

HABITAT-SPECIFIC DIET ANALYSIS OF SACRAMENTO PIKEMINNOW
(*PTYCHOCHEILUS GRANDIS*) AND STRIPED BASS
(*MORONE SAXATILIS*) IN THE
SACRAMENTO RIVER

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to the Faculty of
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In Partial Fulfillment
of the Requirements for the Degree
Master of Science
in
Biological Sciences

by
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Fall 2018

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DEDICATION

I would like to dedicate this thesis to my late grandmother, Maggie Neese,
my parents, Brad and Mary Stompe, and my grandparents,
Brian and Susan Stompe for their
unwavering support.

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This thesis truly has been a collaborative effort and would not have been possible without the assistance of California State University (CSU), Chico students Carlos Estrada, Lue Lo and Drew Nielsen for enduring countless early mornings and late nights on the river, Brian Poxon of Pacific States Marine Fisheries Commission (PSMFC) for volunteering use of crew hours and fyke nets, Dr. Tyler Pilger of Fishbio and Dr. David Keller of CSU, Chico for teaching me everything I know about genetic analysis, and Andrea Schreier of the University of California, Davis Genomic Variation Laboratory and Michael Memeo of the PSMFC Upper Sacramento River Basin Fisheries Program for providing tissue samples for qPCR optimization.

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ABSTRACT

HABITAT-SPECIFIC DIET ANALYSIS OF SACRAMENTO PIKEMINNOW (*PTYCHOCHEILUS GRANDIS*) AND STRIPED BASS (*MORONE SAXATILIS*) IN THE SACRAMENTO RIVER

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This study examined the diets of two predatory fish species, the native Sacramento Pikeminnow (*Ptychocheilus grandis*) and the introduced Striped Bass (*Morone saxatilis*), within the Sacramento River, CA, USA. Sampling occurred between March and December 2017 and was comprised of two primary components. The northern survey component was done via hook and line sampling, on a 35 kilometer reach near Chico, CA, and the southern survey component was done via seven fyke traps located near Sacramento, CA. Stomach contents were collected via non-lethal gastric lavage and were later processed using visual, gravimetric, and genetic techniques. Relative abundance of Sacramento Pikeminnow was significantly higher at man-made structure sites and Striped Bass relative abundance was positively correlated with water temperature. Diets of Sacramento Pikeminnow and Striped Bass captured near Chico, CA were not different, and Striped Bass captured near Chico, CA had significantly different diets to those captured near

Sacramento, CA as determined by PERMANOVA analysis.

INTRODUCTION

Engineered and otherwise altered ecosystems present unique challenges for the species which inhabit them. Changes in abiotic conditions, the amount of suitable habitat available, the amount of usable food resources, hatchery domestication and increased and/or novel sources of mortality by introduced species can lead to population declines and extinction (Raleigh et al. 1986; Moyle and Light 1996; McCullough 1999; Lindley and Mohr 2003; Fritts et al. 2007). Bottom-up factors (e.g. resource limitation) work in concert with top-down factors (e.g. predation pressure) to determine the success of a species (Stochat et al. 2010; Křivan 2011). While natural systems remain relatively stable when unaltered, the often delicate balance struck between these factors can become disrupted when ecosystems are engineered and species are introduced (Moyle and Light 1996; Křivan 2011).

Introduced species generally impact native species negatively in one of two ways; through competition or predation (Moyle and Light 1996). Competition occurs when an introduced species uses the same food resource(s) and/or habitat type as a native species. If the introduced species is better able to exploit resources or inhibits the native species from accessing resources, then the native species will be displaced, either physically or through a lack of nutrition. Impacts of predation are generally more direct in nature, resulting in increased mortality of the native species. However, it may also result in predator avoidance behavior which can have implications for species success (Berejikian 1995; Alvarez and Nicieza 2003).

Predator-Prey relationships may be qualified in a number of different ways. There are two primary response types that predators may experience in relation to prey population density; the first being functional response and the latter numerical response (Holling 1959a, 1959b;

Křivan 2011). Functional response entails density dependent prey consumption by a predator, in which the number of prey consumed is directly associated with prey density (Holling 1959a, 1959b; Křivan 2011). Numerical response is an associated value which refers to the increase or decrease in predator population density in response to increasing or decreasing prey population density (Holling 1959a, 1959b; Křivan 2011). These two related response types are responsible for population cycling and equilibrium in resource limited predator populations, where predator population levels track prey density.

Functional response may be further classified into one of three general models. First proposed in the Lotka-Volterra model, and then later defined as Holling Type I functional response, predators may exhibit a linear functional response to prey density (Volterra 1926; Holling 1959a, 1959b; Křivan 2011). Under the Holling Type I model the consumption of prey increases linearly from zero with increased prey population densities, until reaching some asymptote of predator satiation (Holling 1959a, 1959b; Křivan 2011). This model does not account for prey switching or decreased foraging success at low prey population levels, and thus is generally not realistic in dynamic systems. Despite this, predator-prey dynamics following the Holling Type I model have been observed; notably in the case of predation on juvenile sockeye salmon by piscivorous fish in a British Columbia lake (Ricker 1941; Holling 1959a, 1959b). The next functional response model proposed by Holling (1959a, 1959b), known as the Holling Type II functional response, refers to a predation scenario in which functional response starts off relatively high at low prey densities, then rises to an asymptote at a continuously decreasing rate (Holling 1959a, 1959b; Křivan 2011). The functional response model which is generally regarded as the most realistic under natural conditions, as first conceptualized by Gause, and further defined by Holling (1959a, 1959b), is the Holling Type III functional response (Gause

1934a, 1934b; Gause et al. 1936; Křivan 2011). This model follows a “s-shaped” form, in which functional response is initially low due to factors such as low levels of olfactory cues or predator naivety, then increases exponentially as prey density increases, and finally reaches an asymptote at predator satiation (Gause 1934a, 1934b; Gause et al. 1936; Holling 1959a, 1959b; Křivan 2011). Determination of system specific predator functional response is crucial in determining the relative effects of predation on vulnerable native species.

Any one of the aforementioned models may be further modified by the addition of a critical prey threshold, as first proposed by Gause (Gause et al. 1936; Holling 1959a, 1959b; Křivan 2011). The critical prey threshold refers to a basal level of prey density at which prey are no longer available to predators (Gause et al. 1936; Holling 1959a, 1959b; Křivan 2011). This may be due to a number of different factors; however, a common example is the filling of predator refuge (i.e. cover), and subsequent overflow of prey at densities above the critical prey threshold (Holling 1959a, 1959b). Once there is no longer room for additional prey in an area of predator refuge they are made available to predators and thus are susceptible to mortality by predation. The concept of a critical prey threshold allows for a predator-prey limit cycle to exist, in which prey densities increase above the critical prey threshold, are then made susceptible to predation, and are reduced back to the critical prey threshold (Gause et al. 1936; Křivan 2011). This forms predator and prey density oscillations in which predator numerical response tracks prey density, effectively forming an oscillatory equilibrium (Gause et al. 1936; Křivan 2011). In Gause’s experiments on predator-prey interactions between microorganisms he showed that, in a homogenous environment, a critical prey threshold is crucial for allowing a limit cycle to exist, otherwise the predator would invariably push the prey to extinction and then cease to exist itself in the absence of alternate prey (Gause 1934a, 1934b; Gause et al. 1936; Křivan 2011). Natural

systems are generally highly dynamic and heterogenous, rather than homogenous, complicating the application of Gause's theory to real world scenarios.

Gause also showed experimentally that under homogenous conditions, two organisms which exploit the same resource cannot coexist (Gause 1934a, 1934b). This would seem to have implications for species introductions in instances which an introduced species and a native species share a similar niche space. For example, the lower Sacramento River, in California, USA, harbors two main piscivorous fish species, the non-native Striped Bass (SB, *Morone saxatilis*) and the native Sacramento Pikeminnow (SP, *Ptychocheilus grandis*). The fact that both predatory species have been able to coexist in the same system for an extended period of time would suggest that they have not had enough time to reach a point of competitive exclusion, the dynamic nature of the Sacramento River system negates whatever competitive advantage one species may have over the other, the life history differences between the species mean that they do not share enough niche space to be susceptible to competitive exclusion, or finally that Sacramento Pikeminnow and/or Striped Bass are not food resource limited.

Because predation is a challenge with which nearly all organisms must contend, it is often considered in the management of vulnerable populations. In the Sacramento River system, this challenge may be compounded by a complex water system, adverse environmental conditions, and non-native predatory fish species (NMFS 2018). Engineered river dynamics, a lack of juvenile rearing habitat, and poor Chinook Salmon (*Oncorhynchus tshawytscha*) and steelhead (*Oncorhynchus mykiss*) hatchery release strategies may further exacerbate loss of vulnerable populations to predation (Brown and Moyle 1981). Loss to predation is of particular concern for Sacramento River Chinook Salmon populations due to recent population declines (Lindley and Mohr 2003). Of the four distinct Chinook Salmon runs native to the Sacramento

River, Sacramento River winter-run Chinook Salmon are state and federally endangered, Central Valley spring-run Chinook Salmon are state and federally threatened, and both Central Valley fall-run and Central Valley late fall-run Chinook Salmon are state species of special concern (NMFS 2018). In addition, Green Sturgeon (*Acipenser medirostris*) and steelhead trout, both species native to the Sacramento River, are federally listed as threatened.

