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**INTERACTIVE EFFECTS OF NON-NATIVE PREDATORS AND
ANTHROPOGENIC HABITAT ALTERATIONS ON NATIVE JUVENILE
SALMON**

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Abstract

INTERACTIVE EFFECTS OF NON-NATIVE PREDATORS AND ANTHROPOGENIC HABITAT ALTERATIONS ON NATIVE JUVENILE SALMON

by

Megan Sabal

Multiple human stressors including non-native species and habitat alterations can interact with complex consequences on native species. Human-modified habitats can change non-native predator functional and aggregative responses with additive impacts on native prey species. I assessed how the non-native predator, striped bass (*Morone saxatilis*), and habitat alterations (small diversion dam and other altered habitats) interact to influence mortality on native juvenile Chinook salmon (*Oncorhynchus tshawytscha*) migrating to sea on the lower Mokelumne River, CA (USA). Relative abundance and diet surveys across natural and human-altered habitats assessed functional and aggregative responses of striped bass. Striped bass showed elevated per capita consumption of juvenile salmon and behavioral aggregation (estimated as catch per unit effort – CPUE) at a small diversion dam site (Woodbridge Irrigation District Dam: per capita consumption= 3.54 juvenile salmon per striped bass and CPUE= 0.189) over other altered (0 juvenile salmon per striped bass; CPUE= 0.0024) and natural habitats (N/A; CPUE= 0.0003) creating a localized area of heightened predation. At this predation hotspot, experimental predator removals, diet energetic analysis, and before-after impact assessment estimated

striped bass consumption of the population of out-migrating juvenile salmon to be between 10-29%. Striped bass per capita consumption rates among the three approaches were 0.92%, 1.01-1.11%, and 0.96-1.11% respectively. This study highlights how interactions between multiple stressors can exacerbate consequences for native species and are important to examine when predicting ecological impacts from stressors and planning local management strategies.

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Introduction

Human stressors are leading causes of declines in species and biodiversity, and wholesale changes in ecosystem structure, functions, and services (Dudgeon et al. 2006, Halpern et al. 2008b, Sanderson et al. 2009, Barnosky et al. 2012, Dodds et al. 2013). Typically, impacts of human stressors on species are studied independently, although evidence suggests that multiple stressors interact and exacerbate or ameliorate their consequences (Schindler 2001, Didham et al. 2007). Furthermore, different ecological mechanisms can cause interactions to be non-additive producing an even greater net impact on species (Crain et al. 2008). Human stressors are ubiquitous across ecosystems, and therefore it is important to examine interactive effects of multiple stressors to understand their ecological consequences, potentially predict impacts in altered systems, and design appropriate management strategies to maintain healthy populations of species (Halpern et al. 2008a).

Two significant human stressors driving global change are the establishment of non-native species and habitat alterations. Non-native species may compete with or prey upon native species or interact indirectly and change prey behavior or cause apparent competition (DeCesare et al. 2009, Sorte et al. 2010). Habitat alterations change the physical environment with direct physiological consequences for native fishes or indirect effects such as reduced growth (Schindler et al. 2000, Hojesjo et al. 2004) or reproductive success (Halfwerk et al. 2011). Habitat changes can alter predator-prey overlap (Peters et al. 2013, Kempf et al. 2013), success of invading species (Marchetti et al. 2004), prey vulnerability (Weber and Brown 2012), or

predator foraging success (Bartholomew et al. 2000), and thereby interact with non-native predators to change the magnitude of predation by modifying predator responses (Vucic-Pestic et al. 2010, Alexander et al. 2012). Locally, an aggregation of predators exerts greater net mortality on a prey population, while an increase in predator functional response, specifically per capita consumption of prey relative to prey density, results in higher net predation despite constant predator abundances (Holling 1959, Murdoch and Stewart-Oaten 1989). An increase in both predator responses results in an exponential increase in consumption of native prey also referred to as synergistic or functionally-moderated interaction. Synergistic interactions occur commonly in nature-for example, as predators aggregate at habitats where feeding is profitable (Anderson 2001b, Didham et al. 2007). Additive impacts from multiple stressors may intensify negative consequences on native species and create hotspots of artificially-inflated predation, yet also may allow for spatially-focused management strategies.

Native California salmon populations are in decline and are an integral ecological link between terrestrial, freshwater, and marine ecosystems as well as economically and culturally significant recreational and commercial resources. In the Sacramento-San Joaquin Delta in California (USA), native juvenile Chinook salmon (*Oncorhynchus tshawytscha*) populations experience high mortality during their outmigration to sea (Michel 2010). During outmigration juvenile salmon pass through various anthropogenically-altered habitats such as dams, diversions, marinas, and rip-rap channels, and also encounter multiple non-native predators. Striped bass

(*Morone saxatilis*), introduced from the east coast in 1879, are recognized as a potential threat to juvenile salmon due to their reputation as a voracious fish predator despite inconclusive predation and diet studies (Lindley and Mohr 2002, Nobriga and Feyrer 2008, Loboschefskey et al. 2012). Significant uncertainty exists in the relative and absolute importance of various stressors on salmon mortality, and this challenges management efforts aiming to restore salmon populations. Scientific studies need to assess impacts of human stressors and their interactive effects including, but not limited to habitat alterations and non-native predators (Grossman et al. 2013). A mechanistic understanding of how stressors impact juvenile salmon and context dependence of interactions will allow for more ecologically-aware and effective management strategies.

