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RESEARCH

Diets of Native and Non-Native Piscivores in the Stanislaus River, California, Under Contrasting Hydrologic Conditions

Matthew L. Peterson¹, Tyler J. Pilger^{1*}, Jason Guignard², Andrea Fuller², Doug Demko¹

ABSTRACT

The fish communities of the Sacramento–San Joaquin Delta and its tributaries in California’s Central Valley have been irreparably altered through introductions of numerous fish species, including Striped Bass (*Morone saxatilis*), black bass (*Micropterus* spp.), and catfishes (*Ameiurus* spp. and *Ictalurus* spp.). Research into how predation by non-native piscivores affects native anadromous species has focused on the Sacramento and San Joaquin river mainstems and Delta habitats, through which all anadromous species must pass. Yet, the ranges of non-native fishes extend into upstream tributaries. We collected diets from native and non-native piscivores in the Stanislaus River, a tributary to the San Joaquin River and a remaining stronghold for native fishes. Piscivorous fishes primarily consumed invertebrates and the native species fall-run Chinook Salmon (*Oncorhynchus tshawytscha*) and Pacific Lamprey (*Entosphenus tridentatus*). Juvenile Chinook Salmon and Pacific Lamprey were consumed at higher frequencies

than any other potential fish prey species, particularly by Striped Bass and black bass. The frequency of native fishes in predator diets was similar across years, despite contrasting hydrologic conditions; 2019 (wet year), 2020 (dry year), and 2021 (critically dry year). Our results show that Pacific Lamprey were frequently consumed by native and non-native piscivores, and that juvenile Chinook Salmon experience substantial predation early in their migration, regardless of hydrologic conditions.

KEY WORDS

black bass, Chinook Salmon, Pacific Lamprey, Striped Bass, diet composition, introduced species

INTRODUCTION

Freshwater ecosystems around the world have been severely affected by numerous anthropogenic alterations including fragmentation, habitat degradation, and introductions of non-native species (Dudgeon et al. 2006; Jackson et al. 2016). The intentional and unintentional translocation of fish species into non-indigenous waters has become so widespread that freshwater fish communities are becoming more similar as popular species are translocated and native species are extirpated or go extinct (Rahel 2002; Olden and Poff 2003;

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Cazelles et al. 2019). Increased understanding of the novel species interactions in managed systems is needed to elucidate what extrinsic factors can exacerbate or ameliorate negative effects on native species. Specifically, increased understanding of how predation dynamics vary in response to external factors, such as discharge, can shed light on population-level effects on native fish species.

The Sacramento and San Joaquin rivers in California's Central Valley form one of the largest freshwater deltas and tidal estuaries in North America, which is also one of the most engineered water systems (Nichols et al. 1986) and most invaded ecosystems in the world (Cohen and Carlton 1998). Throughout the Sacramento–San Joaquin watershed, destructive mining practices, extensive dam construction, conversion of wetlands and floodplain to agriculture land use, hydrologic alteration, and biological invasions have fundamentally altered ecosystem processes and biotic interactions (Nichols et al. 1986; Cohen and Carlton 1998). The combination of these stressors has severely reduced abundance and distribution of native fishes such that fish communities in the Sacramento–San Joaquin system are now dominated by non-native species, particularly centrarchids (Brown and Michniuk 2007; Grimaldo et al. 2009; Mahardja et al. 2017).

Whereas predation by non-native fishes has been implicated in the decline of native fishes in the Sacramento–San Joaquin watershed, the role of predation in causing native fish mortality is context dependent and mediated by other environmental stressors (Grossman 2016). For example, wide-spread proliferation of invasive submerged aquatic vegetation, man-made structures, and artificial lighting are considered to be important factors that exacerbate predation on emigrating juvenile Chinook Salmon (Lehman et al. 2019; Nelson et al. 2021). Alternatively, high and variable spring discharge has been associated with improved survival and recruitment of juvenile Chinook Salmon (e.g., Zeug et al. 2014; Michel et al. 2015; Michel 2019), presumably as a result of reduced predation. Increased water velocity, turbidity, and decreased water

temperature—typically associated with higher discharge—are conditions considered to reduce predation on juvenile salmon (Gregory and Levings 1998; Michel et al. 2020; McInturf et al. 2022).

Diet data from piscivorous fishes in the Sacramento–San Joaquin watershed have been accumulating for over 50 years (reviewed by Grossman 2016) revealing that piscivorous fishes are generalist (i.e., do not specialize on any single prey group) and opportunistic (i.e., foraging on whatever prey is available) feeders. Despite a long history of data collection, knowledge gaps related to the context of predation persist. First, spatial coverage of diet and predation studies has been centered in the mainstem Sacramento and San Joaquin rivers as well as in the legal Delta (see Figure 1 inset). Understandably, studies have focused on these areas because they include designated critical habitat for species listed under the Endangered Species Act. However, trophic interactions in upstream tributaries, where fish species composition differs from the river mainstems and estuarine habitats, are not well documented. Fish communities in river mainstems and the Delta are dominated by non-native fish species (Feyrer and Healey 2003; Brown and Michniuk 2007; Maharjda et al. 2017). As such, non-native prey species are frequently observed in predator diets (e.g., Michel et al. 2018; Weinersmith et al. 2019). In contrast, riverine habitats upstream of the Delta have higher proportions of native fishes, especially in upper reaches (Brown and Ford 2002; Kiernan et al. 2012). Thus, opportunistic, generalist predator diets from upstream tributaries should consist of more native fishes compared to non-natives.

Second, taxonomic coverage in diet studies has been limited because they have tended to focus either on recreationally important predators such as Striped Bass (*Morone saxatilis*), or on impacts of listed species as prey, such as Chinook Salmon, Steelhead, and/or Delta Smelt. Early Striped Bass diet studies in the San Francisco Estuary were implemented to understand what prey resources were important to sustain the population (e.g., Stevens 1966; Thomas 1967). Later, the decline

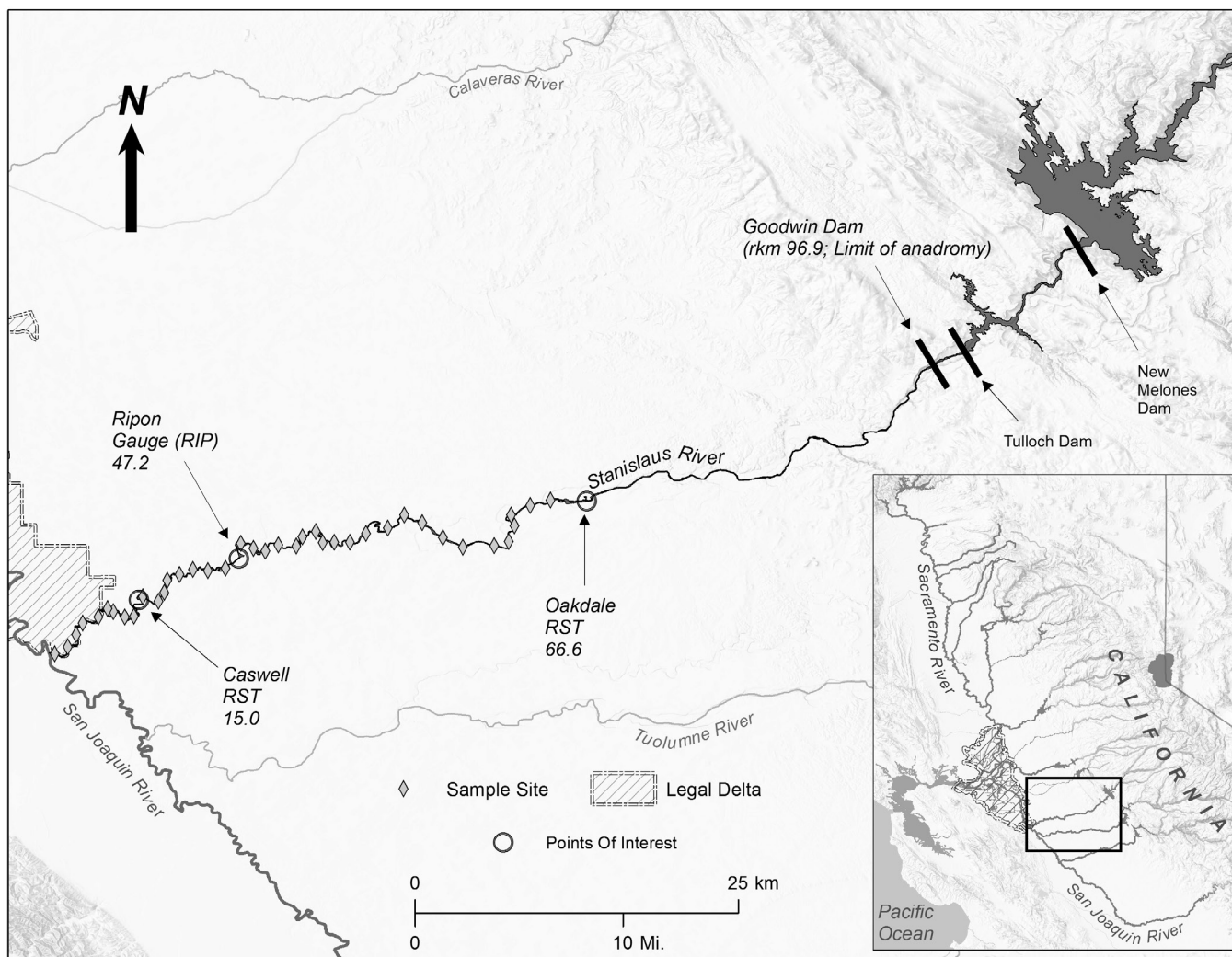


Figure 1 Sampling units (*diamonds*) on the lower Stanislaus River where diets of native and non-native predators were collected in 2019, 2020, and 2021. Additional locations of interest include the boundary of the legal Delta, Oakdale and Caswell rotary screw traps (RSTs), USGS Gauge at Ripon, and Goodwin Dam, which is the upper limit of anadromy. River kilometers are for locations of interest.