In other rivers in western North America, much focus has been given to predator control as a means of supporting salmon populations (Zimmerman 1999). The Columbia River, for example, saw a reduction of 1.1 million predatory Northern Pikeminnow (*Ptychocheilus oregonensis*) between 1991 and 1996 through a number of different removal efforts (Friesen and Ward 1999). As a result, predation on juvenile salmonids by Northern Pikeminnow fell by 25%, which translates to an estimated reduction in juvenile salmonid losses of 3.8 million (Friesen and Ward 1999). As one of the means of salmon predator control, Oregon and Washington operate a sport-reward fishery for Northern Pikeminnow on the Columbia and lower Snake Rivers (Friesen and Ward 1999). Historically, agencies in California implemented fishing derbies and trap and cull measures for Sacramento Pikeminnow around the now defunct Red Bluff Diversion Dam in an effort to reduce predation on juvenile salmon (Tucker et al. 1998, Moyle 2002). While agency sponsored control measures no longer operate, potentially due to concerns over public perception, occasional Sacramento Pikeminnow derbies are still organized by private entities within the Sacramento River system.

Although Sacramento Pikeminnow control is generally no longer discussed by management agencies, in 2011 the California Fish and Wildlife Commission considered severely loosening take restrictions on non-native Striped Bass in an effort to reduce impact on listed species (Bonham 2011). These restrictions were tightened in 1982 in response to angler pressure

and plummeting Striped Bass populations in the Sacramento-San Joaquin delta (Stevens et al. 1985). Stevens et al. (1985) reported a decrease in adult Striped Bass populations of approximately 50% between 1970 and 1982 as calculated by Peterson mark-recapture modeling, annual fyke net surveys, and annual gill net surveys, while Kohlhorst (1999) reported an estimated decrease in fish >18" total length of 1.7-1.9 million individuals from 1969 to 1976, to just 579,000 in 1994. In addition, annual midwater trawl data collected by the California Department of Fish and Wildlife (CDFW) shows a remarkable decrease in captured Striped Bass fry, from an index value of 19,677 in 1967 to 470 in 2017 (White 2017). Unfortunately, current adult Striped Bass population estimates are not available, however the catch per unit effort (CPUE) and total harvest of legal (>18" total length) Striped Bass for commercial passenger fishing vessels east of the Golden Gate Bridge has remained relatively constant between 1980 and 2017 (CDFW 2018). The discrepancy in adult and juvenile index values most likely does not indicate a change in population age structure, as the timescale of available data spans multiple generations. The data more likely reflects commercial passenger fishing vessels' ability to alter their fishing methods to target Striped Bass in changing bay, delta, and river ecosystems, making these data less vulnerable to changes in Striped Bass distribution and behavior (Maunder et al. 2006).

Despite substantially decreased Striped Bass populations, a 2003 study on Sacramento River predator-prey interactions has shown a correlation between Striped Bass predation and salmon population decline. Lindley and Mohr (2003) developed a model which predicted the probability of quasi-extinction (defined as 200 adult individuals, assuming 100 females) for Sacramento River winter-run Chinook Salmon given multiple Striped Bass population levels. They used the estimated adult Striped Bass population at the time (pop=512,000), an eradication

scenario (pop=0), a light stocking scenario (pop=700,000), and an intensive stocking scenario (pop=3,000,000) in their model to estimate quasi-extinction probabilities of winter-run Chinook of 23% given Striped Bass eradication to 55% given intensive Striped Bass stocking over a 50-year time period (Lindley and Mohr 2003). This model suggests that Striped Bass, while not necessarily a driving force in population decline, have an impact on vulnerable salmon populations.

Multiple studies have looked at predation rates by pikeminnow species on juvenile salmonids, however, results vary substantially. Proportions of salmonids in pikeminnow (Northern and Sacramento Pikeminnow) gut content are reported as being as low as 1.4% in the free-flowing portion of the Willamette River, to as high as 88% in the Columbia River (Brown and Moyle 1981). This large discrepancy in predation rates can likely be attributed to river dynamics and hatchery release methods (Brown and Moyle 1981). Researchers have examined predation rates by Sacramento Pikeminnow and Striped Bass on juvenile salmonids in the Sacramento River through limited stomach content analysis, however this research was focused around the now defunct Red Bluff Diversion Dam, and there is little in the literature that examines in-river differences in diet between Sacramento Pikeminnow and Striped Bass (Brown and Moyle 1981, Tucker et al. 1998, Moyle 2002).

The effects of man-made structures, including water-diversion facilities, on predation have been a point of concern. Altered water dynamics near man-made structures may serve as ambush habitat, making conditions more favorable to opportunistic predators such as Striped Bass and Sacramento Pikeminnow (Brown and Moyle 1981). In addition, juvenile Chinook Salmon show a preference for low water velocity areas, possibly compounding predation risk if they utilize the low velocity hydraulics created by man-made structures (Sommer et al. 2001). As

an example, the Red Bluff Diversion Dam (RBDD) on the Sacramento River formerly operated as a ponding device and was used to divert water for agricultural purposes. The hydraulics immediately downstream from RBDD created ideal predation conditions for Sacramento Pikeminnow, which were found to feed heavily on juvenile salmonids in this localized area (Brown and Moyle 1981, Tucker et al. 1998, Moyle 2002).

While there is an abundance of studies which investigate the diets of Striped Bass in the lower reaches of the Sacramento River system, there is relatively little information available on Striped Bass diets in the upper reaches of the river. Likewise, few studies have considered comparing the diets of Sacramento Pikeminnow and Striped Bass concurrently. This study was designed in an effort to further demystify the effects of predation on native fish populations in the Sacramento River through the use of predator diet analysis and demographic information. The goals of this study were two-fold and sought to identify: 1) Environmental and seasonally associated predator distribution and 2) Environmental, seasonal, and spatially associated predator diet composition within the Sacramento River.

METHODS

Study Organisms

The two predatory species considered for this study were Sacramento Pikeminnow and Striped Bass. Sacramento Pikeminnow are native to the Sacramento River, and were historically the primary piscivorous fish throughout the system. They become piscivorous at 10 to 20cm total length and generally exhibit a resident life history strategy, however they have been shown to migrate up to 400km within the Sacramento River system (Moyle 2002).

Conversely, Striped Bass are a non-native piscivorous fish within the Sacramento River system, introduced to California from the East Coast in 1879 as a recreational and commercial species (Moyle 2002). Striped Bass become piscivorous between 10 to 35cm fork length and generally exhibit an anadromous life history strategy, spending much of the year in the Sacramento-San Joaquin Delta, the San Francisco and San Pablo bays and the ocean (Thomas 1967; Moyle 2002). Striped Bass generally enter the Sacramento River system in the spring to spawn before returning to downstream habitats (Moyle 2002, Le Doux-Bloom 2012), and while they have been shown to occasionally exhibit annual residence in their natal East Coast rivers (Morris et al. 2003), recent studies on the movement of California Striped Bass show relatively short residence times within the Sacramento River (Sabal et al. 2018).

Study Reach

Data collection occurred on the Sacramento River, primarily between Ord Bend boat ramp (river kilometer 296) and Glenn County Irrigation District diversion facility (GCID; river kilometer 331; Figure 1). This reach was chosen due to its proximity to the CSU Chico campus,

availability of boat ramps,
 presence of adequate numbers of
 both Striped Bass and Sacramento
 Pikeminnow, presence of man-
 made structures, and limited
 spatial scale.

Site selection was made
 based on three distinct habitat
 types; man-made structures,
 “riprap” bank, and natural sites.
 Since the limiting habitat type in
 our study reach was man-made
 structures, the number of r ripr
 and natural sites corresponded to
 the number of man-made sites
 available. Possible ripr and

unaltered sites were identified and a subset of four of each site-type was randomly selected. The total sampling reach was broken into four sections of similar length, each of which contained one of each site-type.