This study examines how the combined effects of habitat alterations and a non-native predator, striped bass, influence mortality on native, migrating juvenile salmon. I ask if striped bass consumption of juvenile salmon is greater at anthropogenically-altered habitats, if striped bass aggregate at these habitats, and what is the population-level impact on an out-migrating salmon population at an area of high predation. Answers to these questions are fundamental to our understanding of how and to what extent human-modified riverine habitat and introduced predators influence survival of juvenile salmon as they migrate to sea. I used data on diet and the fish community to estimate per capita consumption and aggregative responses of striped bass. I combined predator removal experiments, diet energetic analysis, and a

before-after impact assessment to generate three separate estimates of striped bass' impact on the population of out-migrating juvenile salmon.

Methods

To address the combined effects of habitat alterations and predation by introduced striped bass on juvenile Chinook salmon, I used a combination of field observations, experiments, and laboratory analysis to ask (1) is the per capita rate of juvenile salmon consumption by introduced striped bass greater at human-modified habitats than natural habitat elsewhere in the same river? (2) If so, are predators more likely to aggregate at these sites of greatest per capita salmon consumption? And (3) what is the consumption of juvenile salmon population by striped bass at the altered habitat?

Study system

I address these questions in the lower Mokelumne River in the eastern Sacramento-San Joaquin Delta that drains approximately 1,624 km² of central Sierra Nevada and extends 54 km between Comanche Dam and the confluence of the San Joaquin River. River flows are highly regulated with peak flows occurring typically between November and April. My study sites lie below the Woodbridge Irrigation District Dam (WIDD) (Figure 1), which is approximately 50 m across and creates a relatively deeper pool of water immediately downstream and is distinct from other habitats, which include glides and pools bordered by natural vegetation, levees, and

rip-rap banks (Merz and Setka 2004). The river is tidally-influenced, average river gradient is 0.0003, and substrate is comprised of sand and mud. Over 38 fish species inhabit the Mokelumne River including anadromous, non-native striped bass and native Chinook salmon that spawn naturally without the aid of fish hatcheries. Juvenile Chinook salmon migrate annually from headwaters downstream passing WIDD in two pulses from February-March (approximate fork length (FL) 30-40 mm) and May-June (approximate FL 80-110 mm) (Merz and Workman 2013). The Mokelumne River Fish Hatchery plants juvenile salmon into the river downstream of my study sites, so they are not a pertinent part of the fish community in this study reach. East Bay Municipal Utility District (EBMUD) has been estimating populations of juvenile salmon emigration using rotary screw traps (2.4 meter diameter, E.G. Solutions Inc.) to record juvenile salmon catches, and is operated daily from December-July since 1990 (Volkhardt et al. 2007). Estimates of emigrating juvenile salmon populations vary annually, but ranges on the order of 60,000-280,000 fish passing WIDD. Adult striped bass migrate upstream April-July, and therefore predator and prey overlap during the peak juvenile salmon outmigration in May and June (Le Doux-Bloom 2012).

Striped bass per capita consumption of juvenile salmon by habitat

To test the hypothesis that habitat alterations affect consumption rates by striped bass, I combined relative abundance surveys with diet analysis to compare predation rates of salmon across different habitat types. Because structures, especially

dams and diversions, may disorient salmon and increase predator foraging efficiency (Davis et al. 2012), I predicted that striped bass will have the highest per capita consumption of juvenile salmon at WIDD, followed by other altered, and natural habitats. I surveyed 10 total sites and categorized them into three habitat categories: diversion dam (WIDD) (n=1), other altered (n=7), and natural (n=2). The diversion dam, WIDD, described above significantly alters the physical and hydrodynamic environment and is distinct from all other sites. Other altered habitats included sites with rip-rap channels and sites with man-made structures like docks and bridges. These hardened structures modify the river, but to a lesser extent than WIDD. Natural sites lack hardened structures and are bordered by natural vegetation. Striped bass were captured from the lower Mokelumne River using single-pass boat electrofishing (Smith Root Model SR-18EH) following the methods of Meador et al. (1993) at fixed transects parallel to each shoreline and one in the mid channel at 10 sites between April 23 and May 24, 2013 during peak fall-run Chinook salmon outmigration. I used an automatic timer to record the number of seconds electrofished at each site and used this to calculate striped bass relative abundance: number of striped bass caught per seconds electrofished (CPUE= catch per unit effort). I counted, measured (FL in mm), weighed (g), and took diet samples using non-lethal gastric lavage which were preserved in 95% ethanol (Hakala and Johnson 2004). Striped bass are gape-limited and switch to piscivory around 250 mm FL, therefore striped bass <250 mm FL were not considered as potential juvenile salmon predators (Nobriga and Feyrer 2007).