and subsequent listing of some native species led to diet studies identifying predation as a threat to those species (Sabal et al. 2016; Weinersmith et al. 2019). Documenting predation on increasingly rare, listed species has spurred innovative genetic identification methodologies (e.g., Baerwald et al. 2012; Brandl et al. 2021). These methods can be used to efficiently characterize the full extent of diets from multiple predators in a fish community. These data are needed to better understand the similarity in diets among native and non-native predators, as well as potential effects on non-listed native fishes.

Finally, temporal coverage of diet information has been limited to relatively short-duration studies, spanning at most 2 years. Whereas short-term studies have yielded valuable insights about trophic interactions, longer-duration studies are needed to assess interannual variation in trophic dynamics, especially regarding environmental variation. For example, the Mediterranean climate of the Sacramento–San Joaquin watershed experiences high interannual variation in precipitation (Dettinger and Cayan 2014). Years with greater than average winter precipitation result in higher discharge volume and cooler water temperatures that are associated with

higher native fish abundance (Brown and Ford 2002; Feyrer and Healey 2003) as well as increased survival of juvenile Chinook Salmon (Michel 2019). In contrast, non-native fishes may respond poorly or get displaced during high-precipitation years, although this has not been thoroughly documented. Annual changes in prey and/or predator species composition that result from annual environmental variation could influence trophic interactions. Therefore, multi-year diet studies that span wet and dry years are a first step in evaluating how environmental variation affects trophic dynamics.

Combined, these knowledge gaps limit our understanding of the full breadth of native and non-native predator-prey interactions spatially and temporally in the Central Valley. To address this, we sampled gut contents from native and non-native piscivores on the Stanislaus River to characterize predation on the native fish community. Using a combination of visual and genetic identification, we quantified predation across 3 years with contrasting hydrology. Specific research objectives were to (1) assess variability in diets of native and non-native piscivores, (2) evaluate inter- and intra-annual variation in native and non-native fish species being consumed, and (3) assess the relationship between predator size and the degree of piscivory (i.e., the probability of consuming fish prey). Seasonal sampling spanned the juvenile fall-run Chinook Salmon emigration period; therefore, we expected that the prevalence of Chinook Salmon in the diet collections would coincide with their seasonal abundance. Furthermore, we expected to see less predation on native species during a high flow year compared to low flow years. Lastly, based on research from elsewhere in the watershed (e.g., Michel et al. 2018; Stompe et al. 2020), we expected Striped Bass and black bass species to exhibit the highest degree of piscivory compared to other predator species. Data on these popular non-native sport fish may help inform water and fisheries management in the regulated Stanislaus River.

MATERIALS AND METHODS

Study Area

The Stanislaus River is a major tributary to the San Joaquin River in California's Central Valley (Figure 1), and because the region experiences a Mediterranean climate, discharge patterns in the Stanislaus River can be highly variable within and among years as a result of fluctuations in seasonal precipitation (Dettinger and Cayan 2014; Dettinger et al. 2016). However, because storage reservoirs capture most of the precipitation, the naturally variable hydrograph of the river has been muted (Kondolf and Batalla 2005). Not only is the Stanislaus River an important source for natural production of fall-run Chinook Salmon (*Oncorhynchus tshawytscha*), but it also remains a stronghold for other native fishes. At least 12 native fishes occur in the river as juveniles that form the native fish prey base. Resident species such as Sacramento Sucker (*Catostomus occidentalis*), Hitch (*Lavinia exilicauda*), Rainbow Trout (*Oncorhynchus mykiss*), and Prickly Sculpin (*Cottus asper*) are present year-round. Migratory juvenile Chinook Salmon and Pacific Lamprey (*Entosphenus tridentatus*) ammocoetes and macrophthalmia provide a seasonally abundant prey source during the late winter and spring (Pilger et al. 2019; Parker 2022). Native fishes known to be piscivorous include Sacramento Pikeminnow (*Ptychocheilus grandis*) and Hardhead (*Mylopharodon conocephalus*; Moyle 2002). Non-native fish species richness now outnumbers native fish richness. Non-native piscivores include Striped Bass, four black bass species (*Micropterus* spp.), five sunfish species (*Lepomis* spp.), crappie (*Pomoxis* spp.), and four catfish species (*Ameiurus* spp. and *Ictalurus* spp.). At least ten additional non-native fishes occur in the Stanislaus River, including members of the families Cyprinidae, Clupeidae, Poeciliidae, Atherinopsidae, and Percidae, all of which may serve as prey for piscivores. Our study took place in the lower 65 km of the Stanislaus River. This reach is below the known salmonid spawning grounds and represents the start of the migratory corridor for anadromous fish before they enter the San Joaquin River.

Fish Capture and Diet Collection

Fish sampling via boat-mounted electrofishing occurred at 39 sample units that were selected according to a stratified random design to represent the entire 65-km survey reach (Figure 1). Each unit was approximately 300 m along either the right or left bank, extending out to the centerline of the channel. At the upstream and downstream boundaries of each unit, we recorded latitude and longitude using a GPS and marked with flagging to facilitate repeated visits within and among years. Sampling events consisted of visiting each unit a minimum of once per month from February through June in 2019, 2020, and 2021. Extraneous factors prevented access to some units over the course of this study, including obstructions that prevented unit access, COVID-19 precautions, and water temperatures that exceeded 18 °C (a permit condition). Limited sampling occurred in June of 2018, but because we collected samples from different units and we used a different protocol for prey item identification, we do not present these data herein.

We targeted native Sacramento Pikeminnow, Hardhead, and non-native Striped Bass, black bass, sunfish, and catfish for diet collection. We discontinued collecting diets from sunfish in 2021 because we observed a low degree of piscivory in samples from 2019 and 2020. We captured fish by boat electrofishing (5.0-watt generator-powered pulsator [GPP], direct current only), and initial settings at each site were typically 60 Hertz and 30% duty cycle at either high or low range. We placed all captured fish in a recirculating tank until processing, and we separated fish less than 100 mm from larger fish to prevent consumptions while in the tank. We collected a water sample prior to sampling each unit on each day for turbidity (1 to 22 samples per day, depending on how many units we visited), and we measured with a LaMotte turbidity meter (Model 2020e, LaMotte Company, Chestertown, MD) and reported in nephelometric turbidity units (NTU).

We measured all captured fish for fork length (FL) and total length (TL) to the nearest millimeter. We collected diet samples from target species

> 70 mm FL by modified gastric lavage (Van Den Avyle and Roussel 1980; Kamler and Pope 2001). Depending on individual size, we inserted a clear acrylic tube through the esophagus into the anterior portion of the gut (outside diameters ranging from 1.27 to 6.35 cm). With the head and tube facing up, we poured river water, free from observable particulates, down the tube, filling the foregut. Then the fish was inverted allowing disgorged contents to pour back through the acrylic tube. The flushing procedure was repeated a minimum of three times to completely recover all gut contents. Prey items were collected on a plastic tray, sieved through a fine mesh aquarium net, and transferred to a 2- or 4-oz plastic vial. Gut contents were preserved using 70% ethanol. Each vial was labeled with site, date, species, fork length (FL), and a unique identification number that corresponded to the individual fish. Fish were PIT tagged for a concurrent mark–recapture study. After tagging, they were placed in aerated buckets or returned to the circulating tank to recover. Once recovered, fish were released near the point of capture, typically in a sheltered location in the middle of the sampling unit.

Prey Identification

Visual identification methods were used exclusively for invertebrates (e.g., insects or crayfish) or non-fish vertebrates (e.g., frogs). Visual identification was also used for fish prey that could be readily and confidently identified to species. Diet items that appeared to be fish but could not be conclusively identified through visual means were subjected to genetic methods.