Additional data was collected from Striped Bass caught in fyke traps operated on the Sacramento River near Sacramento, California. Pacific States Marine Fisheries Commission, in collaboration with CDFW, operates seven fyke traps for the purpose of steelhead (*Oncorhynchus mykiss*) capture and pit tagging. Pacific States Marine Fisheries Commission biologists had

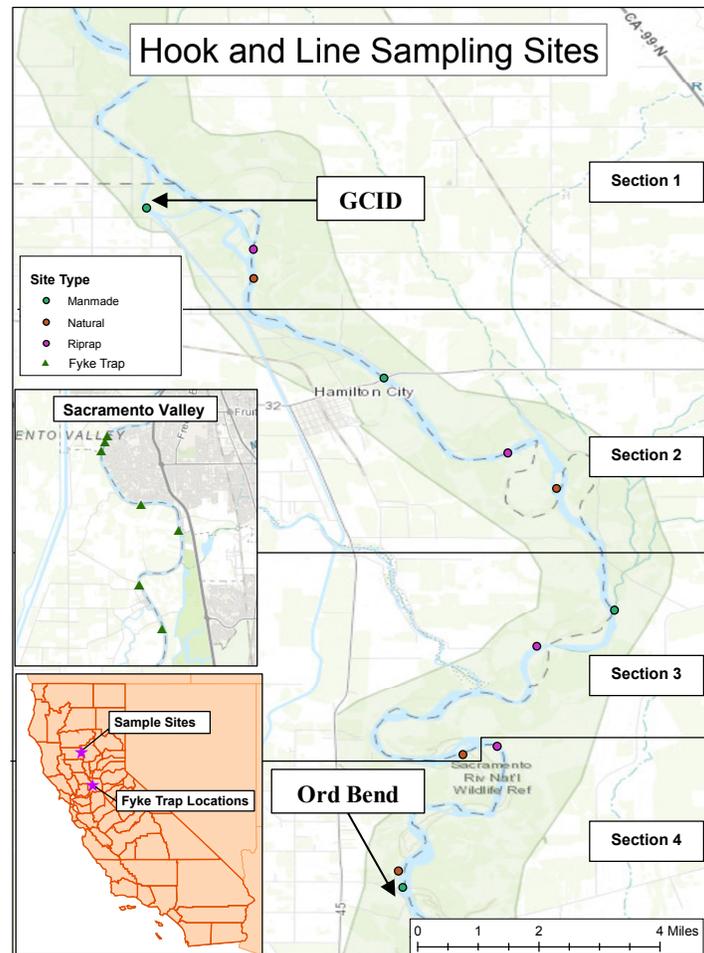


Figure 1.) Distribution of sampling sites by site type, for both hook and line and fyke trap components of study. Map courtesy of Stacey Alexander, CDFW.

reported substantial bycatch of Striped Bass, which presented an opportunity to collect additional stomach content samples. Collection of this additional data allowed for supplementation of hook-and-line survey data, further clarifying research objectives. In addition, samples sourced from fyke traps allowed for increased spatial analysis when compared to samples collected via hook-and-line survey.

Sample Collection

Data were collected from wild Striped Bass and Sacramento Pikeminnow through hook-and-line sampling methods. Hook and line sampling was selected for its low material cost and low incidence of take of listed species. Sampling generally occurred twice weekly, with one morning shift (starting 45 minutes before sunrise) and one evening shift (starting five hours before sunset) in order to control for temporal effects (Fraser et al. 1993). Each site was sampled for 1.25 hours per sampling period, with all three site-types within a section sampled for a total of 3.75 hours. Individual sections were sampled biweekly and alternated between morning and evening shifts in an effort to make sure all sites were sampled across a range of temporal and environmental conditions. The order in which sites were visited was randomly generated prior to going sampling a section.

Once anchored, four rods were fished in randomized order, each of which was assigned a unique bait which would not contaminate downstream sample analysis (large sardine piece, small sardine piece, chicken liver, and nightcrawlers). Bait types were selected to attract target species from a range of sizes. When caught, fish were removed from the water, measured for length and weight, and placed into an aerated holding tank. Fish stomachs were then pumped 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). Stomach content

samples were then captured in a fine mesh bait net, transferred to Whirl-pak[®] bags, labeled, stored on ice and frozen at -20C immediately after returning from the field to retain sample integrity for genetic, visual, and volumetric analysis. In addition, scale samples were collected between the dorsal fin and lateral line and Floy[®] T-bar anchor tags were injected just below the dorsal fin in target species to measure movement and recapture rates. Hook and line sampling began in March 2017 and continued through the end of November 2017. High water and unsafe conditions negated sampling in January to March 2017, and limited crew availability are responsible for the lack of sampling in December 2017.

Data and samples collected from fyke traps followed similar protocol to those obtained through hook-and-line sampling, however low Sacramento Pikeminnow catch meant only Striped Bass were sampled. When time and crew constraints allowed, subsamples of 5 to 20 fish were haphazardly selected during fyke trap sampling, measured for length and weight, and processed for stomach content collection via gastric lavage. Scale samples were taken and Floy[®] T-bar anchor tags were injected. All samples were bagged and labeled in Whirl-pak[®] bags, stored on ice and immediately frozen at -20C upon returning from the field. As fyke sampling was only conducted when crew time constraints allowed, sampling occurred during April, May, June, and December 2017.

Water quality metrics including water temperature and water clarity were measured at each site during field sampling. Water temperature was measured via the transducer from the onboard fishfinder/gps unit (Garmin[®] Striker 4) and water clarity was measured using an 8" white and black Secchi disk mounted to a rigid pole for use in high current areas. During hook and line sampling, crew neglected to record water temperature on one occasion, and water clarity on two occasions, and during fyke sampling, crew neglected to record water quality metrics on a

more frequent basis. When crew failed to take water quality measurements in the field, water temperature data was sourced from the California Data Exchange Center (California Data Exchange Center 2018) and water clarity was taken as an average of the previous and following sampling days.

Lab Analysis

Stomach contents were processed to determine weight, volume, frequency of occurrence and number of prey within each sample. Stomach content samples were transferred from the freezer to a cooler with ice in batches of 4 to 25, at which point they were analyzed individually. Prior to analysis, samples were removed from ice and allowed to fully thaw at room temperature. Once thawed, samples were removed from Whirl-pak[®] bags and placed onto new polystyrene weigh boats using instruments sterilized in 20% bleach solution. Samples were then sorted, and prey was segregated by category. Prey categories included identifiable fish, unidentifiable fish, crayfish, other macroinvertebrates and unknown soft-matrix. Individuals were enumerated using diagnostic parts, such as spinal columns for fish and head parts for macroinvertebrates.

Next, prey group weight was taken to the nearest thousandth of a gram using an Ohaus[®] STX223 Scout portable balance, after being blotted dry with new paper towels, and volume was measured by displacement in 5, 10, 50, or 100mL graduated cylinders. For individual fish which could be clearly identified as such, a sample of tissue ($\leq 0.25\text{g}$) was removed and transferred to a new 1.5mL microcentrifuge tube, labeled, and stored on ice. When individuals could not be clearly differentiated, the soft matrix material was homogenized with dissecting tools and at least one representative grab sample ($\leq 0.25\text{g}$) was taken. When a processing session was completed samples were immediately returned to storage at -20C for genetic analysis. Remaining prey

tissue was retained in Whirl-pak[®] bags at -20C in case of contingency.

Genetic Analysis

Genetic analysis was performed via qPCR in house at California State University, Chico. A reference list of potential prey species was determined through the lead author's (D.K.S.) seining and snorkel survey experience and via *Inland Fishes of California* (Moyle 2002). Previously designed primers were referenced from current literature (Baerwald et al. 2012; Ye et al. 2012; Brandl et al. 2015) and additional primers were designed using Genbank sequence data and the NCBI Primer-BLAST tool (Benson et al. 2005; Ye et al. 2012). All primer sets except for river lamprey and brook lamprey (due to an inability to procure tissue) were tested for validity against known voucher tissue via PCR and qPCR and were optimized for optimum annealing temperatures. Striped Bass and Sacramento Pikeminnow primers were validated, however were not used in testing due to concern of contamination from predator tissue. PCR primer sets which 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, California Department of Fish and Wildlife Upper Sacramento Watershed Fisheries Project, the field component from this study, and the primary author's (D.K.S.) personal freezer. Voucher tissue was either frozen, dried, or stored in ethanol when collected and DNA was extracted using Qiagen[®] DNeasy DNA extraction kits. Prey reference list and associated primers can be seen in Table 1.

QPCR was run using an Eppendorf[®] EP realplex thermal cycler, in 96 well format. Reagents were mixed using 3uL of sample DNA, 3uL DNase free water, 1.5uL primer pair, and 7.5uL of 2X Luminaris[™] Color HiGreen qPCR Master Mix per well. All qPCR runs had at least

two negative controls of water. Brandl et al. (2015) and Baerwald et al. (2012) primers were run 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 universal fish primer set followed similar programs, however the annealing step was changed to 45 seconds at 68°C and 62°C, respectively.

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 content samples. All sample DNA was extracted and tested for DNA concentration and quality using a Thermo Scientific™ NanoDrop One Microvolume UV-Vis Spectrophotometer.