Diet samples were processed in the lab to quantify relative and absolute consumption of juvenile salmon. I identified prey items to lowest taxonomic level, and enumerated, measured, and weighed each prey group. I used diagnostic bones to distinguish between common digested prey species (Hansel et al. 1988, Frost 2000). If only one fish prey category was present in a stomach, unidentified fish tissue was included in that group weight, if more than one category was present, unidentified fish tissue was divided equally and added to each fish prey category, and non-food items were excluded from diet calculations (Poe et al. 1991). To determine if consumption of juvenile salmon increases with striped bass size or peaks at a middle size, I compared striped bass FL (mm) and number of juvenile salmon found in each diet using both a linear and second degree polynomial relationship. Multivariate methods using PRIMER v.6 were used to compare striped bass diet composition between habitat types (WIDD and other altered). Only 1 striped bass was caught at natural sites and its diet was empty, therefore the natural habitat category is not included in this analysis. I computed a similarity matrix using Bray-Curtis distance on square root transformed weights (g) of prey categories for each fish. Distance-based permutation multivariate analysis of variance PERMANOVA; (Anderson 2001a) was used to test (significance level $\alpha=0.05$) the null hypothesis of no difference of diet composition between habitat types. Analyses were based on 999 unrestricted permutations of raw data. Non-metric multidimensional scaling (nMDS) with diet vector overlay plot was used to visualize multivariate patterns. I also

analyzed diet composition by percent by weight and percent by number for each prey category, and calculated per capita consumption of salmon by habitats.

Striped bass aggregation by habitat

I tested the hypothesis that if there is a greater per capita consumption of juvenile salmon at one or more habitat(s) relative to others, then predators will also aggregate at that habitat(s) with highest rates of salmon consumption. I predicted striped bass will aggregate at man-made structures, seeing the largest aggregation at WIDD followed by other altered habitats, and lowest at natural habitats because structure may increase prey vulnerability and predator foraging success creating profitable feeding locations. I compared catch per unit effort (CPUE), a measure of relative abundance of striped bass (FL >250 mm) from sites in habitat categories: WIDD (diversion dam), other altered, and natural. CPUE data were taken from EBMUD's long-term spring fish community surveys from 1998 to 2013. These data were collected using the same single-pass electrofishing methods described in the previous section. I used one-way ANOVA and Tukey's HSD test to compare mean striped bass CPUE, a measure of aggregation, among WIDD, other altered, and natural habitats. I tested assumptions for these analyses and performed a square root transformation on CPUE data to meet these assumptions. Pearson's chi-squared test was used to compare differences in frequency of striped bass caught across sampling events for each habitat.

Impact on the population of out-migrating juvenile salmon

To further assess the impact of striped bass predation on the population of emigrating juvenile salmon at an area of high predation (WIDD), I used three independent approaches: 1) striped bass removal/salmon survival experiment, 2) diet energetic analysis, and 3) before-after impact assessment.

Striped bass removal/salmon survival experiment

I evaluated how striped bass removal affects juvenile salmon survival by marking and recapturing paired releases of juvenile Chinook salmon before and after striped bass removal. By comparing before and after releases, I hypothesize there will be greater percent of recaptures (i.e. survival) of experimental fish after striped bass removal. This experiment was conducted twice during the peak juvenile salmon migration period in 2013; from May 6 to May 10, and from May 20 to May 24. To remove striped bass I conducted four sequential passes of electrofishing, cumulatively depleting predators at WIDD. To satisfy the assumption of a closed population, required for applying the recapture method of estimating predator abundance, a block net enclosed the study area to prevent predator escapement. I concluded that depletion was complete when the catch-per-pass declined by 75% or more between successive passes (Peterson et al. 2004). To ensure equal capture efficiency between passes I used a pulsed current and kept the total seconds electrofished consistent between passes (Raleigh and Short 1981). Captured fish were held in a live well and transferred to holding tanks until I achieved depletion. I counted, weighed (g),

measured (FL; mm), and collected diet samples using gastric lavage from striped bass >250 mm FL. To assess the relative contribution of an alternative predator to patterns of juvenile salmon mortality, I also collected diet samples from black bass (includes largemouth bass-*Micropterus salmoides* and spotted bass-*Micropterus punctulatus*) to compare striped bass salmon consumption with an alternate non-native predator. After depletion passes were completed, striped bass were transported and released at an alternative location (King's Island) while all other fish species collected were released back into the study area.

To estimate survival of juvenile Chinook salmon, I marked juvenile salmon obtained from the Mokelumne River Fish Hatchery with unique external visible implant elastomer tags. These tags have high retention rates, are easily detected, have no observed effect on survival and growth of juvenile fish (Hale and Gray 1998, Bilski et al. 2011, Leblanc and Noakes 2012). Therefore I did not account for tag loss in our estimates of survival. The first release (before removal treatment, n=1000) was performed at the base of WIDD in the evening two days prior to striped bass removal. A rotary screw trap (2.4 meter diameter, E.G. Solutions Inc.) approximately 200 meters downstream of WIDD was checked every morning and juvenile salmon recaptures were recorded (Volkhardt et al. 2007). The second release (after predator removal treatment, n=1000) was performed in the evening after striped bass removal. Recapture rate was calculated from the number of tagged fish recaptured in the screw trap extrapolated to the total river by volume divided by total number of tagged fish released. Both release and recapture estimates were divided by corresponding daily

flow (EBMUD's Golf gauging station) to standardize recaptures by volume of water sampled. We examined the difference between proportion of recaptures before and after striped bass removal. After final salmon recaptures were recorded, I conducted a single-pass of electrofishing to assess if striped bass remained removed over the duration of the experiment and if other fish species remained roughly consistent to what I caught on the first pass on day of removal. Changes in the fish community occurring throughout the experiments, could confound my treatment making it difficult to attribute change in salmon survival to striped bass removal.