A sub-sample of tissue (at least 2 mm³ in size) was collected from each discrete item and preserved in 95% laboratory-grade ethanol. Mitochondrial DNA (mtDNA) was extracted from tissue samples using Chelex methods (Walsh et al. 1991). Polymerase chain reaction (PCR) was used to amplify a 572-base-pair fragment of the 16S mtDNA gene in reactions consisting of 6.25 µl of PCR Master Mix (Promega M7505), 0.5 µl of forward primer (400 nM; 16S_{AR}-CGCCTGTTTATCAAAAACAT; Palumbi 1996), 0.5 µl of reverse primer (400 nM) (16S_{BR}-CCGGTCTGAACTCAGATCACGT; Palumbi 1996),

and 1 μ l of DNA template and nuclease free water to bring the total reaction volume to 12.5 μ l. The thermocycle profile consisted of 94 °C for 2 min, 35 cycles of 94 °C for 30s, 52 °C for 40s, and 72 °C for 1 min, with a final extension at 72 °C for 10 min. Amplified PCR products were Sanger sequenced at MCLAB (San Francisco, California). Sequences were identified by comparison to reference sequences archived in GenBank using the Basic Local Alignment Search Tool (National Center for Biotechnology Information). Samples with poor PCR amplification or low sequence similarity to reference sequences were considered unidentifiable.

Data Analyses

Mean daily discharge in cubic feet per second (cfs) and water temperature for each year were downloaded from the USGS Ripon gauging station (#11303000; accessed 2/9/22), which is near the middle of the study reach (Figure 1). Because each sampling event occurred across multiple days (typically 8 days), mean and standard deviation of discharge and water temperature across days in each sampling event were calculated to represent aquatic conditions during each event. Water-year classification for the San Joaquin River watershed during each year of sampling was downloaded from the California Department of Water Resources (CDWR; <https://cdec.water.ca.gov/reportapp/javareports?name=WSIHIST>; accessed 2/9/22).

Predators were assigned to one of six groups for data analysis: Striped Bass, black bass, catfish, sunfish, Sacramento Pikeminnow, and Hardhead. Black bass, catfish, and sunfish were treated as functional groups, which helpfully maximized sample sizes of catfish and sunfish. Counts of each identified prey taxa for individual predators were transformed to presence–absence and then used to calculate the frequency of occurrence (FO), i.e., the proportion of individuals for a given predator group that contained a specific diet item. The FO metric provides a robust quantification of diet composition, especially when the size of prey items varies on orders of magnitude (Baker et al. 2014; Amundsen and Sanchez–Hernandez 2019). This method is also frequently used in other

diet studies in the Central Valley (e.g., Michel et al. 2018; Weinersmith et al. 2019; Stompe et al. 2020), to allow direct comparison between our findings and others. Diet data for each group were summarized at the monthly sampling event and annual-time scales, depending on research objectives.

Variation in Diets among Native and Non-Native Piscivores

We visualized trophic niche space and similarity among predator diets using principal coordinates analysis (PCoA). A PCoA uses ordination to reduce the dimensionality of multivariate diet data so that it can be represented in fewer dimensions (ter Braak 1995). We used the FO of prey items by sampling event to quantify diets for each predator group. We excluded diet items we could not identify. We grouped diet items that occurred at low frequencies (< 1%) across all individuals sampled into rare categories. These included rare native fish, rare non-native fish, other vertebrates (e.g., birds, rodents, and frogs), rare terrestrial invertebrates, and aquatic macroinvertebrates. After grouping, all diet categories were present in 1% or more of all diet samples collected. Diet category FOs by predator group and sampling event were transformed into a Bray–Curtis dissimilarity matrix and we implemented the PCoA using the labdsv package in R (Roberts 2019). Output from the PCoA was visualized to evaluate similarity among diets of predator groups and years. All data analysis was implemented with the programming language R (R Core Team 2020).

Inter-Annual and Intra-Annual Variation in Native and Non-Native Fishes Being Consumed

We tested how frequently (FO) predators consumed fish within and among years using multivariate and univariate approaches. We used permutational multivariate analysis of variance (PERMANOVA; Anderson 2001) to partition variation in the FOs of all prey fishes attributed to predator group (black bass, Striped Bass, catfish, Sacramento Pikeminnow, and Hardhead), sample year (2019, 2020, and 2021), and sequential sampling event (1-13). We excluded sunfish from analysis since diets were not collected in 2021.

We also tested for the effects of mean discharge, mean water temperature, and mean turbidity from each sampling event. We implemented PERMANOVA using the R package (Oksanen et al. 2020) with 1,000 permutations for each test. We ran six single variable models and evaluated models according to their pseudo-P values and partial R^2 . We used Bonferroni correction to adjust the significance level ($\alpha=0.05/6=0.008$) to account for multiple tests. We performed tests on both Bray–Curtis and Euclidian distance matrices to ensure the choice of distance metric did not influence results. We observed no differences in the test outcomes between the distance metrics; therefore, we only report results from Euclidean distance.

Our univariate approach consisted of multiple pairwise comparisons that tested for differences in the FO of prey fishes between different predator groups, between sampling events, and between years to identify any differences not observed with the multivariate approach. We treated FO as a proportion (i.e., the proportion of predator x that consumed prey fish i during sampling event e) and used the ‘prop.test’ function to perform tests of equal proportions (Wilson 1927, hereafter proportion tests). We excluded sampling events where fewer than 15 individuals per predator group were captured to minimize random variation associated with small sample sizes. Again, we applied Bonferroni corrections to adjust the significance level, depending on the number of tests performed. For any significant proportion test, we implemented a permutation test (Millard 2013; R package EnvStats) based on Fisher’s exact test (Fisher 1935) to evaluate if the difference in proportions was from random chance. For each comparison between two FOs, a total of 1,000 permutations was used.

Relationship Between Predator Size and Degree of Piscivory

We used binomial generalized linear models (GLM) to examine how predator size affected the probability that a black bass or Striped Bass consumed *any* fish (regardless of species), Chinook Salmon, or Pacific Lamprey. We conditioned the probability on predators that

had recently fed (i.e., not empty) for two reasons. First, empty samples do not provide data on what a predator has consumed, and second, the addition of zeros from empty samples could cause overdispersion in presence–absence data. For both predators and each prey fish category (any fish, Chinook Salmon, or lamprey) we compared an intercept and FL slope model with a model that contained a quadratic term for FL. The latter model was to account for a possible change in direction of probability as FL increased. We compared models based on the Akaike information criterion (AIC) and how well the predicted values fit the data.

RESULTS

Environmental Conditions

Water years 2019 through 2021 were classified as wet, dry, and critically dry, respectively. Mean discharge during multi-day sampling events was lowest in February 2021 (247 cfs, SD=44.7) and greatest during the March 2019 event (4,628 cfs, SD=20.4; Figure 2). Mean water temperatures were coolest during February events in 2020 (9.8 °C, SD=0.48) and 2021 (10.9 °C, SD=0.74); no samples were collected in February 2019. Warmest water temperatures each year occurred in June 2019 (16.2 °C, SD=0.46), June 2020 (15.8 °C, SD=0.26) and mid-May 2021 (16.2 °C, SD=0.84); no sampling occurred in June 2021 because water temperatures exceeded 18 °C. Across all years, turbidity was low, but highest in 2019 (mean=4.1 NTU; SD=3.1) compared to 2020 (mean=3.1 NTU; SD=2.3) and 2021 (mean=3.1 NTU, SD=2.1).

Predator Diets

A total of 2,844 individual predators were sampled for diets over 3 years (Table 1). Black bass comprised 62% (n=1,770) of samples and Striped Bass 16% (n=441) of samples. Catfish were infrequently encountered, and we stopped collecting diets from sunfish after 2020. Combined, native Sacramento Pikeminnow (n=255) and Hardhead (n=155) comprised 14% of diet samples. For all species, diet samples were collected from a broad range of sizes (see Table A1 and Figure A1 in Appendix A), especially from Striped Bass (166 to 1,090 mm FL), Sacramento

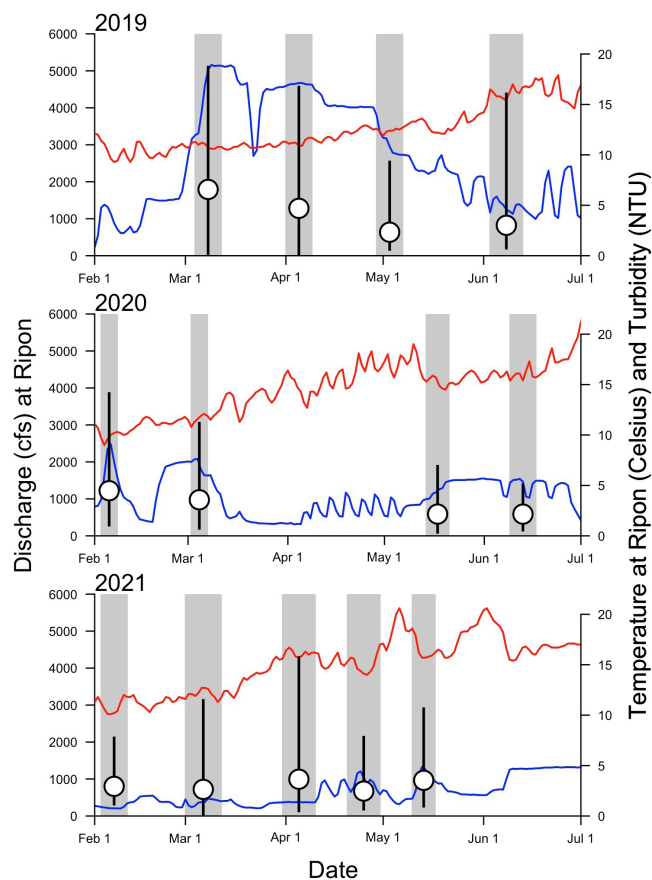


Figure 2 Environmental conditions in the lower Stanislaus River during each year 2019 (top), 2020 (middle), and 2021 (bottom). Grey shaded areas indicate multi-day sampling events. Discharge (left y-axis) is represented by the blue line. Water temperature (right y-axis) is represented by the red line. Points indicate mean turbidity (right y-axis), black lines indicating the range of measured turbidity values during the sampling event.