Initially, all samples labeled as soft matrix were tested against the universal primer set to determine if further testing was required, and samples which did not amplify with the universal fish primer set were excluded from further analysis. Soft matrix samples which did amplify against the universal primer set were then tested against a limited assay of species which included Chinook Salmon, rainbow trout, white sturgeon, green sturgeon, and Pacific lamprey for samples collected from the hook-and-line portion of the study. The same assay was used for fyke soft matrix samples, with the addition of Delta Smelt, Longfin Smelt, and Threadfin Shad to reflect locally available prey species. Soft matrix samples which tested positively for one or more species were conservatively counted as one individual from each positive amplification.

Non soft matrix samples were tested against targeted assays until a positive result was reached. Notes on prey morphology taken during raw sample processing were used to inform primer set selection, targeting the most likely prey items in an effort to increase processing

efficiency. Occasionally, a single individual sample would amplify for multiple species (potentially due to inter/intra-sample contamination), in which case the species with the lowest Ct value was selected.

Table 1. Prey reference list including mitochondrial reference gene, primer sequences, gene segment length, and accession number. Superscript denotes primer sequence source: (Benson et al. 2005³; Baerwald et al. 2012², Brandl et al. 2015¹). *Primers amplified both riffle and prickly sculpin DNA. **Primers were not validated against known voucher tissue and experienced partial cross amplification; strongest signal was selected for analysis.

| Common Name (<i>latin name</i>) | Gene | Primers (5' to 3') | Segment Length | Accession Number |
|---|------|---|----------------|------------------|
| American Shad ³ (<i>Alosa sapidissima</i>) | CYTB | FOR - TGCACGCAAACGGGGCATCA REV - CCTCGGCCAATGTGGGCGTAAA | 58bp | GU556214.1 |
| Chinook Salmon ¹ (<i>Oncorhynchus tshawytscha</i>) | CYTB | FOR - CCTAAAAATCGCTAATGACGCACTA REV - GGAGTGAGCCAAAGTTTCATCAG | 80bp | KF013235 |
| Delta Smelt ² (<i>Hypomesus transpacificus</i>) | CYTB | FOR - AATGGCCAACTTCGGAAA REV - GARATATTRGAGGGTGCAGG | 90bp | HQ667171 |
| Green Sturgeon ¹ (<i>Acipenser medirostris</i>) | COI | FOR - AGGGAAAAATGGTTAGGTCTACAGA REV - CCCCACTGGCGGGAAA | 61bp | KF558288 |
| Hardhead ³ (<i>Mylopharodon conocephalus</i>) | CYTB | FOR - TGCCGGCGCAACCATCTACA REV - CGGCCGGGTTGTTTGATCCGGT | 62bp | EU747218.1 |
| Longfin Smelt ¹ (<i>Spirinchus thaleichthys</i>) | CYTB | FOR - CTCTGCCGGGACGTCAAT REV - CCCGTTAGCGTGCATATTCC | 53bp | KF013249 |
| Mississippi Silverside ² (<i>Menidia beryllina</i>) | CYTB | FOR - CCGTTTGATGCATATTTCG REV - CCTTTTCGTCTGTTGCACACA | 73bp | JN008748 |
| Pacific Lamprey ³ (<i>Entosphenus tridentatus</i>) | COI | FOR - TTGAAGCAGGGGCTGGCACAGG REV - GGAGGCCCTGTGTGGGCTAA | 74bp | KX389877.1 |
| Prickly Sculpin ^{3*} (<i>Cottus asper</i>) | CYTB | FOR - ATTGCCCTCACAGCCCTCGCAC REV - TCACCAGCGGTTAGCAGGGG | 82bp | KX353550.1 |
| Riffle Sculpin ^{3*} (<i>Cottus gulosus</i>) | COI | FOR - GCGGCCCTTTTGGGGGACGA REV - GGGCGCCGATCATTAAGGGGA | 137bp | JN025103.1 |
| River Lamprey ^{3**} (<i>Lampetra ayresii</i>) | CYTB | FOR - CTGACTAATGTCCCACCACCAACT REV - GCAGGAGAAGGAAGGTCAACTAGCA | 93bp | KR422617.1 |
| Sacramento Sucker ³ (<i>Catostomus occidentalis</i>) | COI | FOR - AATCTTGGCCACGCCGGAGCC REV - TTGAGAGATGGCTGGGGGCTTCA | 132bp | JN024942.1 |
| Sacramento Tule Perch ³ (<i>Hysterocarpus traskii</i>) | COI | FOR - GGGCAGAACTAAGCCAACCAGGCG REV - ACAAGGCGTGGGCGGTACAA | 79bp | JN026852.1 |
| Steelhead/RBT ¹ (<i>Oncorhynchus mykiss</i>) | COI | FOR - AACATAAACTCCAGCCATCTCT REV - AGCACGGCTCAAACGAAAA | 59bp | KF558313 |
| Threadfin Shad ¹ (<i>Dorosoma petenense</i>) | CYTB | FOR - AAGTCCTCGCCGATGTG REV - CATGCAAACGGAGCATCTCT | 39bp | KF013218 |
| Western Brook Lamprey ^{3**} (<i>Lampetra richardsoni</i>) | CYTB | FOR - TCGGACGAGGAATCTACTACGGCT REV - TGCCCTCATGGGAGAACGTAACCGA | 118bp | KY499461.1 |
| White Sturgeon ¹ (<i>Acipenser transmontanus</i>) | CYTB | FOR - CCCCGTTTGCATGAATGTTT REV - CGCCACATCTGCCGAGAT | 62bp | KF013247 |

Data Analysis

Predator demographics and distribution were analyzed using ANOVA, Tukey's honest significant difference (HSD) post hoc test, Welch two sample t-tests, and linear models. Demographic information considered included fork length and weight, from which differences in means were analyzed by species and survey type. Predator distribution was analyzed using CPUE data as an index of abundance and was tested for associations with variables including habitat type, month, water temperature, and water clarity.

The component values measured through lab and genetic analysis were then used to calculate the index of relative importance (IRI) of each prey taxon by predator species. 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:

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

Where %N is the prey percent by number, %W is the prey percent by weight, and %FO is the percent frequency of occurrence. Volumetric measurements may be used in place of %W (Hyslop 1980), however given the small size of prey, we chose to use gravimetric measurements as the instruments available were more far more precise. In order to reduce sample processing time wet weight was used as opposed to dry weight, as Glenn and Ward (1968) showed that prey wet and dry weights are highly correlated.

Once IRI was determined for each prey taxon, it was then converted to %IRI, which allows for easier comparisons of dietary information to prior and future studies (Cortés 1997). While multiple index values for the relative importance of prey species exist, IRI and %IRI are the most widely used and have been proposed by Cortés (1997) as the standard measures for diet

studies in order to increase study comparability. %IRI is calculated as follows:

$$\%IRI_i = 100 * IRI_i / \sum_{i=1}^n IRI_i$$

At the end of the data collection period, sample size adequacy was determined using cumulative prey curves, as outlined by Ferry and Cailliet (1996). 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 (Ferry and Cailliet 1996). The R package ‘vegan’, function ‘specaccum’, was utilized for constructing cumulative prey curves (Oksanen et al. 2013; Hernandez 2016; R Core Team 2018).

Additional analyses was conducted by looking at dietary niche breadth overlap between Striped Bass and Sacramento Pikeminnow, and between Striped Bass captured via hook and line and fyke survey. Dietary niche breadth overlap uses aggregate values of prey observed to calculate an index of overlap between two species, in effect measuring the similarity of their diets. To obtain these values, both total number of prey observed and prey index of relative importance were used as the prey metrics, and values were calculated using Pianka’s index of overlap (Pianka 1974) in R package EcoSimR, with the number of permutations set at 50,000 (Gotelli et al. 2013; R Core Team 2018). This metric allows for determination of similarity of Striped Bass and Sacramento Pikeminnow diets, which has implications in determining the potential effects of reduced Striped Bass populations in the Sacramento River.

Finally, diet composition was analyzed using nonmetric multi-dimension scaling (NMDS) and permutational analysis of variance (PERMANOVA). NMDS was chosen for its effectiveness in visualizing ecological distances and was run using Bray-Curtis dissimilarity distance as its ordination method (Bray and Curtis 1957; Abookire et al. 2007; Zhang et al.,

2018). NMDS was run using prey numerical data for diets of Sacramento Pikeminnow vs Striped Bass captured via hook and line survey, and for Striped Bass from both hook and line and fyke surveys. NMDS analysis was conducted using R package 'vegan', with 1,000 permutations to reduce stress.

PERMANOVA was chosen for 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). Prior to analysis, the PERMANOVA assumption of homogeneity of variances between groups was tested using R package 'vegan', function 'betadisper', for hook and line species groups and Striped Bass survey groups (Oksanen et al. 2013; R Core Team 2018). For hook and line captured fish, PERMANOVA models were run using both prey numerical and frequency of occurrence data versus variables species, fork length, water temperature, Secchi depth, site type, and month of capture. Two more models were run using prey numerical and frequency of occurrence data, however these models only included Striped Bass (due to an absence of Sacramento Pikeminnow in the fyke traps) and were run against variables survey, fork length, and water temperature. All PERMANOVA analysis was run with 10,000 permutations, which was chosen as the point at which p-values stabilized.