Diet energetic analysis

To determine if the change in survival found in the first striped bass removal/salmon survival experiment was due to predation, I also calculated percent salmon consumed using diet analysis from the same predators. I calculated the average number of salmon consumed per striped bass removed from the first removal experiment, and because fish predators frequently digest prey under 24 hours, I used a range of fast (10 hours; 0.416 days) and slow (15 hours; 0.625 days) gastric evacuation rates to extrapolate to daily individual consumption (Elliott and Persson 1978, TID/MID 1992). Individual daily consumption rates were multiplied by the number of striped bass removed (11) to calculate daily population-level consumption. I used the known number of experimental fish released at WIDD and ratio of known number of recaptures of experimental fish to natural fish caught in the screw trap to estimate the number of natural fish passing WIDD. I then assumed a constant ratio of

natural fish caught in the trap to total number passing WIDD to calculate juvenile salmon populations at WIDD for the day striped bass were removed. I calculated the percent of juvenile salmon consumed by striped bass using the daily population-level consumption rate.

A black bass population estimate at WIDD was determined from multiple-pass depletion electrofishing, using least squares linear regression of black bass catch per effort (CPUE) against cumulative catch, lagged for one unit of effort (Maceina et al. 1995, Cavallo et al. 2012). Using the same methods, I also calculated population-level consumption of black bass on juvenile salmon for both first and second removal experiments.

Before-after impact assessment

I used existing data from EBMUD to retrospectively determine whether striped bass removal affects juvenile emigration survival in Mokelumne River natural Chinook salmon populations, and if the magnitude of impact is related to number of striped bass removed. The rotary screw trap below WIDD captures migrating juvenile salmon daily and because catches are highly auto-correlated, I hypothesize that juvenile salmon catch will increase the day following a predator removal and the magnitude will increase with increasing numbers of striped bass removed. I tested this prediction by calculating percent change in salmon survival $(\text{After} - \text{Before} / \text{After} + \text{Before}) * 100$ using juvenile salmon catches in the screw trap the day before and day after an impact (predator removal) and control (no predator removal). This

value scales from 100% to -100% where 0 indicates catches before and after are identical, positive values indicate an increase, and negative values a decrease in juvenile salmon catch.

EBMUD conducted predator removals in 2009 and 2010; they used boat electrofishing to catch, deplete, and remove both striped bass and black bass from WIDD, multiple passes were not separated, and there was no block net in place. Ten total predator removal events from 2009 (n=4), 2010, (n=4), and 2013 (n=2) were included in the impact treatment. Electrofishing during predator removal can injure or cause mortality to Chinook salmon, which may diminish salmon catch in the screw trap the first day following removal (Schreer et al. 2004). For this reason, I calculated percent change in salmon survival between both the day before and the first day after removal and the second day after removal. For the control treatment I calculated percent change in salmon survival before and after all pairs of days in 2009, 2010, and 2013 excluding the day before and two days after predator removals and days there was debris in the screw trap preventing it from fishing properly (n=139). I used Welch two-sample t-tests to compare mean percent change in salmon survival between control and each impact treatment and estimate the impact of striped bass removal on juvenile salmon survival. To assess if percent change in salmon survival correlated with numbers of striped bass removed, I conducted a linear mixed regression analysis where percent change in salmon survival was the response variable, striped bass number removed was the predictor variable, and period (first or second day after removal) was a random effect.

Results

Striped bass per capita consumption of juvenile salmon by habitat

Striped bass diet composition including juvenile Chinook salmon consumption differed markedly between WIDD and other altered habitats (Figure 2; Appendix 1 and 2). Striped bass ranged from 225 to 925 mm FL with an average size of 530 mm at WIDD (n=22) and an average size of 424 mm at all other sites (n=30). Diet data showed striped bass consumption of juvenile salmon was not significantly size dependent using either linear ($R^2 = -0.033$, $p = 0.572$) or second degree polynomial ($R^2 = 0.057$, $p = 0.219$; Appendix 3) relationships, and therefore diets were not separated into size classes of striped bass for energetic analysis. Multivariate PERMANOVA showed significant differences in striped bass diets between WIDD and other altered habitats ($p = 0.001$, $df = 1$, psuedo-F = 17.3). nMDS plot indicated strong grouping of striped bass diet samples by location and diet vector overlay shows the presence of juvenile salmon primarily drives diet differences (Figure 2). Juvenile Chinook salmon was the predominant prey item from striped bass caught at WIDD (56.52% number, 94.82% weight) while there was no occurrence of salmon in diets from any other locations. Striped bass consumed primarily crayfish at other locations (18.18% number, 90.87% weight; Appendix 1 and 2). Striped bass per capita consumption of juvenile salmon was 3.54 at WIDD and 0 at other altered habitats.

Striped bass aggregation by habitat

Striped bass aggregated at WIDD with an eight-fold increase in CPUE (WIDD mean= 0.0189) relative to other altered (mean= 0.0024) and sixty-fold increase relative to natural habitats (mean= 0.0003) (Figure 3). One-way ANOVA and Tukey's HSD tests indicated significant differences between all pair combinations: WIDD and other altered ($p < 0.001$), WIDD and natural ($p < 0.001$), and other altered and natural ($p = 0.03$). Striped bass were caught in 13/15 (86.6%) surveys at WIDD, 37/100 (37.0%) surveys at other altered, and 6/21 (28.6%) surveys at natural habitats (Chi-squared test: $df=4$, $p = 0.0048$). Striped bass ranged from 204 to 904 mm FL with an average size of 526 mm at WIDD ($n = 132$), ranged from 201 to 705 mm FL with an average size of 391 mm at other altered habitats ($n = 90$), and ranged from 225 to 510 mm FL with an average size of 363 mm at natural habitats ($n=18$).