Pikeminnow (63 to 700 mm FL), and black bass (67 to 511 mm FL).

Native predators had a higher percentage of empty guts (49% empty) than non-native predators (30% empty, Figure A1). Percent of empty guts was lowest for catfish (28%) and highest for Sacramento Pikeminnow (55%; Table 1). From the predators that did not have empty guts, we recovered 18,815 prey items and visually identified them. We genetically identified tissue samples from 1,079 presumed fish. Because of poor sequence quality, we could not identify 7% of those samples. In total, 4% of all recovered items were unidentifiable using visual and genetic

methods, and thus excluded from analyses. Of identified prey items, 88% were invertebrates, 8% were fish, and a small fraction were non-fish vertebrates (0.001%). Consumed fishes were identified to 15 genera that represented, at minimum, 21 species, of which six were native species and 15 were non-native (Table A1). We enumerated 1,493 identifiable fishes consumed by all predators examined, and 95% of those were native species.

Striped Bass, black bass, and Sacramento Pikeminnow were the most piscivorous species, in terms of FO and number of different taxa consumed (10, 12, and 6, respectively; Table A1). Striped Bass consumed Pacific Lamprey most frequently (FO=0.29), followed by Chinook Salmon (FO=0.17). Sacramento Sucker were found in 3% of Striped Bass guts, whereas the remaining taxa were less frequently observed. Although most black bass guts contained invertebrates (crayfish FO=0.19, dragonflies FO=0.15, caddisflies FO=0.14, and mayflies FO=0.24), Sacramento Sucker and Prickly Sculpin were the most frequently consumed fishes (FOs=0.08 and 0.05, respectively). Juvenile salmon and lamprey were observed in 4% and 3% of black bass, respectively. The most frequently observed fish in Sacramento Pikeminnow guts was lamprey (FO=0.03), while salmon, suckers, sculpin and juvenile centrarchids (black bass and Bluegill, *Lepomis macrochirus*) each had FO=0.01. The only fish prey observed in catfishes were lamprey and suckers, whereas Hardhead had consumed lamprey, suckers, pikeminnow, and Hitch. A small percentage of sunfish diets contained larval suckers and Common Carp (*Cyprinus carpio*). Overall, black bass consumed the greatest number of native species (n=6), followed by Striped Bass (n=5).

Identified prey items were grouped into one of 21 prey categories for the PCoA (Table 2). The first two principal coordinate axes accounted for 40.5% of variation in diets among predators. Overall, there was a high degree of overlap in predator diets (Figure 3). The first axis distinguished black bass diets, consisting of crayfish and Sacramento Sucker, from other species that had high FOs of

Table 1 Summary of the total number of diet samples collected, mean predator fork length (standard deviation; SD), and percentage of empty guts from predators sampled on the Stanislaus River between 2019 and 2021. Predator codes used in [Figure 3](#) and [Table 3](#).

Group	n	Mean length (mm)	Length SD (mm)	Minimum length (mm)	Maximum length (mm)	Percent empty (%)
Black Bass (BB)	1,770	216	82.5	67	511	30
Catfishes (CAT) ^a	90	299	123.9	138	575	28
Hardhead (HH)	155	385	59.9	80	505	39
Sacramento Pikeminnow (SAPM)	255	272	141.5	63	700	55
Striped Bass (STB)	441	388	150.2	166	1,090	31
Sunfishes (SUN) ^b	133	149	33.5	70	226	32

a. Total length used for catfish.

b. Diets from sunfishes were only collected in 2019 and 2020.

annelid worms in their diets. High scores on the second axis were associated with diets that had high frequencies of Chinook Salmon and lamprey, whereas low scores indicated diets that contained zooplankton and snails. Striped Bass typically had high second-axis scores while sunfishes had low scores. Catfishes, Hardhead, and Sacramento Pikeminnow exhibited the greatest variation and overlap in trophic niche space.

Inter-Annual and Intra-Annual Variation in Native and Non-Native Fishes Being Consumed

Of the six PERMANOVA models used to partition variation in FO of fish prey, only predator group explained a significant amount of variation (76%, P -value < 0.001). No other variable explained more than 11% of variation in diets.

All predators examined consumed native prey fish species at higher frequencies than non-native fish prey in all 3 years ([Figure 4](#)).

- In **2019**, the FO for non-native predators that consumed native fish prey (FO=0.23, 95% CI=0.20–0.26) was 8.1 times higher ($P < 0.001$, $n=771$) than the FO for non-native fish prey (0.03, 0.02–0.04).
- In **2020**, the proportion of native fish prey (0.28, CI=0.25–0.31) exceeded the proportion of non-native fish prey (0.02, CI=0.01–0.03) by 12 times ($P < 0.001$, $n = 736$).
- In **2021**, the frequency of native prey (0.19, CI=0.17–0.22) consumed was 7.7 times higher

($P < 0.001$, $n=926$) than non-native prey (0.02, CI=0.01–0.03).

Only Striped Bass and black bass, which accounted for 78% of diet samples, had sufficient sample size for univariate comparisons between and within years. And, since Pacific Lamprey and Chinook Salmon were the most frequently encountered prey fish species, we focus subsequent comparisons on these two predators and prey species.

The proportion of Striped Bass that consumed Chinook Salmon on a yearly basis was different ($P=0.012$) with 2019 being greatest (FO=0.24, CI=0.17–0.30) followed by 2021 (FO=0.15, CI=0.09–0.21) and 2020 being the least (FO=0.11, CI=0.06–0.17; [Figure 5](#)). There was no difference between 2019 and 2021, but 2019 and 2020 were different ($P=0.007$). For lamprey, interannual differences were also significant ($P < 0.001$), with lower FO in 2019 (0.17, CI=0.11–0.23) and higher in 2020 (0.42, CI=0.33–0.50) and 2021 (0.31, CI=0.24–0.39). Within years, juvenile Chinook Salmon FO for Striped Bass differed across sampling events in 2019 ($P=0.031$) and 2020 ($P=0.008$), but not in 2021 ($P=0.081$). Sample sizes of Striped Bass for the first three events in 2021 were low (2, 7, and 5 individuals, respectively), and thus not included in comparisons. Chinook Salmon FO was greatest in May 2019 and 2020 and late April of 2021. There were no within-year differences in the FO of lamprey consumed by Striped Bass.

Table 2 Frequency of occurrence for each prey category by each group of predators, excluding unknown or unidentified diet items and empty guts. Values in parentheses are total counts for each item.

