTAGCGTGCATATTCC	53bp	KF013249
Mississippi Silverside <sup>c</sup> ( <i>Menidia audens</i> )	CYTB	FOR – CCGTTTGCATGCATATTTTCG REV – CCTTTTCGTCTGTTGCACACA	73bp	JN008748
Pacific Lamprey <sup>a</sup> ( <i>Entosphenus tridentatus</i> )	COI	FOR – TTGAAGCAGGGGCTGGCACAGG REV – GGAGGCCCTGTGTGGGCTAA	74bp	KX389877.1
Prickly Sculpin <sup>a, e</sup> ( <i>Cottus asper</i> )	CYTB	FOR – ATTGCCCTCACAGCCCTCGCAC REV – TCACCAGCGGGTTAGCAGGGG	82bp	KX353550.1
Riffle Sculpin <sup>a, e</sup> ( <i>Cottus gulosus</i> )	COI	FOR – GGCGCCCTTTTGGGGGACGA REV – GGGGCGCCGATCATTAAAGGGGA	137bp	JN025103.1
River Lamprey <sup>a, f</sup> ( <i>Lampetra ayresii</i> )	CYTB	FOR – CTGACTAATGTCCCACCCACCAACT REV – GCAGGAGAAGGAAGGTCAACTAGCA	93bp	KR422617.1
Sacramento Sucker <sup>a</sup> ( <i>Catostomus occidentalis</i> )	COI	FOR – AATCTTGCCACGCCGGAGCC REV – TTGAGAGATGGCTGGGGGCTTCA	132bp	JN024942.1
Sacramento Tule Perch <sup>a</sup> ( <i>Hysterocarpus traskii</i> )	COI	FOR – GGGCAGAATAAGCCAACCAGGCG REV – ACAAAGGCGTGGGCCGTTACAA	79bp	JN026852.1
Steelhead/Rainbow Trout <sup>d</sup> ( <i>Oncorhynchus mykiss</i> )	COI	FOR – AACATAAAACCTCCAGCCATCTCT REV – AGCACGGCTCAAACGAAAA	59bp	KF558313
Threadfin Shad <sup>d</sup> ( <i>Dorosoma petenense</i> )	CYTB	FOR – AAGTCCTCGGCCGATGTG REV – CATGCAAACGGAGCATCCT	39bp	KF013218
Western Brook Lamprey <sup>a, f</sup> ( <i>Lampetra richardsoni</i> )	CYTB	FOR – TCGGACGAGGAATCTACTACGGCT REV – TGCCCTCATGGGAGAACGTAACCGA	118bp	KY499461.1
White Sturgeon <sup>d</sup> ( <i>Acipenser transmontanus</i> )	CYTB	FOR – CCCCGTTTGCATGAATGTTT REV – CGCCACATCTGCCGAGAT	62bp	KF013247
Universal Fish Primer <sup>b</sup>	12S	FOR – GCTTAAAACCCAAAGGACTTG REV – CTACACCTCGACCTGACGTT	148bp	—

a. Benson et al. (2012).

b. Jordan et al. (2010).

c. Baerwald et al. (2012).

d. Brandl et al. (2015).

e. Primers amplified both Riffle and Prickly Sculpin DNA.

f. Primers were not validated against known voucher tissue and experienced partial cross-amplification; strongest signal was selected for analysis.



We used cumulative prey curves, as outlined by Ferry and Cailliet (1996), to determine sample size adequacy by species, habitat type, and season. With this technique, the number of new prey items is plotted against the number of stomachs analyzed, in random order. If the plot reaches an asymptote, then a sufficiently large sample size has been obtained to describe the diet of a species under the conditions studied (Ferry and Cailliet 1996). We used the R package 'vegan,' function 'specaccum,' to construct cumulative prey curves (Oksanen et al. 2013; Hernandez 2016; R Core Team 2018).

We used gravimetric values and prey enumerations, as determined through lab and genetic analysis, to calculate the index of relative importance (IRI) of each prey taxon by predator species. We used visual and genetic identifications interchangeably; however, we did not include soft-matrix samples in IRI calculations since we could not determine prey weight for these samples. IRI is a compound value used to determine the importance of any given prey taxon in a predator species diet (Pinkas et al. 1971; Hyslop 1980) and is calculated as follows:

$$IRI = (\%N + \%W) * \%FO \quad (1)$$

where %N is total prey percent by number, %W is total prey percent by weight, and %FO is total prey percent frequency of occurrence for a given predator group. Volumetric measurements may be used in place of %W (Hyslop 1980); however, given the small size of prey, we chose to use gravimetric measurements because the instruments available were more precise. We used wet weight of prey because Glenn and Ward (1968) showed that prey wet and dry weights are highly correlated.