Impact on the population of out-migrating juvenile salmon

Striped bass removal/salmon survival experiment

Estimated Chinook salmon survival increased 10.21% after first removal of 11 striped bass (0.92% per capita impact), and decreased 2.06% after second removal of 1 striped bass. Majority of striped bass caught in the first experiment were >400 mm FL, and although I did see re-colonization of WIDD during the 12 days between experiments all but one striped bass was <250 mm FL in the second removal experiment (Appendix 4). I depleted 78.4% and 89.9% of the total striped bass

populations including all size ranges (Appendix 5), but only removed 11 and 1 predatory striped bass capable of consuming juvenile salmon in first and second removal experiments respectively. Environmental conditions were similar between both experiments: water temperature (17.0°C, 17.7°C) and water flow (4.56 cms, 4.51 cms). Release groups of experimental salmon were similar in size between first and second removal experiments (mean FL= 78.95 mm and 82.31 mm, respectively) and slightly smaller than natural fish populations (mean FL= 87.3 mm and 92.11 mm, respectively). Greater than 99% of experimentally tagged fish were recaptured in the screw trap the morning following the release suggesting fish are migrating through the basin immediately, and the first release group is out of the system by the time the second group is released. After the removal experiments were completed, single-passes of electrofishing indicated I maintained removal of striped bass in the first experiment, but did not maintain removal in the second experiment (Appendix 6). Because I removed 1 predatory striped bass and caught 1 after the end of the second experiment, there was approximately no change in striped bass predation impact between tagged salmon releases. The remaining fish community had variable responses with some species increasing and others decreasing in abundance (Appendix 6).

Diet energetic analysis

Diet samples from striped bass caught in the first removal experiment contained an average of 4.75 juvenile salmon per striped bass. Gastric evacuation

rates (slow and fast range) generated individual daily consumption rates of 7.60-11.40 juvenile salmon per day. Using the 11 striped bass that I removed in the first experiment, I scaled individual consumption to daily population-level consumption of 86.9-125.4 juvenile salmon per day. Mark and recapture estimates of salmon population size were 770 salmon and 796 salmon for the first and second days of removal respectively. During the first removal experiment, the 11 striped bass removed would have consumed between 11.2% (slow) and 16.2% (fast) (1.01%-1.47% per capita impact) of the migrating juvenile salmon population passing WIDD. Despite having introduced tagged hatchery salmon into the system for my removal experiments two days before, striped bass diets were likely comprised only of natural fish because >99% of experimentally tagged fish migrated through the reach within 12 hours of release and would have been absent when diet samples were taken.

The same methods showed black bass consumed an average of 0.08 juvenile salmon and individual daily consumption rates of 0.13-0.19 juvenile salmon per day. Depletion regression estimated a population of 16.5 ($R^2 = 0.6209$, $p = 0.0708$) and 38.0 ($R^2 = 0.9987$, $p = 0.0004$; Appendix 7) black bass at WIDD during first and second removals respectively, which scales population level consumption to (2.08-3.13) and (4.80-7.2) juvenile salmon per day. Black bass consumed between 0.27-0.41% (0.01%-0.18% per capita impact) of the migrating juvenile salmon population passing WIDD during the first removal experiment and 0.60-0.90% (0.01%-0.02% per capita impact) during the second removal experiment.

Before-after impact assessment

The before-after impact assessment indicated a mean increase in natural salmon survival of 25-29% after predator removal. Ten removal events from 2009, 2010, and 2013 occurred in the range of May 7th to June 16th and between 1 and 68 striped bass (average 26.3) were removed. For the control, the mean percent change in salmon survival between pairs of days with no predator removal was 0.3%. For the impact treatments, percent change in salmon survival between day before and first day after predator removal was 25.9% ($t = -2.02$, $df = 10.52$, $p = 0.06$), and for day before and second day after predator removal was 29.2% ($t = -2.61$, $df = 11.05$, $p = 0.024$). Welch two-sample t-tests indicated both predator treatments showed an increase in salmon caught compared to control treatment (Figure 4). The average number of striped bass removed among all removal events was 26 striped bass; therefore, the striped bass per capita impacts are 0.96% and 1.11% for first day after removal and second day after removal respectively. Mixed linear regression indicated increasing proportional change with increasing number of striped bass removed ($t = 2.43$, $df = 17$, $p = 0.026$; Figure 5).

Discussion

Multiple stressors can interact with complex consequences on native species. In this example, habitat alterations, likely through an increase in foraging efficiency, increase the magnitude of predation by a non-native predator. This interaction is synergistic as habitat increases both functional and aggregative responses of a

predator. A local predation hotspot, WIDD, was associated with increased striped bass per capita salmon consumption and attracted larger numbers of striped bass decreasing migrating juvenile salmon survival by 10-29%.