Diet Category	Black Bass	Catfish	Hardhead	Sacramento Pikeminnow	Striped Bass	Sunfish ^a
Pacific Lamprey	0.033 (63)	0.106 (12)	0.013 (4)	0.031 (10)	0.288 (309)	0 (0)
Chinook Salmon	0.043 (97)	0 (0)	0 (0)	0.011 (3)	0.169 (132)	0 (0)
Sacramento Sucker	0.079 (484)	0.053 (31)	0.006 (1)	0.011 (3)	0.029 (46)	0.03 (83)
RareNatFish ^b	0.006 (13)	0 (0)	0.108 (16)	0 (0)	0.002 (1)	0 (0)
Prickly Sculpin	0.049 (97)	0 (0)	0 (0)	0.011 (4)	0.002 (2)	0 (0)
Centrarchid ^c	0.016 (34)	0 (0)	0 (0)	0.011 (3)	0.02 (11)	0 (0)
RareNNFish ^d	0.007 (13)	0 (0)	0 (0)	0 (0)	0.022 (12)	0.022 (6)
TerrVert ^e	0.006 (10)	0.043 (4)	0 (0)	0.019 (5)	0 (0)	0 (0)
Annelids	0.029 (134)	0.106 (250)	0.185 (230)	0.118 (119)	0.13 (504)	0.193 (107)
Beetles	0.022 (145)	0.074 (9)	0.013 (36)	0.031 (53)	0.004 (156)	0.022 (19)
Caddisflies	0.135 (713)	0.309 (168)	0.013 (10)	0.069 (97)	0.135 (531)	0.059 (17)
Clams	0.001 (1)	0.032 (26)	0.134 (177)	0 (0)	0.002 (1)	0.015 (2)
Crayfish	0.19 (381)	0.149 (16)	0.057 (9)	0.023 (6)	0.065 (35)	0.03 (4)
Dragonflies	0.153 (533)	0.117 (22)	0.006 (1)	0.019 (6)	0.061 (55)	0.119 (47)
Flies	0.069 (517)	0.213 (78)	0.057 (66)	0.042 (34)	0.045 (186)	0.281 (402)
Isopods	0.007 (31)	0.106 (53)	0.032 (51)	0.019 (10)	0.013 (11)	0.03 (23)
Mayflies	0.242 (4869)	0.266 (117)	0.013 (2)	0.008 (2)	0.061 (268)	0.111 (67)
Snails	0.003 (6)	0.074 (15)	0 (0)	0.023 (11)	0 (0)	0.081 (332)
True Bugs	0.129 (807)	0.053 (8)	0.006 (1)	0.004 (1)	0.011 (7)	0.089 (51)
RareInverts ^f	0.02 (48)	0.16 (41)	0.045 (18)	0.023 (6)	0.016 (7)	0.052 (44)
Zooplankton	0.028 (698)	0.064 (101)	0.006 (1)	0 (0)	0.016 (2544)	0.23 (333)

a. Sunfish diets were not collected in 2021.

b. Rare Native Fishes: Sacramento Pikeminnow, Hitch.

c. Largemouth Bass (*Micropterus salmoides*), Redeye Bass (*M. coosae*), Smallmouth Bass (*M. dolomieu*), Bluegill (*Lepomis macrochirus*), Green Sunfish (*L. cyanellus*), Redear Sunfish (*L. microlophus*), Black Crappie (*Pomoxis nigromaculatus*), White Crappie (*P. annularis*).

d. Rare Non-native Fishes: Channel Catfish, White Catfish, Black Bullhead (*Ameiurus melas*), Fathead Minnow (*Pimephales promelas*), Striped Bass, Goldfish (*Carassius auratus*), Common Carp.

e. Terrestrial Vertebrates: birds, frogs, rodents.

f. Rare Invertebrates: bees, wasps, ants, butterfly or moth, centipedes, millipedes, grasshoppers, spiders, dobsonflies, and stoneflies.

Black bass consumed Chinook Salmon and Pacific Lamprey at lower frequencies than Striped Bass (Figure 5). On a yearly basis, the proportion of black bass that consumed salmon was significantly greater in 2019 (0.09, CI=0.06–0.12) compared to 2020 (0.03, CI=0.01–0.04) and 2021 (0.02, CI=0.01–0.04; $P < 0.001$). No within-year differences in Chinook Salmon FO were observed in black bass diets during 2019, but differences between sampling events were observed in 2020 ($P=0.023$) and 2021 ($P=0.035$). In 2020, Chinook Salmon FO in black bass diets was greatest in February, while in 2021, the greatest FO was in

early April. No within-year differences in FO for lamprey consumption were observed in any year.

Relationship Between Predator Size and Degree of Piscivory

We detected fish in the diets of black bass as small as 79 mm FL. The smallest that consumed juvenile Chinook Salmon was 90 mm FL. Individuals between 205 and 263 mm FL accounted for half of Chinook Salmon predation. Black bass in this size range represented 26% of the total number of black bass captured. For all three fish prey categories, the quadratic binomial models had AIC values 15 to 35 points lower than the linear

Table 3 Estimated annual proportions and 95% confidence interval of each predatory species that had consumed native fishes in the Stanislaus River from 2019 to 2021

Group	Year	n	Chinook Salmon	Lamprey	Sacramento Pikeminnow	Sacramento Sucker	Hitch	Prickly Sculpin
BB	2019	487	0.09 ± 0.03	0.03 ± 0.01	0 ± 0	0.07 ± 0.02	0.01 ± 0.01	0.05±0.01
	2020	512	0.03 ± 0.01	0.04 ± 0.02	0.01 ± 0.01	0.16 ± 0.03	0 ± 0	0.04±0.02
	2021	771	0.02 ± 0.01	0.04 ± 0.02	0 ± 0	0.04 ± 0.01	0 ± 0	0.06±0.02
CAT	2019	47	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0
	2020	25	0 ± 0	0.12 ± 0.13	0 ± 0	0.08 ± 0.11	0 ± 0	0 ± 0
	2021	18	0 ± 0	0.22 ± 0.19	0 ± 0	0.06 ± 0.11	0 ± 0	0 ± 0
HH	2019	83	0 ± 0	0.01 ± 0.02	0 ± 0	0.01 ± 0.02	0.18 ± 0.08	0 ± 0
	2020	67	0 ± 0	0.01 ± 0.03	0.01 ± 0.03	0 ± 0	0 ± 0	0 ± 0
	2021	5	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0
SAPM	2019	47	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0
	2020	95	0.02 ± 0.03	0.03 ± 0.04	0 ± 0	0 ± 0	0 ± 0	0 ± 0
	2021	113	0 ± 0	0.04 ± 0.03	0 ± 0	0.03 ± 0.03	0 ± 0	0.01 ± 0.02
STB	2019	170	0.24 ± 0.06	0.17 ± 0.06	0.01 ± 0.01	0.04 ± 0.03	0 ± 0	0 ± 0
	2020	134	0.11 ± 0.05	0.42 ± 0.08	0 ± 0	0.03 ± 0.03	0 ± 0	0.01 ± 0.01
	2021	137	0.15 ± 0.06	0.31 ± 0.08	0 ± 0	0.02 ± 0.02	0 ± 0	0 ± 0
SUN ^a	2019	67	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0
	2020	65	0 ± 0	0 ± 0	0 ± 0	0.06 ± 0.06	0 ± 0	0 ± 0

a. Gut contents were not collected in 2021.

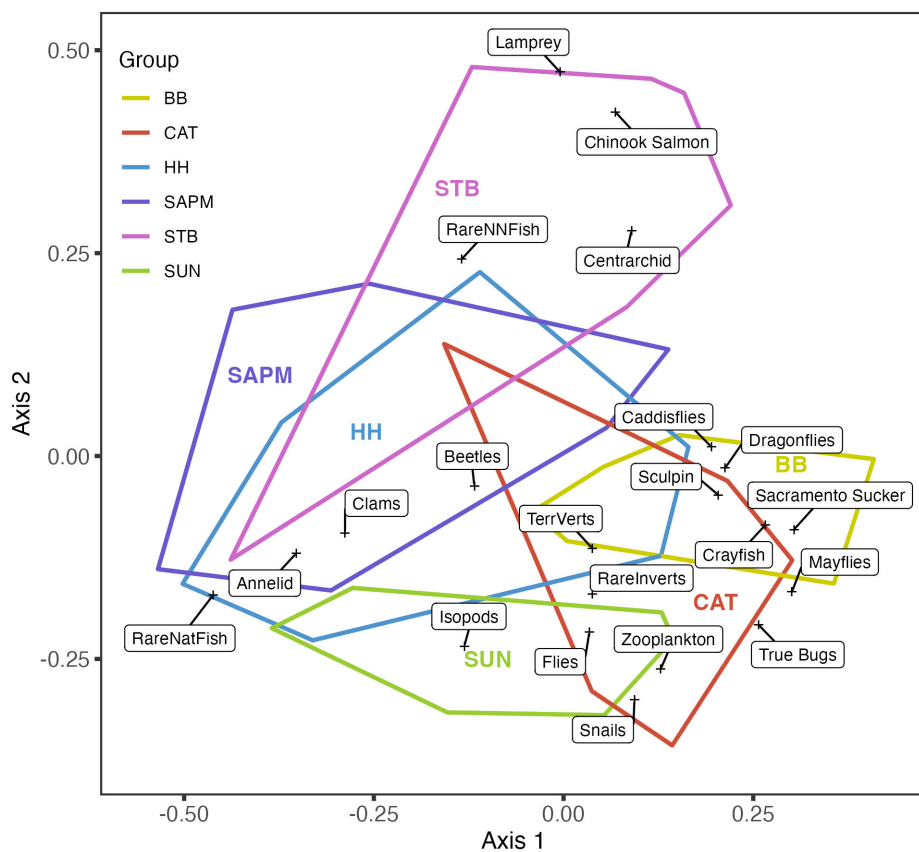


Figure 3 Principal coordinates analysis of Stanislaus River predator diets collected from 2019 to 2021. Diet categories (+) are displayed in ordination space along axes 1 and 2. Convex hulls surround points (not shown) for each species-by-event sample. Colors indicate predator groups. Note: sunfish diets were not collected in 2021.