RESULTS

Demographics

Over the course of the sampling period 409 target species were captured, of which 255 were Striped Bass captured in fyke traps, 87 were Striped Bass captured via hook and line sampling, and 67 were Sacramento Pikeminnow captured via hook and line sampling. Percentage of empty stomachs was higher for fyke trap Striped Bass than for either species captured via hook and line sampling (Table 2). Since fyke traps were only checked once per 24 hour period it is likely that the higher rate of empty stomachs for fyke trap Striped Bass is simply a result of fish not being able, or willing, to feed within the traps. Welch two sample t-tests showed that mean fork length (FL) and weight of non-empty Striped Bass and Sacramento Pikeminnow captured via hook and line sampling were not significantly different (FL: $t = -1.97$, $df = 59.95$, $p = 0.053$, 95% CI = -6.44 to 0.04cm; Weight: $t = -0.63$, $df = 46.91$, $p = 0.530$, 95% CI = -0.19 to 0.10kg), however Striped Bass captured via fyke trap were significantly larger than their hook

Table 2. Demographics of target species captured via hook and line and fyke trap. 'Fyke SB' denotes Striped Bass captured via fyke trap near Sacramento, CA, 'H&L SB' denotes Striped Bass captured via hook and line sampling near Chico, CA, and 'H&L SP' denotes Sacramento Pikeminnow captured via hook and line sampling near Chico, CA.

| Variable | Fyke SB | H&L SB | H&L SP |
|--------------------------------|-------------------|------------------|------------------|
| Sample Size | 255 | 87 | 67 |
| Fork Length range (cm) | 35.0 - 96.0 | 22.5 - 50.5 | 16.5 - 63.0 |
| Fork Length mean \pm SD (cm) | 47.82 \pm 10.25 | 32.45 \pm 7.18 | 34.98 \pm 9.16 |
| Weight range (kg) | 0.50 - 12.00 | 0.14 - 1.32 | 0.10 - 2.90 |
| Weight mean \pm SD (kg) | 1.52 \pm 1.40 | 0.43 \pm 0.28 | 0.51 \pm 0.54 |
| Empty rate | 83.14% | 42.53% | 55.22% |

and line counterparts, likely a reflection of size specific sampling efficiency (FL: $t = 10.04$, $df = 80.97$, $p < 1e-04$, 95% CI = 12.70 to 19.03cm; Weight: $t = 7.42$, $df = 47.88$, $p < 1e-04$, 95% CI = 0.70 – 1.23kg).

Distribution

Within the hook and line component of the study, ANOVA did not reveal an association between CPUE and site type ($F = 2.59$, $df = 2$, $p = 0.078$). This relationship changed when species was introduced as a moderating variable, in which Tukey's HSD post hoc revealed a significantly lower CPUE of Sacramento Pikeminnow at natural sites than at man-made sites

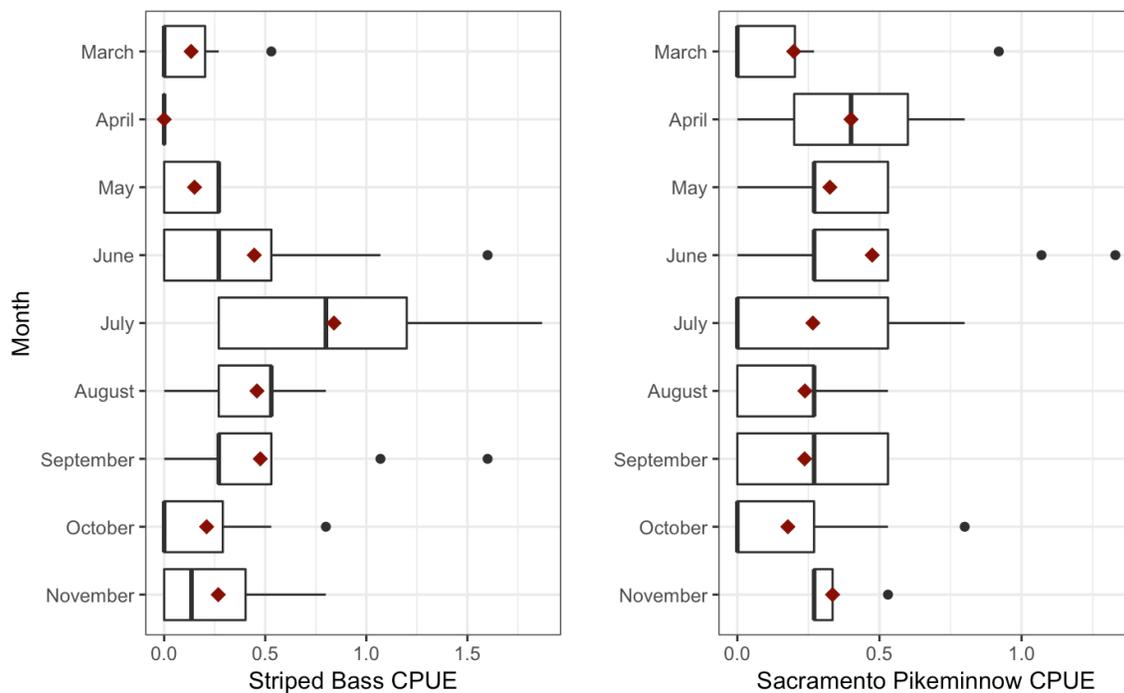


Figure 2. CPUE of Striped Bass and Sacramento Pikeminnow captured via hook and line survey by month of capture. CPUE was not affected by month for Sacramento Pikeminnow ($F = 0.73$, $df = 8$, $p = 0.667$), however it was for Striped Bass ($F = 2.35$, $df = 8$, $p = 0.030$). Tukey's HSD post hoc test revealed mean Striped Bass CPUE was not different for all months except for May and July, in which CPUE was 0.69 less in May (95% CI = -1.35 to -0.03, $p = 0.034$; Wickham 2016; R Core Team 2018). Red diamonds denote means and black circles are outliers.

(difference = -0.21, 95% CI = -0.41 to -0.01, $p = 0.042$). While CPUE does not measure true abundance, it serves as an index value which can be interpreted in a similar manner.

Similarly, ANOVA did not reveal an association between total target species CPUE and month of capture via hook and line survey ($F = 1.89$, $df = 8$, $p = 0.081$). When species was added as a moderating variable however, an association was seen between Striped Bass CPUE and month of capture ($F = 2.35$, $df = 8$, $p = 0.030$) while Sacramento Pikeminnow CPUE remained unassociated with month of capture ($F = 0.73$, $df = 8$, $p = 0.667$; Figure 2). Further analysis via Tukey's HSD post hoc test showed that the association between Striped Bass CPUE and month of capture was driven by the difference in means between May and July (difference = -0.69, 95% CI = -1.35 to -0.03), $p = 0.034$).

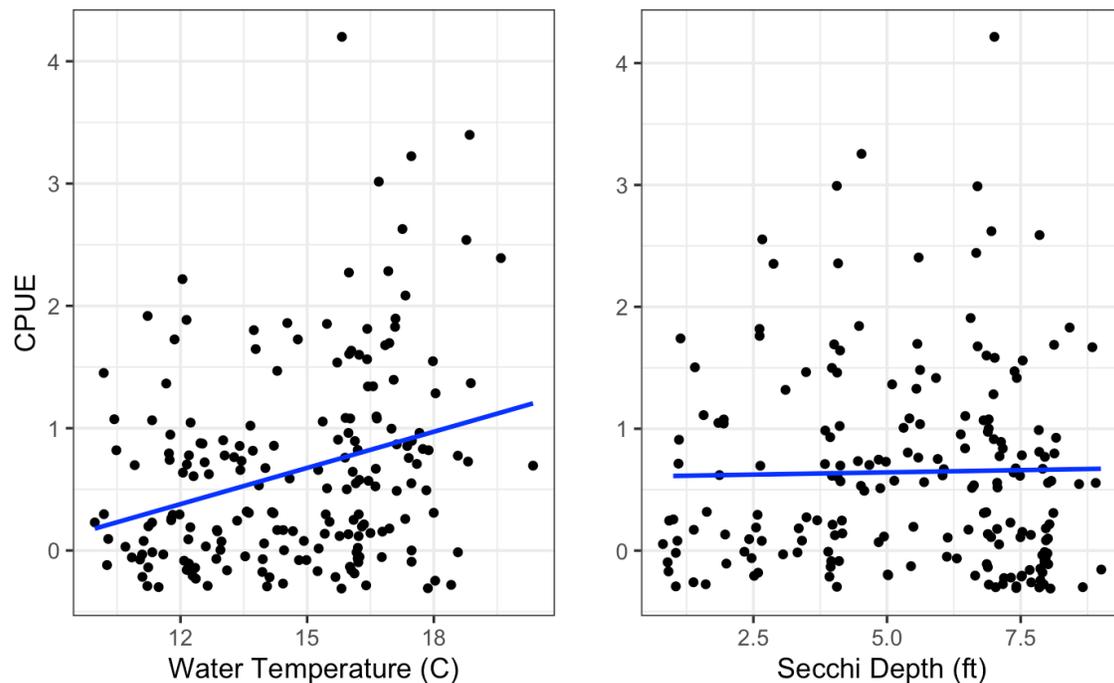


Figure 3. Total target species CPUE captured via hook and line sampling versus water temperature and Secchi depth. Person's product-moment correlation shows a moderate positive relationship between CPUE and water temperature ($r = 0.30$, $t = 4.36$, $df = 189$, $p < 1e-04$), however there was no relationship between CPUE and Secchi depth ($r = 0.02$, $t = 0.29$, $df = 189$, $p = 0.77$; Wickham 2016; R Core Team 2018). Blue lines denote linear regression.