I found that striped bass diets from WIDD consisted primarily of juvenile salmon, and the per capita impact of striped bass on salmon was higher at WIDD than other altered locations. Alterations at WIDD may create profitable feeding conditions by concentrating prey density because of shortened river width or upstream location before salmon experience additional downstream mortality, or disorienting migrating salmon coming over the dam with sudden changes in water velocity (Deng et al. 2010), or favoring visual predators because of reduced turbidity (Gregory and Levings 1998, Horodysky et al. 2010). Increased juvenile salmon consumption behind dam-like structures has also been observed by Sacramento pikeminnow (*Ptychocheilus grandis*) and striped bass on the Sacramento River (Tucker et al. 1998), by Northern pikeminnow (*Ptychocheilus oregonensis*), walleye (*Sander vitreus*), and small mouth bass (*Micropterus dolomieu*) on the Columbia River (Rieman et al. 1991), and on the U.S. East Coast by striped bass on the Merrimack River (Blackwell and Juanes 1998). These studies attribute increased juvenile salmon predation to disoriented prey, increased transit time through study reaches, and aggregations of predators. I cannot truly distinguish a functional response because I lack data on prey density of juvenile salmon at sites during diet sampling. I conclude there was a large difference in per capita consumption of juvenile salmon between

WIDD and other altered locations potentially due to increased foraging efficiency at WIDD.

Striped bass did aggregate at WIDD with an eight-fold increase in CPUE compared to other altered locations and sixty-fold increase compared to natural locations. This aggregation corresponds to where per capita consumption of juvenile salmon was also greatest suggesting striped bass may aggregate to areas of profitable feeding. Feeding aggregations are common in nature and include striped bass aggregating behind dams on the U.S. East Coast to feed on migrating blueback herring (*Alosa aestivalis*) (Davis et al. 2012). Alternatively, spawning aggregations or blocked upstream migration could account for the observed aggregation at WIDD, however there are no documented striped bass spawning areas on the Mokelumne River and I observed very few ripe male fish. Aggregation at other altered over natural habitats may still be due to hardened structures increasing foraging efficiency despite absence of juvenile salmon in striped bass diets. Regardless of the reason for aggregation, I saw an increase in striped bass, which increases predation on juvenile salmon relative to other locations. The habitat alteration, WIDD, interacts with the non-native predator, striped bass at WIDD, to increase both functional and aggregative predator responses. This creates a local hotspot of juvenile salmon mortality, which is artificially inflated above natural levels.

I used three separate approaches to assess striped bass impact on the population of out-migrating juvenile salmon and generated a range of 10-29% of the juvenile salmon population consumed by striped bass at WIDD. These population-

level impact values were generated for different numbers of striped bass at WIDD, but are comparable through striped bass per capita impacts which ranged from 0.92%, 1.01-1.11%, and 0.96-1.11% for striped bass removal/salmon survival experiments, diet analysis, and before-after impact assessment respectively. Despite limitations in each approach, these findings point in the same direction and similar magnitude. The first approach was the striped bass removal/salmon survival experiments which showed a 10.2% increase in salmon survival after 11 striped bass were removed and a 2% decrease in survival after 1 striped bass was removed. The 10.2% increase in survival supports my hypothesis that survival would increase after I removed striped bass. The 2% decrease suggests there was minimal change in salmon survival when only 1 striped bass was removed, which is logical given I was unsuccessful keeping striped bass removed in the second experiment. Possible other effects are electrofishing and handling stress on other fish predators that were not removed could have caused them to migrate out of the study area (Appendix 4), reduce feeding, or change other behaviors, which could confound the effect of striped bass removal on juvenile salmon survival. However, if stressing of other predators was responsible for some of the observed increase in salmon survival in the first removal experiment, I would have expected to see an increase in survival during the second removal experiment when there was minimal change in predation impact. Salmon survival minimally decreased in the second experiment suggesting striped bass are the primary influence on salmon survival in this reach.

The second approach to estimate striped bass impact on population of out-migrating juvenile salmon included a diet energetic analysis from striped bass removed during first removal experiment which showed 11-16% of the juvenile salmon population consumed. This estimate is relatively similar to the 10% increase from the first removal experiment. It is important to note that uncertainty exists in these diet estimates. Even though gastric evacuation rates I used came from the nearby Delta, using similar temperature and based on consumption of juvenile Chinook salmon, they are from a largemouth bass study (TID/MID 1992). This magnitude of consumption estimate is only for one sampling instance (population of 11 striped bass), and it is important to note that surveys at WIDD in other years have shown populations of striped bass to be upwards of 60 fish and magnitude of predation could have been even higher. The relatively low numbers of striped bass at WIDD in May 2013 may be due to basin-wide low flow conditions. Diet energetic analysis provides an alternative method to validate the magnitude of striped bass predation found in the striped bass removal/salmon survival experiment. Comparative predator analysis indicated black bass consumed <1% of the population of juvenile salmon at WIDD, suggesting WIDD may not create heightened salmon predation for all predatory fish species.

The third and most robust approach to population-level impact is the before-after impact assessment which estimated 26% or 29% increase in salmon survival after removal of striped bass populations from WIDD. This analysis included 10 replicate removal events spanning three years, differences in timing throughout the

Chinook salmon emigration period, and variation in environmental conditions. Therefore I am confident that observed increases in juvenile salmon survival is due to striped bass predation and not a correlated alternate variable. I do not know the percentage of striped bass population removed from all events, but I do know the numbers of fish removed. For eight removal events both striped bass and black bass were removed from the basin. However, diet data from black bass at WIDD showed <1% consumption of juvenile salmon, and I feel confident the increase in survival is driven primarily by striped bass. Collectively, these three approaches estimate 10-29% juvenile salmon mortality from striped bass predation at WIDD. In comparison, on the Columbia River the McNary Dam is approximately 15 times longer than WIDD and average population-level consumption of juvenile salmon by three predators (small mouth bass, walleye, and Northern pikeminnow) was 14% in the John Day Reservoir (123 km), of which 21% of loss occurred in the area immediately after the McNary Dam (0.5 km) (Rieman et al. 1991).