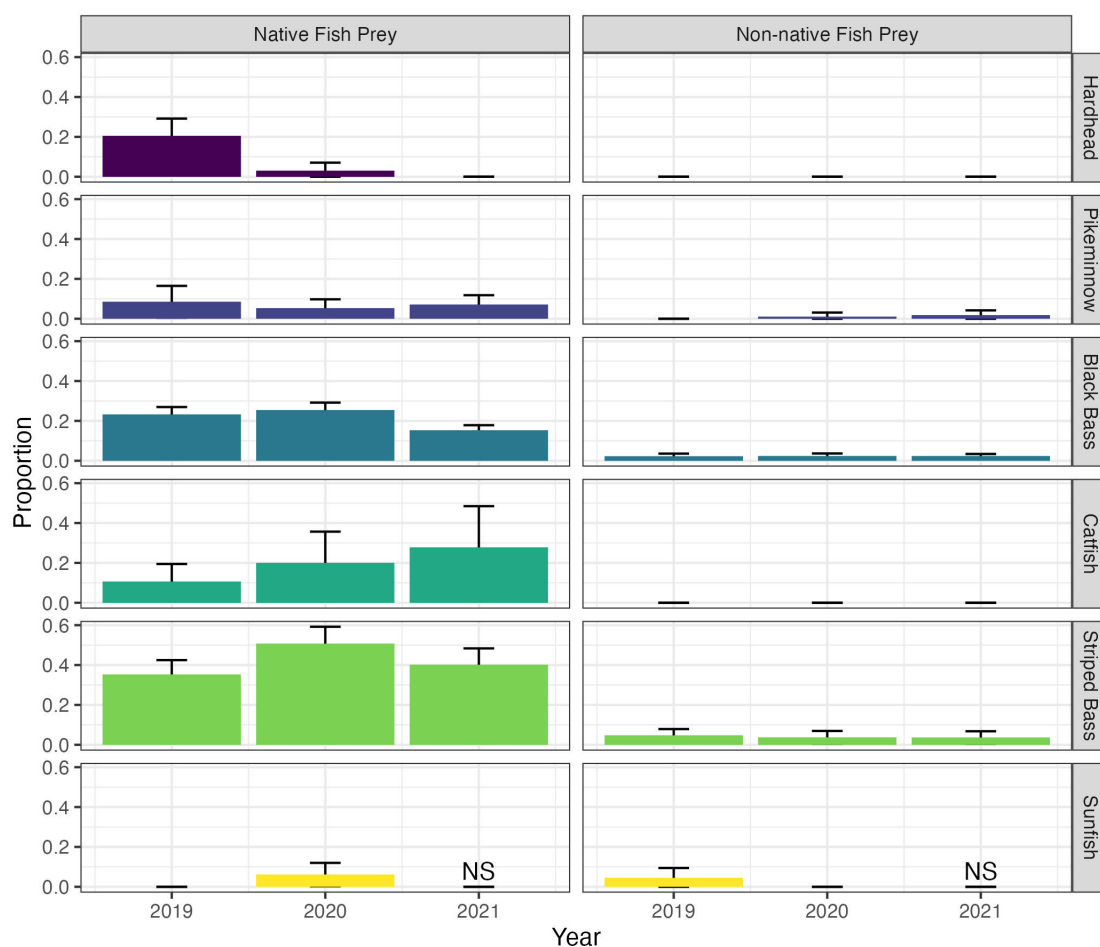


Figure 4 Estimated annual proportion of major predators that consumed native (left) or non-native (right) fish prey. Error bars represent the 95% confidence interval around each estimated proportion. NS indicates no sample collected.

models (Table A2 in Appendix A). The probability of consuming a fish, regardless of prey species, increased for black bass up to 290 mm FL. The probability of consuming a Chinook Salmon peaked at approximately 260 mm FL, and the probability of consuming a Pacific Lamprey peaked around 325 mm FL (Figure 6). The probability of consuming fish prey decreased for increasingly larger black bass.

The smallest Striped Bass that consumed any fish was 169 mm FL, and 64% of individuals that consumed any fish were between 450 and 500 mm FL. Although the AIC value for the linear model that predicted the probability of consuming any fish was greater than the quadratic model by 2.3 (Table A3), the linear model produced a better fit to the data (Figure 6, lower left panel). Striped Bass greater than 565 mm FL had a 0.90 or greater probability that they

consumed any fish. Striped Bass between 315 and 471 mm FL accounted for half of Chinook Salmon predation. Striped Bass in this size range represented 41% of the total number of Striped Bass captured. The binomial models for the probability of consuming Chinook Salmon or a lamprey had AIC values lower by 22 and 35 than the linear models, respectively. The probability of consuming a juvenile Chinook salmon increased for Striped Bass up to 635 mm FL (0.34), but a 900 mm FL Striped Bass had a 0.03 probability of consuming a juvenile salmon. The probability of consuming juvenile lamprey increased for Striped Bass up to 470 mm FL (0.59) and decreased for larger Striped Bass.

DISCUSSION

We used diet data collected from the main piscivores of the Stanislaus River fish community

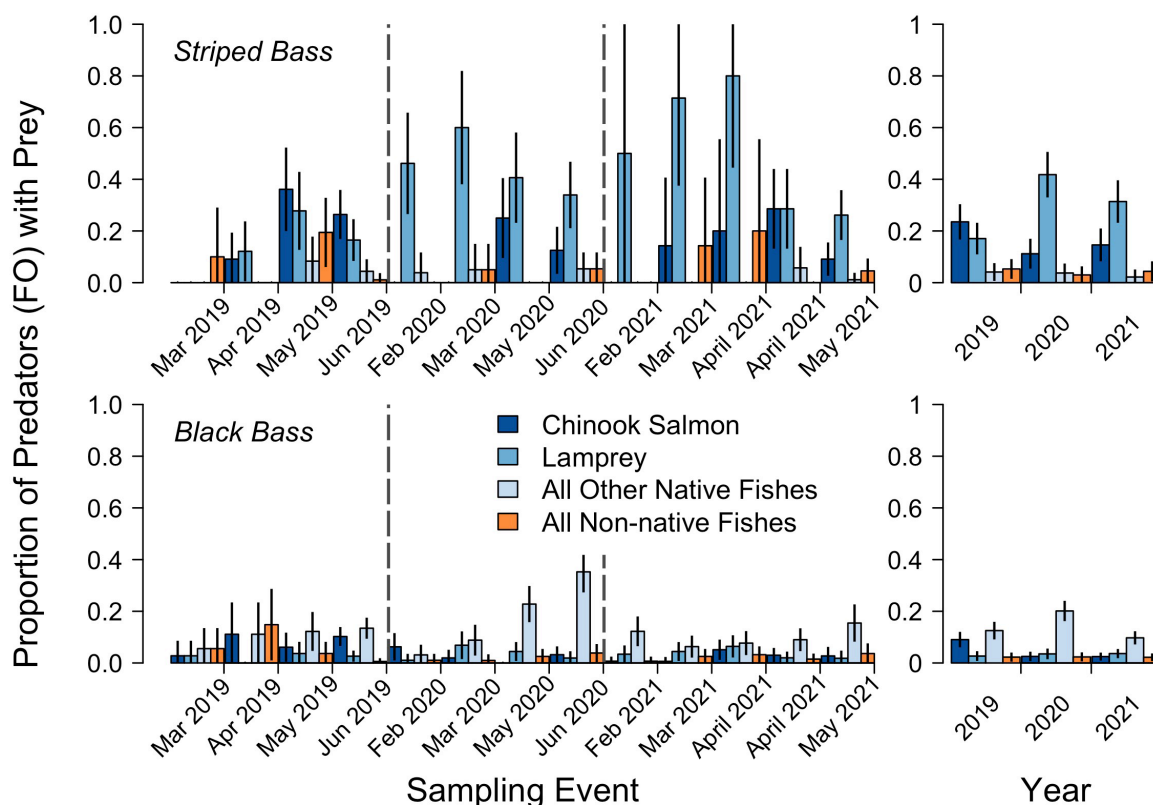


Figure 5 Estimated proportions of Striped Bass and black bass that consumed native and non-native fishes by sampling event and year on the Stanislaus River between 2019 and 2021. 95% confidence intervals are provided around each estimated proportion.

to provide the most comprehensive assessment to date of consumption of native and non-native species within this river. Because our diet samples were collected across 3 years, we were able to evaluate the interannual magnitude and variation of predation on native fishes. Despite there being substantially different hydrologic conditions in each year, we observed remarkably little variation in the diets of non-native predators, specifically the proportion of native to non-native prey. In the Stanislaus River, Striped Bass, black bass, and Sacramento Pikeminnow were the most piscivorous species. Unlike diet studies downstream in the Sacramento–San Joaquin Delta (e.g., Michel et al. 2018; Weinersmith et al. 2019), these predators consumed native prey more frequently than non-native prey. The frequency of native fish prey in the diets of non-native predators was about nine times higher than it was for non-native fish prey. We also found that juvenile lamprey were an under-

appreciated prey resource for both non-native and native piscivores. Whereas previous studies have documented occasional or infrequent consumption of lamprey (see review by Grossman 2016; Weinersmith et al. 2019; Stompe et al. 2020), ours is the first to document such a high magnitude of predation as well as the breadth of species that consume lamprey.