CPUE of all target species showed a moderate positive correlation with water temperature ($r = 0.30$, $t = 4.36$, $df = 189$, $p < 1e-04$), and no relationship with Secchi depth ($r = 0.02$, $t = 0.29$, $df = 189$, $p = 0.770$) when tested with Pearson's product moment correlation (Figure 3). Fitting a linear model combining the variables returned similar results (Table 3).

When CPUE was analyzed by individual species, the relationship between CPUE and water temperature dissolved for Sacramento Pikeminnow ($t = 1.09$, $SE = 0.02$, $p = 0.276$; Table 3) and strengthened for Striped Bass ($t = 4.56$, $SE = 0.02$, $p < 1e-04$; Table 3). This potentially reflects the resident behavior of Sacramento Pikeminnow versus the anadromous behavior of

Table 3. Linear models showing relationships between total target species CPUE, Sacramento Pikeminnow CPUE, Striped Bass CPUE and water quality variables. Water quality variables include Secchi depth and water temperature.

| Variable | Estimate | Std. Error | t value | Pr(>t) |
|--|----------|------------|---------|--------------|
| CPUE ~ Secchi Depth + Water Temperature | | | | |
| Intercept | -0.77 | 0.35 | -2.24 | 0.027 * |
| Secchi Depth | -0.01 | 0.02 | -0.04 | 0.696 |
| Water Temp. | 0.10 | 0.02 | 4.36 | 2.18e-05 *** |
| Striped Bass CPUE ~ Secchi Depth + Water Temperature | | | | |
| Intercept | -0.09 | 0.28 | -3.27 | 0.001 ** |
| Secchi Depth | 0.01 | 0.02 | 0.38 | 0.707 |
| Water Temp. | 0.08 | 0.02 | 4.56 | 9.08e-06 *** |
| Sac. Pikeminnow CPUE ~ Secchi Depth + Water Temperature | | | | |
| Intercept | 0.01 | 0.23 | 0.57 | 0.569 |
| Secchi Depth | -0.02 | 0.02 | -1.06 | 0.292 |
| Water Temp. | 0.02 | 0.02 | 1.09 | 0.276 |
| Significance codes: '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 | | | | |

Striped Bass, as ANOVA showed a strong association between month of capture and water temperature ($F = 76.59$, $df = 8$, $p < 1e-04$). Conversely, considering species specific CPUE did not affect the lack of association between CPUE and Secchi depth (Table 3).

Tag Recaptures

Out of 320 Striped Bass and 62 Sacramento Pikeminnow which were tagged with Floy® T-bar anchor tags, 10 Striped Bass (3.1%) and 4 Sacramento Pikeminnow (6.5%) were recaptured during 2017. Of these, 100% of Striped Bass recaptures and 25% of Sacramento Pikeminnow recaptures were angler reported, with the remaining 75% of Sacramento Pikeminnow recaptured via the hook and line survey. All four Sacramento Pikeminnow recaptures occurred within the hook and line survey study reach, whereas Striped Bass were more varied in their distribution. While not nearly a large enough sample size to build population estimates or confidently describe distribution, this does correspond with the anadromous life history strategy of Striped Bass and the resident life history of Sacramento Pikeminnow.

Index of Relative Importance

Observed %IRI values for fyke trap Striped Bass revealed Threadfin Shad and crayfish (54.84% and 25.54%, respectively) as the most important prey items, while the two most important prey items for both predator species captured via hook and line sampling were macroinvertebrates (excluding crayfish) and Chinook Salmon (SB: 78.09% and 17.03%, respectively; SP: 76.90% and 14.57%, respectively). Observed %IRI values are shown in Table 4.

Table 4. Observed %IRI values for Striped Bass captured via fyke trap near Sacramento, CA (Fyke SB), Striped Bass captured via hook and line sampling near Chico, CA (H&L SB), and Sacramento Pikeminnow captured via hook and line sampling near Chico, CA (H&L SP).

| Prey Species | Fyke SB | H&L SB | H&L SP |
|------------------------|----------------|-------------------|-------------------|
| American Shad | 3.83 | 0.64 | 0.08 |
| Brook Lamprey | 7.53 | 0 | 0 |
| Chinook | 4.56 | 17.03 | 14.57 |
| Crayfish | 25.54 | 0.17 | 2.56 |
| Green Sturgeon | 0 | 0.08 | 0 |
| Hardhead | 0 | 2.75 | 0.48 |
| Macroinvertebrate Spp. | 0.37 | 78.09 | 76.9 |
| Mykiss | 0.17 | 0 | 0 |
| Pacific Lamprey | 3.11 | 0.11 | 0.9 |
| Threadfin Shad | 54.84 | 0 | 0 |
| Sculpin Spp. | 0 | 1.03 | 4.51 |
| Tule Perch | 0 | 0.1 | 0 |
| White Sturgeon | 0.05 | 0 | 0 |

Niche Breadth Overlap

Dietary niche breadth overlap was calculated between species captured via hook and line survey, and between Striped Bass captured via hook and line and fyke trap sampling. Values were calculated using both prey numerical data (count) and using %IRI. Values closer to one indicate a high degree of dietary niche breadth overlap, whereas values closer to zero indicate low dietary niche breadth overlap. As can be seen in Table 5, Sacramento Pikeminnow and Striped Bass captured via hook and line sampling near Chico exhibited a high degree of dietary niche breadth overlap using both count and IRI data (count: 0.982, %IRI 0.998, respectively),

Table 5. Pianka's dietary niche breadth overlap index values for Striped Bass between survey components (hook and line/fyke), and between Striped Bass and Sacramento Pikeminnow within the hook and line component of this study. Values reported using both prey counts and percent index of relative importance (Pianka 1974; Gotelli et al. 2013; R Core Team 2018).

| Survey/species | H&L SB - Count | H&L SB - %IRI |
|-----------------------|---------------------------|--------------------------|
| Fyke SB | 0.064 | 0.023 |
| H&L SP | 0.982 | 0.998 |

while Striped Bass captured via hook and line sampling and fyke traps exhibited low dietary niche breadth overlap (count: 0.064, %IRI: 0.023).

Analysis of Diets

Diets were analyzed using both prey counts and prey frequency of occurrence, visualized with the use of NMDS, and modeled with PERMANOVA analysis. NMDS indicated more similar diets between Sacramento Pikeminnow and Striped Bass captured via hook and line sampling than between Striped Bass captured via hook and line sampling and those captured via fyke trap (Figure 4 and 5).