In the Sacramento-San Joaquin Delta there is debate about the relative importance of the major drivers of juvenile salmon mortality: water exports, habitat loss, water pollution, and non-native predators. Management decisions depend on these relative rankings to designate effort to the most significant stressor. With so much uncertainty, it is critical to assess the relative and population-level impact on juvenile salmon, and the interactive effects of these different anthropogenic stressors. There is value in local studies to assess population-level impact, and test feasibility for management strategies such as predator removals to understand mechanistic

interactions and context-dependent attributes of predator-prey interactions (Hunsicker et al. 2011, Grossman et al. 2013). My project focuses on the non-native predator, striped bass, its relative importance and interaction with habitat alterations, and local impact on population of emigrating juvenile salmon at a predation hotspot. Future studies need to assess basin-wide migration survival after predator removal because delayed downstream compensatory mortality may eliminate long term survival increases. I also examined one predation hotspot at WIDD. There are many man-made structures throughout the Sacramento-San Joaquin Delta and it is important to compare these findings to more sites and determine which common characteristics create this synergistic interaction. My findings highlight that habitat, especially large man-made structures, can create predation hotspots through modifying predator functional and aggregative responses. Therefore it is important to consider habitat alterations and interactive effects when estimating large-scale predation impacts and when planning local management strategies.

Impacts of multiple anthropogenic stressors on native populations are often studied independently despite the fact that they can interact (Didham et al. 2007, Crain et al. 2008). Interactions can be complex and further studies are necessary to examine the context-dependent nature of interactions. This study illustrates how certain habitat alterations can change both functional and aggregative predator responses with additive consequences on native prey populations. On a larger scale, widespread global change including habitat alterations and introduction of non-native species across ecosystems and taxa increases the probability of interactive effects

influencing native prey populations and heightens the importance of studies focusing on these interactions.

Figures

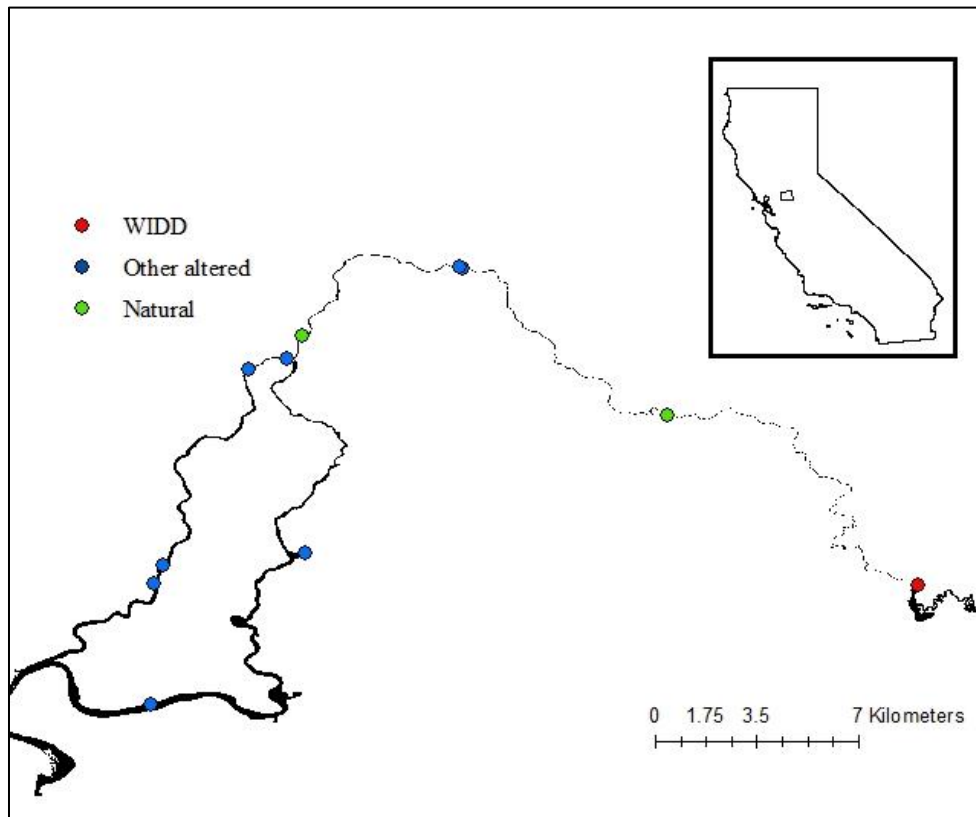


Figure 1. Map of electrofishing study sites on the Lower Mokelumne River, CA. Red circle is WIDD, blue circles are other altered habitats, and green circles are natural sites. Inset demonstrates study location in relationship to California and the San Francisco Bay.