Predator Diets

All target species in this study were known to be generalist feeders (Grossman 2016); as such, we expected to observe non-fish prey items. Invertebrates (mainly insects, annelids, and crayfish) were the most frequently observed prey items across all predators examined, followed by native fishes, non-native fishes, and a variety of miscellaneous prey (i.e., frogs, birds). Previous Central Valley studies from rivers and the Delta have found that invertebrates were a common but variable prey resource for these

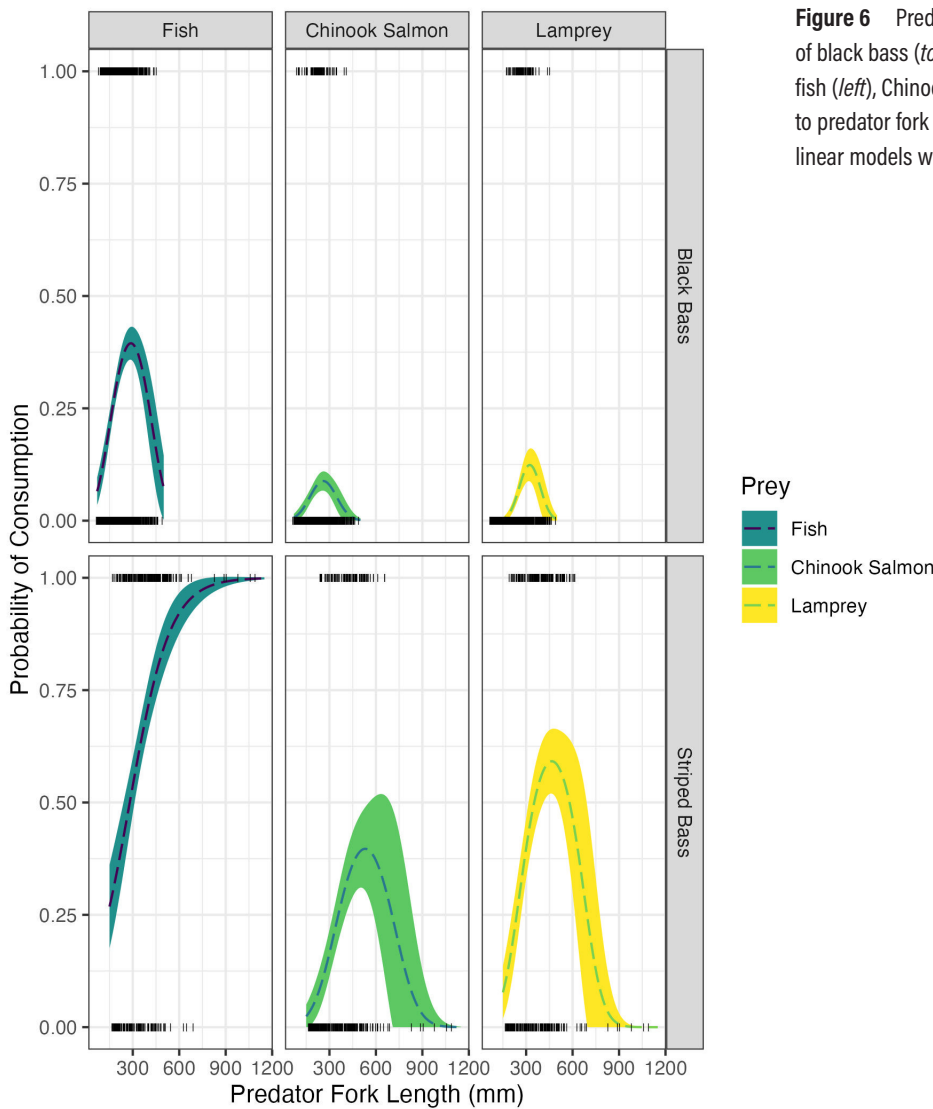


Figure 6 Predicted probability and 95% confidence intervals of black bass (*top*) and Striped Bass (*bottom*) consuming any fish (*left*), Chinook Salmon (*center*), or lamprey (*right*) in relation to predator fork length. Relationship was fit using generalized linear models with a binomial distribution

species. For sunfish, catfish, and Hardhead diets, invertebrates were frequently observed with FOs of 0.60, 0.35, and 0.30, respectively, which was consistent with dietary descriptions for these taxa (Moyle 2002). The proportion of Striped Bass we observed that consumed invertebrates (FO = 0.45) was similar to what Stompe et al. (2020) observed (0.52) and higher than 0.20 reported by Sabal et al. (2016). The frequency in which Sacramento Pikeminnow consumed invertebrates in this study (0.35) was lower than the 0.48 recorded by Stompe et al. (2020) but higher than the 0.20 reported by Tucker et al. (1998). In the Stanislaus River, black bass of all sizes consumed invertebrates at the highest frequency (0.70) across all 3 years.

Invertebrates were commonly observed in the diets of Largemouth Bass in the Delta (Norbriga and Feyrer 2007; Weinersmith et al. 2019), as well as Striped Bass in the estuary (Young et al. 2022). Overall, Stanislaus River predators exhibited a high degree of trophic overlap. This was, in part, the result of the high prevalence of invertebrates in the diets of all predators and because we coarsely identified invertebrate prey items to the taxonomic level of Order.

The high FO of Pacific Lamprey in the diet samples suggested that they are at least seasonally abundant in the Stanislaus River and acted as an important prey resource for piscivores.

Other diet studies from the Central Valley have observed predation on lamprey and have ranged from low frequencies (e.g., 0.0 to 0.10 for a variety of predators; FISHBIO 2013; Sabal et al. 2016; Weinersmith et al. 2019; Brandl et al. 2021) to the highest frequency previously reported in Stompe et al. (2020). In that study, Striped Bass (FO=0.22) and Sacramento Pikeminnow (FO=0.16) consumed Pacific Lamprey. Striped Bass consumed River Lamprey (*Lampetra ayresi*) in estuarine habitats in June (Young et al. 2022). We observed higher annual FOs of Striped Bass with Pacific Lamprey with 0.17, 0.42, and 0.31 in 2019, 2020, and 2021, respectively. Whether this difference was the result of our upstream location where more lamprey occur, seasonal timing of sampling, or a higher detection probability for lamprey in diets, is unknown. In addition, we documented that most of the Stanislaus River predators consumed lamprey. Parker (2022) observed that the Oakdale rotary screw trap (RST) on the Stanislaus River had the highest relative catch of lamprey of all rivers that had RST monitoring programs in the Central Valley. However, unlike Chinook Salmon, no estimates of trap efficiency for lamprey were available to expand seasonal catch into abundance estimates. We are not aware of abundance or production estimates for lamprey elsewhere in the Central Valley; however, some information is available on their migration patterns (Goodman et al. 2015; Parker 2022) and occupancy in the estuary (Goertler et al. 2020). Throughout the year, Lamprey were captured by RSTs in the upper Sacramento River, though the peak period of emigration or downstream movement appeared to be from October to May and associated with rainfall events (Goodman et al. 2015). From November to March, further downstream in the Delta, Goertler et al. (2020) found that juvenile lamprey were most frequently captured by a variety of sampling gears.

Native Sacramento Splittail (*Pogonichthys macrolepidotus*), Hardhead, and steelhead/Rainbow Trout were not detected in the diets of predators, despite being present in the Stanislaus River and captured during the study. Lack of detections may be a result of low abundance,

insufficient sampling effort, mismatch between prey size and predator gape size, and/or increased predator avoidance ability. In 3 years of sampling, only 22 steelhead/trout and 120 Sacramento Splittail were captured while electrofishing. Taken together, our sample units covered approximately 10% of total available area, and were sampled for 2 days per month each year. Increased sampling effort in time and space would increase the chance of detecting rare diet items. Rainbow Trout have primarily occurred in the Stanislaus upstream of the sampling area, and steelhead smolts were rarely captured on the Stanislaus River (Eschenroeder et al. 2022). Hardhead were more numerous in electrofishing catch (n=608), but only 21% were less than or equal to 150 mm. Sacramento Splittail and trout in the catch were also large with minimum FLs of 235 mm and 184 mm, respectively. In addition, steelhead smolts may be less susceptible to predation as they predominantly migrate at night (Chapman et al. 2013).