Once we calculated IRI for each prey taxon, we then converted it to %IRI to increase study comparability (Cortés 1997). %IRI is calculated as follows:

$$\%IRI_i = 100 * IRI_i / \sum_{i=1}^n IRI_i \quad (2)$$

We chose permutational multivariate analysis of variance (PERMANOVA) to analyze diets because of its robustness in analyzing ecological data, as well as its ability to handle heavily zero-weighted data sets (Lek et al. 2011; Anderson and Walsh 2013; Oksanen et al. 2013). While PERMANOVA is robust in analyzing data sets with heterogeneous multivariate spread, it becomes more sensitive to heterogeneity when groups are unbalanced (Anderson and Walsh 2013). Since our sample sizes of Sacramento Pikeminnow and Striped Bass containing identifiable stomach contents were unbalanced (n=30 vs. n=47, respectively), we first tested for homogenous multivariate spread between species groups (R package EcoSimR::betadisper; Gotelli et al. 2015; R Core Team 2018).

We used PERMANOVA to analyze the effect of species, habitat type, and water temperature on diet composition, measured as frequency of occurrence. We tested a suite of other environmental and demographic variables during model construction; however, their effects on diet were insignificant, so we excluded them from our final model. We then subset our data (n=20 Sacramento Pikeminnow, n=36 Striped Bass) by excluding the macroinvertebrate and crayfish prey groups. Using this subset data, we again ran our model to test whether invertebrates were confounding potential differences in piscivory. We ran the PERMANOVA analysis using marginal testing and 10,000 permutations, which we determined as sufficient to stabilize p-values. Results from all statistical tests were considered significant at  $\alpha=0.05$ .

## RESULTS

### Size and Distribution

Over the course of the sampling period, 155 target species were captured, of which 68 were Sacramento Pikeminnow and 87 were Striped Bass. Of these individuals, approximately 46% of Sacramento Pikeminnow (n=31) and 57% percent of Striped Bass (n=50) contained

stomach contents (Table 2). We were unable to identify prey from several of the individuals that contained stomach contents, which reduced the sample size of Sacramento Pikeminnow and Striped Bass included in dietary analysis to  $n=30$  and  $n=47$ , respectively.

Sacramento Pikeminnow were evenly distributed across all habitat types (Kruskal–Wallis, chi-squared = 5.48,  $df=2$ ,  $p=0.06$ ), as were Striped Bass (Kruskal–Wallis, chi-squared = 1.85,  $df=2$ ,  $p=0.40$ ). Given the closeness of the test of Sacramento Pikeminnow distribution to our significance threshold of  $\alpha=0.05$ , we ran Dunn’s post hoc test of multiple comparisons to test what was driving this result. Dunn’s test showed that CPUE of Sacramento Pikeminnow increased by 2.1 fish per hour at engineered sites when compared to natural sites ( $p=0.02$ ).

When temporal distribution was considered, Kruskal–Wallis tests showed no difference in CPUE by season for Sacramento Pikeminnow (chi-squared = 0.37,  $df=2$ ,  $p=0.83$ ), although a difference was seen for Striped Bass (chi-squared = 17.13,  $df=2$ ,  $p<0.001$ ). Dunn’s post hoc test showed this result was driven by significantly higher CPUE of Striped Bass during summer than in fall (difference = 2.62 fish  $hr^{-1}$ ,  $p=0.004$ ) or spring (difference = 4.02 fish  $hr^{-1}$ ,  $p<0.001$ ).

The average fork length (FL) and weight of Sacramento Pikeminnow included in dietary analysis were 35.2 cm and 0.45 kg (Table 2), and Striped Bass was 31.8 cm and 0.40 kg,

respectively. There was not a significant difference in FL or weight between empty and non-empty individuals for either Sacramento Pikeminnow (Kruskal–Wallis, FL: chi-squared = 0.001,  $df=1$ ,  $p$ -value = 0.98; weight: chi-squared = 0.001,  $df=1$ ,  $p=0.98$ ) or Striped Bass (Kruskal–Wallis, FL: chi-squared = 0.13,  $df=1$ ,  $p=0.72$ ; weight: chi-squared = 0.17,  $df=1$ ,  $p=0.68$ ). Kruskal–Wallis tests showed that, for individuals containing identifiable stomach contents, Striped Bass FL was less than for Sacramento Pikeminnow (chi-squared = 5.27,  $df=1$ ,  $p=0.02$ ), while weights were not different (chi-squared = 0.42,  $df=1$ ,  $p=0.52$ ). Dunn’s post hoc test confirmed that Striped Bass FL was less, however, only by approximately 2.3 cm ( $p=0.01$ ).