Prior to analysis with PERMANOVA, the model assumption of homogenous multivariate spread was tested between species and surveys using R package 'EcoSimR' function 'betadisper' (Gotelli et al. 2015; R core team 2018), and survey size adequacy was determined using R package 'vegan' function 'specaccum' (Oksanen et al. 2013; R core team 2018). Multivariate spread was not different between species within hook and line survey, or between survey types within Striped Bass ($p = 0.129$, $p = 0.145$, respectively), therefore meeting PERMANOVA model assumptions. Likewise, it was determined that sample sizes were adequate given that

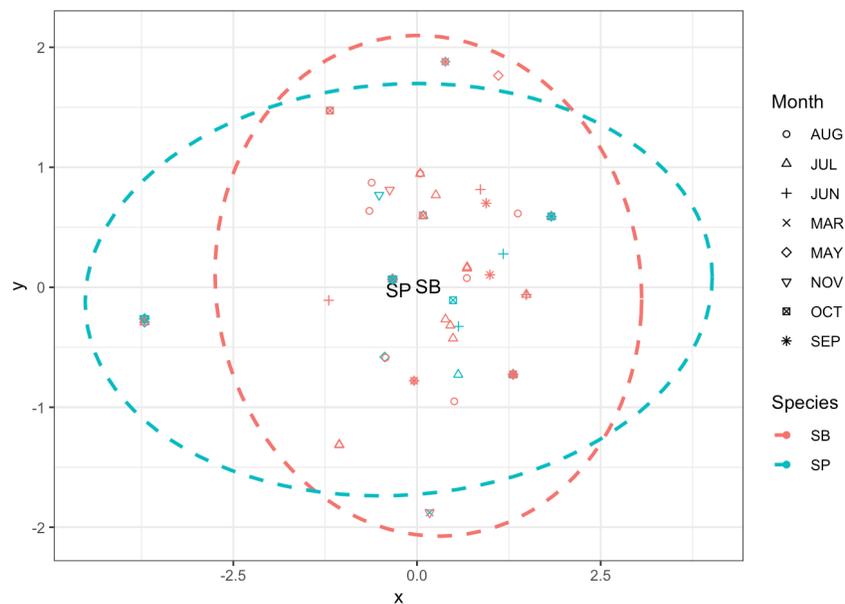


Figure 4. Non-metric Multidimensional scaling distribution of diets for Striped Bass and Sacramento Pikeminnow collected via hook and line sampling near Chico, CA. Blue ellipse denotes Sacramento Pikeminnow and red ellipse denotes Striped Bass. Modeling conducted via R package ‘vegan’ using Bray dissimilarity distance and 1000 permutations to reduce stress (Oksanen et al. 2013; Wickham 2016; R core team 2018).

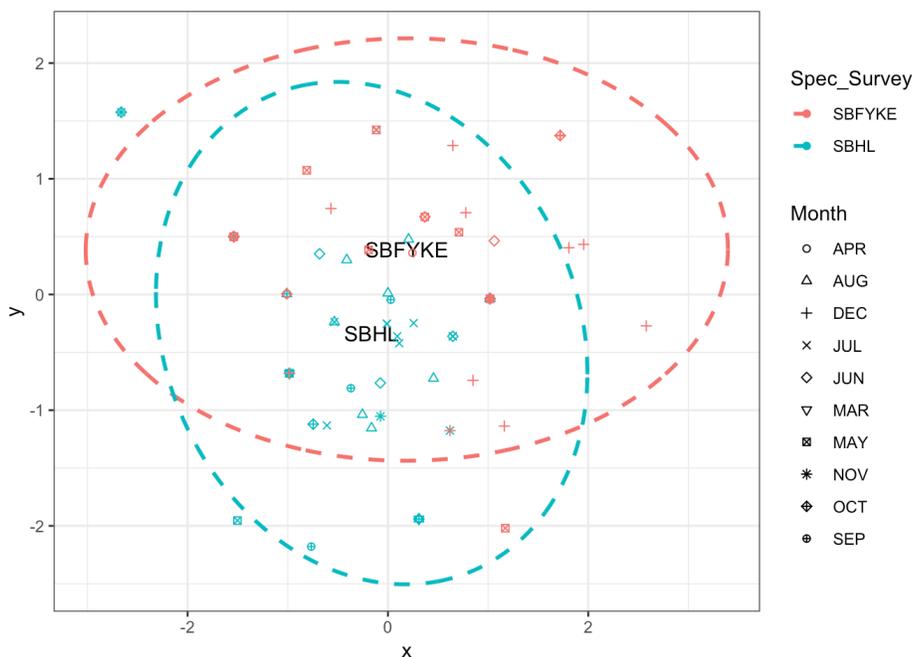


Figure 5. Non-metric Multidimensional scaling distribution of diets for Striped Bass collected via hook and line sampling near Chico, CA, and Striped Bass collected via fyke trap near Sacramento, CA. Blue ellipse denotes hook and line fish and red ellipse denotes fyke trap fish. Modeling conducted via R package ‘vegan’ using Bray dissimilarity distance and 1000 permutations to reduce stress (Oksanen et al. 2013; Wickham 2016; R core team 2018).

Table 6. PERMANOVA model testing species (Sacramento Pikeminnow and Striped Bass), fork length, water temperature, Secchi depth, site type (man-made, rip-rap, natural), and month of capture for fish captured via hook and line sampling near Chico, CA. Top table run using prey numerical data (count), bottom table run using prey frequency of occurrence (FO). Model run in R package 'vegan', using function 'adonis2' with marginal testing and 10,000 permutations (Oksanen et al. 2013; R core team 2018).

| Source | Df | Sum of squares | R ² | F | Pr(>F) |
|--|----|----------------|----------------|------|--------|
| Prey count ~ species + FL + WT + SD + Site Type + Month | | | | | |
| Species | 1 | 0.23 | 0.01 | 0.60 | 0.763 |
| Fork Length | 1 | 0.54 | 0.02 | 1.43 | 0.190 |
| Water Temp. | 1 | 0.37 | 0.01 | 0.97 | 0.462 |
| Secchi Depth | 1 | 0.29 | 0.01 | 0.76 | 0.622 |
| Site Type | 2 | 0.58 | 0.02 | 0.77 | 0.699 |
| Month | 7 | 3.67 | 0.13 | 1.38 | 0.060 |
| Residual | 67 | 25.40 | 0.82 | | |
| Total | 80 | 31.10 | 1.00 | | |
| Prey FO ~ species + FL + WT + SD + Site Type + Month | | | | | |
| Species | 1 | 0.12 | 0.004 | 0.35 | 0.857 |
| Fork Length | 1 | 0.52 | 0.02 | 1.52 | 0.186 |
| Water Temp. | 1 | 0.33 | 0.01 | 0.96 | 0.453 |
| Secchi Depth | 1 | 0.44 | 0.02 | 1.30 | 0.272 |
| Site Type | 2 | 0.45 | 0.02 | 0.66 | 0.734 |
| Month | 7 | 3.14 | 0.11 | 1.32 | 0.134 |
| Residual | 67 | 22.83 | 0.93 | | |
| Total | 80 | 27.52 | 1.00 | | |
| Significance codes: '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 | | | | | |

Table 7. PERMANOVA model testing survey (hook and line and fyke trap), fork length, and water temperature for Striped Bass captured via hook and line sampling near Chico, CA and Striped Bass captured via fyke trap near Sacramento, CA. Top table run using prey numerical data (count), bottom table run using prey frequency of occurrence (FO). Model run vegan R package 'vegan', using function 'adonis2' with marginal testing and 10,000 permutations (Oksanen et al. 2013; R core team 2018).

| Source | Df | Sum of squares | R ² | F | Pr(>F) |
|--|----|----------------|----------------|------|-------------|
| Prey count ~ Survey + FL + WT | | | | | |
| Survey | 1 | 1.15 | 0.03 | 3.06 | 0.004 ** |
| Fork Length | 1 | 0.79 | 0.02 | 2.12 | 0.034 * |
| Water Temp. | 1 | 1.33 | 0.03 | 3.55 | 0.001 ** |
| Residual | 89 | 33.36 | 0.88 | | |
| Total | 92 | 38.11 | 1.00 | | |
| Prey FO ~ Survey + FL + WT | | | | | |
| Survey | 1 | 1.49 | 0.04 | 4.46 | 7.9e-04 *** |
| Fork Length | 1 | 0.81 | 0.02 | 2.44 | 0.035 * |
| Water Temp. | 1 | 1.28 | 0.04 | 3.84 | 0.002 ** |
| Residual | 89 | 29.68 | 0.84 | | |
| Total | 92 | 35.28 | 1.00 | | |
| Significance codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 | | | | | |

cumulative prey curves for both predator species within hook and line sampling, and for Striped Bass from both survey types, reached an asymptote (Ferry and Cailliet 1996, Oksanen et al. 2013).

PERMANOVA modeling confirmed the visual indication given by NMDS. Separate models were run to test the effects of species within the hook and line component, and to test the effects of survey type/location for Striped Bass. The variables included in the model testing

effects of species on diet included species, fork length, water temperature, Secchi depth, site type, and month of capture. PERMANOVA analysis did not reveal any significant associations between variables included and diet at or below a threshold p-value of 0.05 (Table 6).

Conversely, PERMANOVA analysis did detect significant associations between survey type/location (count: $F = 3.06$, $df = 1$, $p = 0.004$; FO: $F = 4.46$, $df = 1$, $p = 7.9e-04$), fork length (count: $F = 2.11$, $df = 1$, $p = 0.034$; FO: $F = 2.43$, $df = 1$, $p = 0.035$), water temperature (count: $F = 3.55$, $df = 1$, $p = 0.001$; FO: $F = 3.84$, $df = 1$, $p = 0.002$), and diet, using both count and frequency of occurrence data, when only examining Striped Bass (Table 7). When variables from the Table 7 models were tested for interaction effects, PERMANOVA did not find a significant interaction between survey and fork length ($F = 1.84$, $df = 1$, $p = 0.099$), however, an interaction was seen between survey and water temperature ($F = 3.54$, $df = 1$, $p = 0.005$), potentially reflecting the temperature dependence of prey assemblages.