Although we detected more non-native than native fish species in the diets of predators, all non-native fishes combined were consumed at significantly lower frequencies than native fishes. Native species made up 95% of identified fish prey consumed in this study. This result was markedly different than the ratio between native and non-native fish prey observed in the lower San Joaquin River (Michel et al. 2018). In that study, which also sampled predators during peak Chinook Salmon migration, non-native fish prey were more frequently consumed by Striped Bass, Largemouth Bass, White Catfish (*Ameiurus catus*), and Channel Catfish (*Ictalurus punctatus*) than native fishes. Chinook Salmon, Sacramento Splittail, Rainbow Trout, and Delta Smelt were consumed by less than 10% of Striped Bass, Largemouth Bass, and White Catfish; however, Channel Catfish consumed those prey species at more elevated rates (Michel et al. 2018). We did not observe catfish preying on Chinook Salmon in the Stanislaus River, but the low number of catfish we examined may have limited our ability to detect this prey species. Non-native fish have high relative abundance in the lower San Joaquin River and south Delta (Brown and Michniuk

2007), resulting in a prey base dominated by non-native fish. In the north Delta, which remains a stronghold for native fish species (Moyle et al. 2012), Brandl et al. (2021) found that FO of native fish prey was 51% higher than what Michel et al. (2018) observed. On the Stanislaus River, native species have higher relative abundance than in the lower San Joaquin River, especially during the juvenile Chinook Salmon migration season when estimates of abundance can range from 127,000 to over 2 million (Pilger et al. 2019).

Inter-Annual and Intra-Annual Variation in Native and Non-Native Fishes Consumed

In the Stanislaus River, juvenile fall-run Chinook Salmon hatch and rear upstream of the Oakdale RST from January through February, then begin to migrate through the lower Stanislaus River as fry, parr, and smolts beginning in February, typically peaking in mid to late April (Pilger et al. 2019). The number of migrating salmon declines sharply in May, and by June, few salmon remain in the river. This seasonality of juvenile salmon abundance was reflected in the monthly diet samples, particularly in Striped Bass and black bass. Although Chinook Salmon were infrequently observed in the diets of Sacramento Pikeminnow, when they were detected, it coincided with the highest frequencies observed in Striped Bass. The greatest probability of detecting salmon in diets of these three predators occurred in April and May, and this pattern was similar across years. Lamprey were more frequently captured in the RST from February through April (Parker 2022), and this was when we observed peaks in FO of lamprey in the diets of Striped Bass. Predator diets tended to be more variable across sampling events within years rather than among years, likely because of seasonal changes in relative abundance of prey species.

Over the 3 years that this study was implemented, the Stanislaus River fish community experienced a broad range of hydrologic conditions, and this allowed for a qualitative assessment of how consumption of native and non-native fishes varied with discharge. We found a higher frequency of predation on juvenile Chinook salmon by black bass in 2019, a wet year,

compared to 2020 and 2021, dry and critically dry years, respectively. Striped Bass predation on Chinook Salmon was also highest in 2019, compared to 2020 and 2021. One potential explanation for higher FO of Chinook Salmon in 2019 is that they were more abundant in 2019 compared to the drier years. Estimates of annual abundance of juvenile Chinook Salmon at the Oakdale RST (at the top of the study reach) and the Caswell RST (near the bottom of the study reach) were highest in 2019 and declined thereafter (Table A4, Appendix A). In contrast to juvenile Chinook Salmon, Striped Bass predation on lamprey increased during 2020 and 2021. Total catch of lamprey at the Oakdale RST was greatest in 2019 ($n=8,671$) compared to 2020 and 2021 ($n=1,666$ and $n=1,353$, respectively; FISHBIO unpublished data, see “Notes”). If RST catch were proportional to lamprey availability, this may suggest Striped Bass are more effective consumers of lamprey at lower flows. However, lamprey may be more susceptible to capture by the RST at high flows. Without knowing the empirical relationship between flow and lamprey capture probability, these catch numbers cannot be expanded to abundance. Thus, abundance estimates of all prey species are needed to better understand predator–prey dynamics when multiple prey species are present.

Higher and more variable discharge during the spring is associated with improved survival and recruitment of juvenile Chinook Salmon (Zeug et al. 2014; Michel et al. 2015; Sturrock et al. 2015; Michel 2019). Therefore, we expected to observe lower frequency of predation on Chinook Salmon in the wet year 2019 compared to drier years 2020 and 2021. Although river discharge was substantially different across years, turbidity in the Stanislaus River remained low, even during high flow events. Our findings suggest that predatory fish, particularly Striped Bass and black bass, still effectively detected, pursued, captured, and ultimately consumed juvenile Chinook Salmon even in periods of high discharge and cool water temperatures. However, because juvenile Chinook Salmon were more abundant in 2019, predator capture efficiency per attempt on a juvenile Chinook Salmon may have been lower,

thus resulting in FOs similar to dry years. These results suggest that mechanisms beyond the scope of this study may play a larger role in mediating the relationship between discharge and survival. Exploring these alternative mechanisms would be a valuable avenue of future research, especially in the San Joaquin River watershed where recent survival rates of emigrating Chinook Salmon have been very low (Buchanan and Skalski 2020).

Influence of Size on Piscivory

Black bass exhibited piscivory at the smallest size compared to any other predator. We observed piscivory by black bass as small as 79 mm FL and consumption of Chinook Salmon by black bass as small as 90 mm FL, whereas the smallest Striped Bass observed to have consumed a fish was 169 mm FL. Nobriga and Feyrer (2007) found Largemouth Bass of 50 to 150 mm FL from Delta nearshore habitats had an increasing propensity for piscivory. We saw a similar increase in the probability of consuming fish for black bass species in the Stanislaus River, but unlike Largemouth Bass in the Delta, larger black bass in the Stanislaus River tended to consume more crayfish than fish. We also found that size affected piscivory in Striped Bass; this contrasts with results for Striped Bass by Nobriga and Feyrer (2007), which showed that Striped Bass exhibited seasonal changes in their probability of consuming fish. One reason for this discrepancy is that our study was centered on the Chinook Salmon emigration period (February to May), whereas Nobriga and Feyrer (2007) collected samples from March through October, thus representing broader seasonal variation in prey availability. Piscivory of Striped Bass in the Stanislaus River increased with size, but larger Striped Bass tended to consume smaller fish prey (e.g., juvenile salmon and lamprey) less frequently. Larger Striped Bass targeted larger fish prey. For example, a Sacramento Sucker that measured approximately 450 mm was removed from a Striped Bass that measured 1,090 mm FL. Although size influenced predators' probability of consuming fish, even the smallest black bass and Striped Bass had non-zero probabilities of consuming fish. Black bass species have self-sustaining populations in the Stanislaus River

(FISHBIO unpublished data, see "Notes") and can become piscivorous in their first year. Ongoing research into black bass growth and survival will aid in understanding the full impact of these species on native fishes. All sizes of Striped Bass observed in the Stanislaus River were capable of piscivory, but size-specific seasonal occupancy patterns (Ware et al. 2023, unreferenced, see "Notes") suggest their interactions with prey may vary seasonally, depending on the size of prey available and the size of Striped Bass in the river.

Study Limitations

The seasonal scope of this study was limited to the emigration period of juvenile Chinook Salmon (February–June) because they were the main prey species of interest. Nonetheless, we were able to document important predator–prey interactions on the Stanislaus River over 3 years. Although we successfully identified most of the recovered diet items, some rarer, small-bodied (and highly digestible) fishes could have been missed (Brandl et al. 2021). In this study we visually identified and genetically validated discrete diet items, which likely yielded precise estimates of consumption for larger prey fishes (i.e., juvenile Chinook Salmon and lamprey), but estimates for smaller (larval) fishes that were more digestible should be considered conservative. In other studies, predators are sacrificed to facilitate collection of complete gastric contents (e.g., Brandl et al. 2021; Michel et al. 2018). We opted to conduct non-lethal collections because individuals were also being used in a concurrent mark–recapture study. Some diet items may possibly have been missed as a result of our method of capture. Electrofishing may cause a regurgitation response, and regurgitated items would not get collected. However, regurgitation was rarely observed during sampling.

CONCLUSIONS

Our study contributes much needed information to close three knowledge gaps related to predation in the Sacramento–San Joaquin watershed.

- **First**, ours is one of very few studies performed in an upstream tributary with a relatively

intact native fish community. We show that non-native predation on native fishes occurs at higher frequencies than has been observed from studies in the Sacramento and San Joaquin rivers and in the Delta. For juvenile Chinook Salmon in the Stanislaus River, exposure to predation by non-natives begins at the start of their migration.

- **Second**, our broad taxonomic scope of both predators and prey species revealed that juvenile Pacific Lamprey are, at least seasonally, an important resource for native and non-native piscivores.
- **Third**, our collection of diet data spans 3 years that had contrasting hydrologic conditions. Across high- and low-flow conditions, the frequency with which non-native piscivores consumed native fishes—including juvenile Chinook Salmon—remained stable. Given lower juvenile Chinook Salmon production in dry and critically dry years, predation by non-native piscivores may affect Chinook Salmon population levels more than the wet years that have greater production. However, additional studies are needed to disentangle the effects of environmental conditions and prey abundance on non-native predators' ability to detect, pursue, and capture prey.

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