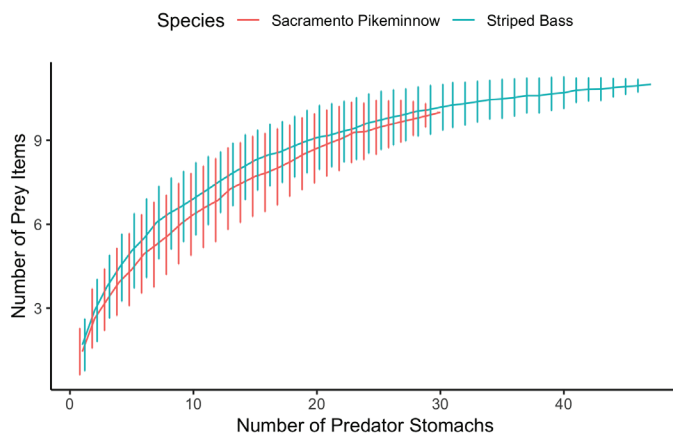
### Diet Composition

Of the individuals that contained stomach contents, piscivory was observed in 71% of Sacramento Pikeminnow and in 84% of Striped Bass. We were unable to identify a minimum size of piscivory for either species, because the smallest Sacramento Pikeminnow (27 cm) and Striped Bass (22.5 cm) that contained stomach contents were both found with fish parts in their stomachs.

Multivariate spread was not different between Sacramento Pikeminnow and Striped Bass ( $p=0.13$ ), therefore meeting PERMANOVA model assumptions. Likewise, sample sizes were determined to be adequate to describe diets by species and habitat type, given that cumulative prey curves for both predator species (Figure 2) and all habitat types reached an asymptote (Ferry

**Table 2** Demographics of Sacramento Pikeminnow and Striped Bass that contained identifiable stomach contents. Empty rate refers to the percentage of individuals captured that did not contain any stomach contents, identifiable or otherwise.

Variable	Sacramento Pikeminnow	Striped Bass
Number of individuals	30	47
Fork length range (cm)	27.0 – 57.0	22.5 – 47.0
Fork length mean $\pm$ SD (cm)	35.2 $\pm$ 7.4	31.8 $\pm$ 6.9
Weight range (kg)	0.20 – 1.60	0.14 – 1.00
Weight mean $\pm$ SD (kg)	0.45 $\pm$ 0.35	0.40 $\pm$ 0.24
Empty rate	54%	43%
Observed onset of piscivory (cm)	27.0	22.5



**Figure 2** Species accumulation curves for Sacramento Pikeminnow and Striped Bass. *Error bars* represent the possible number of new prey species added for the addition of a single randomly selected predator stomach. Species plots offset for visual distinction.

and Cailliet 1996; Oksanen et al. 2013). Although cumulative prey curves reached an asymptote for summer and fall, they did not for fish captured during the spring, precluding season as a predictor variable in our PERMANOVA model.

The two most important prey items for both predator species, as enumerated by %IRI, were macroinvertebrates (excluding crayfish) and Chinook Salmon (Sacramento Pikeminnow: 77% and 15%, respectively; Striped Bass: 78% and 17%, respectively; Table 3). PERMANOVA modeling confirmed the similarity of diets indicated by %IRI. Prey frequency of occurrence showed no relationship with species or habitat type; however, it was significantly influenced by water temperature, although it only explained ~4% of the variation in diet composition ( $F = 3.22$ ;  $df = 1, 72$ ;  $p = 0.01$ ; Table 4). This result did not change when the macroinvertebrate and crayfish prey groups were excluded from the PERMANOVA analysis. The lack of association between diet and habitat type must be qualified by the fact that much of the stomach contents recovered were highly degraded, and prey may have been consumed in areas other than where predators were captured.

**Table 3** %IRI values for Sacramento Pikeminnow and Striped Bass captured via hook and line sampling near Chico, CA

Prey species	Sacramento Pikeminnow	Striped Bass
American Shad	0.08	0.64
Chinook	14.57	17.03
Crayfish	2.56	0.17
Green Sturgeon	0	0.08
Hardhead	0.48	2.75
Macroinvertebrate spp.	76.9	78.09
Pacific Lamprey	0.9	0.11
Sculpin spp.	4.51	1.03
Tule Perch	0	0.1

**Table 4** PERMANOVA model testing effects of species (Sacramento Pikeminnow and Striped Bass), habitat type, and water temperature on diets of predators captured via hook and line sampling near Chico, CA. Analysis run using frequency of occurrence as prey metric.