DISCUSSION

Predation by native and non-native predators in the Sacramento River system is often cited as one of the major contributing factors to native species decline, without sufficient available data on in-river species interactions. By examining the diets of the two primary predatory fish species within the Sacramento River upstream of the Sacramento-San Joaquin delta, this study aimed to approach the issue of native species loss through better understanding of predator life history. While clearly only a snapshot of diets, during a particularly high-water year, we were able to demonstrate the similarity of diets among Striped Bass and Sacramento Pikeminnow near Chico, CA (Table 4-6; Figure 4), as well as the dissimilarity in diets between Striped Bass captured via hook and line survey near Chico, CA, and those captured via fyke trap near Sacramento, CA (Table 4,5,7; Figure 5).

Predator Distribution

CPUE was used as an index of abundance for the hook and line survey portion of this study. Since CPUE was not associated with water clarity it is unlikely that poor water clarity had an effect on the efficacy of CPUE as an index value, potentially due to the use of bait as a fishing method. The olfactory cues given off by bait are present regardless of water clarity, further adding to the effectiveness of CPUE as a density index value (Rowe and Dean 1998; Rowe et al, 2003; Stoner 2004). CPUE analysis showed that Striped Bass distribution was even across all habitat types considered, while Sacramento Pikeminnow were more likely to be found at the man-made sites along this study reach. Conversely, Sacramento Pikeminnow CPUE was unaffected by all other variables considered while Striped Bass CPUE was associated with water temperature and month of capture, likely a consequence of their anadromous life history strategy.

This study attempted to describe movement and residence behavior of predators through external tagging, however recaptures were not frequent enough to return conclusive results. Striped Bass did seem to show higher rates of movement than Sacramento Pikeminnow which aligns with anadromy in Striped Bass and resident behavior in Sacramento Pikeminnow. Striped Bass are known to exhibit both anadromous and resident behavior in their native waters (Morris et al. 2003), however this is relatively uncommon in the Sacramento River, at least among subadult individuals (Sabal et al. 2018). Given the fluctuating in-river populations of sensitive prey species (i.e. salmon, sturgeon, etc.), the concept of Striped Bass residence may have implications for predation effects and would certainly have implications for interspecific competition/predation with Sacramento Pikeminnow. The movement of Striped Bass should be further investigated in future studies using more sophisticated tagging technology and/or larger sample sizes in order to return a higher definition of distribution and to clarify Sacramento-San Joaquin Striped Bass life history.

Diet by Location

It has been noted in previous publications that predation may be higher near man-made structures due to the altered hydraulics in these environments (Sommer et al. 2001; Brown and Moyle 1981); however, we did not observe this phenomenon over the course of this study. While there are undoubtedly predation hot spots within the Sacramento River, there was no association between diet and habitat type for predators captured near Chico, CA. This can likely be attributed to two factors. First, while man-made 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 which act in similar ways. The section of the Sacramento River near Chico, CA, contains many submerged trees, or snags, which impede flow

and are often targeted by recreational anglers, in much the same way they target bridge pilings, for their ability to hold Striped Bass. Second, the two water diversion facilities selected as man-made sampling locations, GCID and a smaller private pumping station, were, in the opinion of the primary author, well-engineered to reduce predation risk. Notably, the GCID fish screen runs parallel to flow and did not appear to create any low water velocity areas in which to concentrate predators and prey. 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).

While there were no associations between habitat and diet seen locally, Striped Bass diets were significantly different between hook and line and fyke trap surveying. This result is confounded by different sampling methodology and sampling period, however the differences in diet clearly reflect the different prey available between sampling locations. Striped Bass have been shown to exhibit prey switching behavior over relatively short times scales when new prey species are introduced to a system (1-2 years; Nobriga and Feyrer 2008), and the same concept can be applied to predation locally. The two most important prey species to Striped Bass collected near Sacramento, Threadfin Shad and crayfish, may very well have been more available in the lower reaches of the Sacramento River, reflecting spatial prey switching behavior. While little data is available to show the upstream boundaries of Threadfin Shad, they are regarded as a warm-water species (Moyle 2002) and USGS records show more collections lower in the system (U.S. Geological Survey 2018), indicating a higher density near the Sacramento fyke traps.

Species-Specific Diets

Observed %IRI, dietary niche breadth overlap, and PERMANOVA modeling all indicate no difference in diets between Striped Bass and Sacramento Pikeminnow captured via hook and line sampling near Chico, CA. There are obvious life history differences between these two species, namely anadromy in Striped Bass versus residence in Sacramento Pikeminnow, however on a per capita basis it would appear that neither of these species has a higher impact on any particular prey than the other. There are currently no estimates of Sacramento Pikeminnow abundance in the Sacramento River, and only indexes of Striped Bass abundance available, therefore total effect of predation on native species cannot be accurately enumerated from diet composition. Future studies should focus on building accurate population estimates for both Striped Bass and Sacramento Pikeminnow in order to clarify their role as predators in the Sacramento River system.

Given that Striped Bass and Sacramento Pikeminnow captured near Chico, CA, did not have statistically different diets, there are management implications for both species in regard to reducing predation on valuable native species such as Chinook Salmon. While maximal carrying capacities of two species may differ, Gause's 1934 experiments on the growth of yeast species in a homogenous environment show that, in the exclusion of an interspecific competitor, a species will reach a higher maximum population level (Gause 1934a, 1934b). The Sacramento River system is clearly not homogenous; however, the concept holds true. If at any point either Striped Bass or Sacramento Pikeminnow are resource limited within the Sacramento River, then their high dietary niche breadth overlap would mean that the exclusion of one species would increase available resources for the other, potentially increasing maximum population levels. Conversely, Pianka's "niche-overlap hypothesis", which states that higher niche breadth overlap indicates a

lower environmental saturation, or “ecological vacuum”, would seem to indicate that neither species is resource limited (Pianka 1972, 1974). Of course, the high degree of niche breadth overlap may simply reflect prey switching behavior by predators due to anadromous prey population fluctuations, eliciting functional response as prey populations exceed a critical prey threshold (Gause et al. 1936; Holling 1959a, 1959b, Buckel and Stoner 2000).

In an effort to reduce DNA contamination, this study did not address the issue of predation by Sacramento Pikeminnow and Striped Bass on one another. Within the recreational fishing community, it is well known that Sacramento Pikeminnow make excellent bait for Striped Bass on the Sacramento River; implying interspecific predation. Given the anadromous life history of Striped Bass larvae, as well as the resident behavior of Sacramento Pikeminnow, it is likely that interspecific predation is more heavily weighted towards predation by Striped Bass on Sacramento Pikeminnow. As interspecific predation is potentially confounding to the concept of competition and impact on prey between these two species, this should be further investigated.

Implications and Future Directions

While not intended to completely describe the diets of Sacramento Pikeminnow and Striped Bass, this study was successful in displaying the similarity of diets between the two species, the irrelevance of certain man-made structures in determining diet in the study reach considered during the course of this study and the spatial differences in diet amongst Striped Bass. Our results show that while Striped Bass and Sacramento Pikeminnow do consume vulnerable native species such as Chinook Salmon and green sturgeon, they do not make up the majority of either species’ diet and are more likely the result of opportunism amongst fluctuating prey populations. It is reasonable to assume that Sacramento Pikeminnow and Striped Bass will

exhibit prey switching behavior in the presence high densities of certain prey, as is the case with in-river hatchery Chinook Salmon releases; however, high water and turbidity did not allow us to effectively sample when out-migrating hatchery Chinook populations were highest.

Future diet studies in the Sacramento River system should consider the use of alternate sampling techniques, as hook and line sampling is both time consuming and returns relatively few individuals per unit effort, and the use of higher throughput stomach content processing methods. While it would preclude the calculation of IRI values, high throughput qPCR or next generation sequencing of whole homogenized stomachs would return quality frequency of occurrence data for dietary niche breadth overlap, NMDS, and PERMANOVA analysis. Additionally, while the effects of temperature on digestion rate have been clearly shown and enumerated for Sacramento Pikeminnow (Vondracek 1987), a correction factor for temperature dependent digestion rate has not been determined for Striped Bass. For this reason, diets were not temperature corrected and daily consumption was likely greater than observed when water temperatures were high. Further laboratory studies are required to determine Striped Bass temperature dependent digestion rates and to fully understand seasonally and environmentally associated diets. Additionally, sampling across multiple water years would add clarity to the dietary data reported here, allowing fisheries managers to identify conditions and strategies most suitable to successful hatchery Chinook releases. Finally, as it has been shown that certain structures and other impediments to flow can act as predation hot spots (Brown and Moyle 1981), further study should focus on identifying these locations within the Sacramento River for mitigation by utilities or management agencies.

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