<i>Model: Prey Frequency of Occurrence ~ Species + Habitat Type + Water Temperature</i>					
Source	df	Sum of squares	$R^2$	F	P
Species	1	0.09	0.003	0.27	0.88
Habitat type	2	0.43	0.02	0.66	0.72
Water temp.	1	1.04	0.04	3.22	0.02*
Residual	72	23.17	0.93		
Total	80	24.91	1.00		

Significance codes: '\*\*\*\*' 0.001 '\*\*\*' 0.01 '\*\*' 0.05

## DISCUSSION

Predation by native and non-native predators in the Sacramento River system is often cited as a major factor that contributes to native species decline (NOAA Fisheries 2019), but without sufficient information on in-river species interactions. By examining diets of the two important predatory fish species within the Sacramento River, this study aimed to approach the issue of native species loss through better understanding of predator diets. Although our study is only a snapshot of diets during a high-water year, it nonetheless demonstrates similarity of diets between Striped Bass and

Sacramento Pikeminnow in the Sacramento River (Tables 3 and 4; Figure 2).

### Predator Diets

%IRI and PERMANOVA modeling indicate no difference in diets between Sacramento Pikeminnow and Striped Bass. While there are obvious life-history differences between these two species, on a per capita basis, neither appears to have a higher impact on any particular prey—including Chinook Salmon—than the other. Our observed proportion of Chinook Salmon in predator diets was lower than was seen by Thomas (1967) within the Sacramento river, and, overall, diets were substantially different than those observed within the Delta (Stevens 1966; Nobriga and Feyrer 2007). Because there are currently no estimates of adult Sacramento Pikeminnow or Striped Bass abundance in the Sacramento River, the total effect of predation on native species cannot be quantified from diet composition alone. Future studies should focus on building accurate population estimates for both Sacramento Pikeminnow and Striped Bass, to clarify their role as predators and to quantify potential effects on prey species in the Sacramento River system.

Given the similarity of diets of Sacramento Pikeminnow and Striped Bass, the compensatory effects of predator control should be considered. If either Sacramento Pikeminnow or Striped Bass is resource-limited at times in the Sacramento River, then their high dietary overlap suggests that control of one species would increase resources for the other. This could potentially increase the population of the species that has *not* been subject to control, undermining any net benefit on predation.

Predation in the Sacramento River is likely higher near some engineered structures because of the favorable hydraulics that attract prey and predators alike (Brown and Moyle 1981). However, we did not observe an association between diet and habitat type in our study. This can likely be attributed to two factors. First, although engineered structures such as bridge pilings do create low-water-velocity pockets, which may act

as predator ambush habitat, there is no shortage of natural structures in this section of the Sacramento River that act similarly (Whiteway et al. 2010). The study reach contains many submerged trees, or snags, which impede flow and are often targeted by recreational anglers in much the same way anglers target bridge pilings, for their ability to hold Striped Bass. Second, the two water diversion facilities selected as engineered sampling locations—GCID and a smaller private pumping station—did not appear to substantially influence surface flows. This is in contrast to other Sacramento River diversion facilities, such as the now defunct Red Bluff Diversion Dam, which used to span the entire channel, altering hydraulics and increasing predation on juvenile salmonids by Sacramento Pikeminnow (Brown and Moyle 1981).

PERMANOVA modeling showed that water temperature was the only variable we measured that significantly affected predator diets. Because of the association between water temperature and seasonality, this may indicate a temporal association of predator diets, which would support the conclusion that both Sacramento Pikeminnow and Striped Bass are opportunistically feeding on seasonally available prey populations. Had we been able to capture more predators in the spring, we would have been able to directly test the association of diets with season.

### Predator Distribution

Based on the results of our CPUE analysis, there were likely more Sacramento Pikeminnow present at engineered sites and more Striped Bass present overall during summer months. Although diet did not differ between site types, it is important to note that the increased abundance of Sacramento Pikeminnow at engineered sites may increase their overall predatory effect in these locations. Likewise, the greater abundance of Striped Bass present during the summer months may scale their predatory effect on prey present within the Sacramento River during that time.

## CONCLUSIONS

Our study demonstrated high similarity of diets between the two predator species. Although Sacramento Pikeminnow and Striped Bass do consume juveniles of native fishes such as Chinook Salmon and Green Sturgeon, these fishes did not make up the majority of either species' diet during the study period. Our results, coupled with previous diet studies, support the notion that Sacramento Pikeminnow and Striped Bass exhibit prey-switching behavior, both spatially and temporally. This likely occurs in the presence of high densities of certain prey, such as during in-river releases of hatchery Chinook Salmon. Unfortunately, high water and turbidity did not allow us to sample effectively when outmigrating hatchery Chinook Salmon populations were highest. Further study should be directed at describing per capita predation by Sacramento Pikeminnow and Striped Bass on Chinook Salmon outmigrants in the Sacramento River when spring flows and turbidity are low.

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