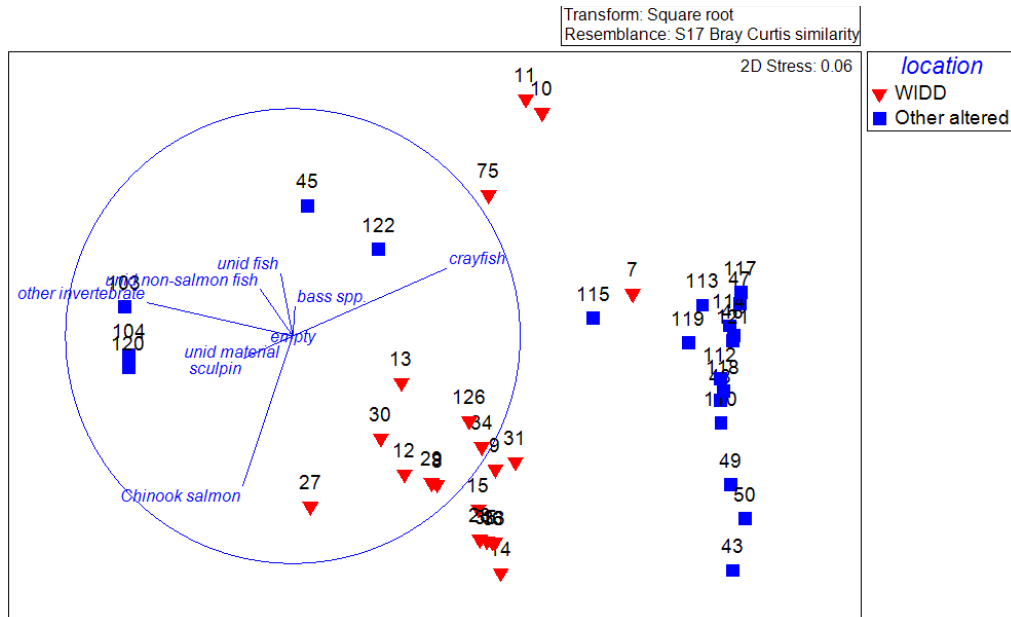


Figure 2: Non-metric multi-dimensional scaling plot with diet vector overlay. Striped bass individual relationships grouped by habitat type (WIDD and other altered) ($p=0.001$).

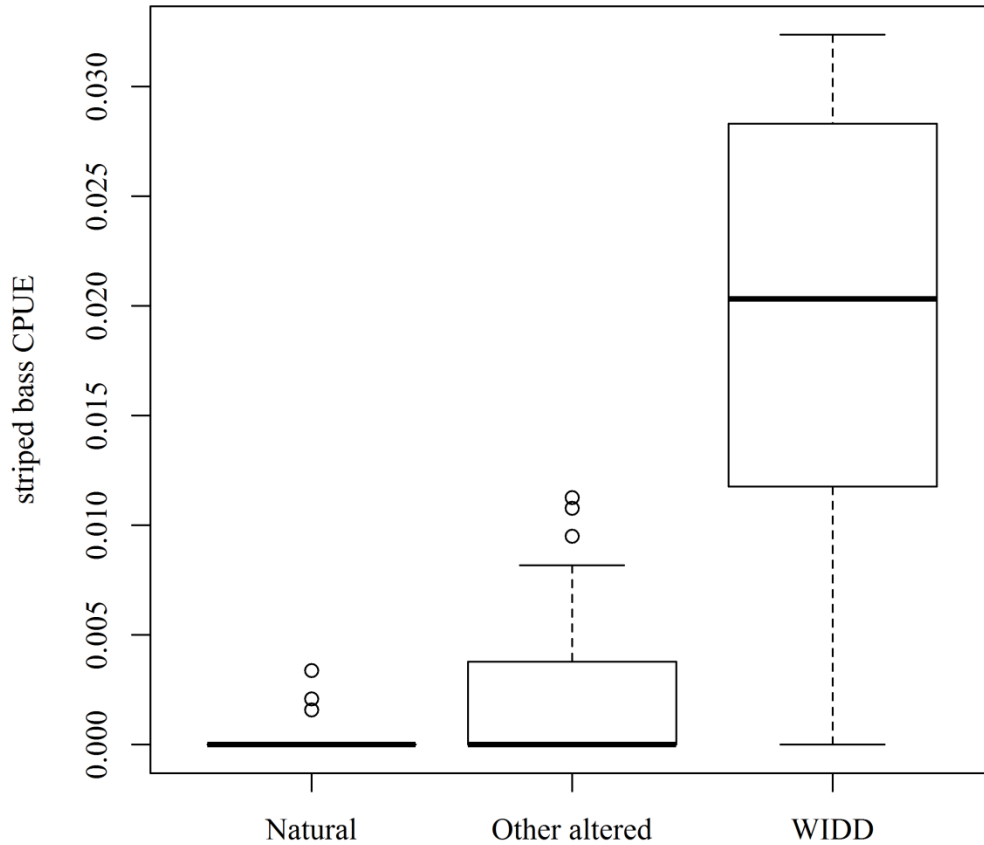


Figure 3. Striped bass (<250 mm FL) CPUE from electrofishing surveys 1998-2013 at other locations combined and WIDD. One-way ANOVA and Tukey's HSD tests indicate significant differences between WIDD and natural ($p < 0.001$), WIDD and other altered sites ($p < 0.001$), and other altered and natural habitats ($p = 0.03$).

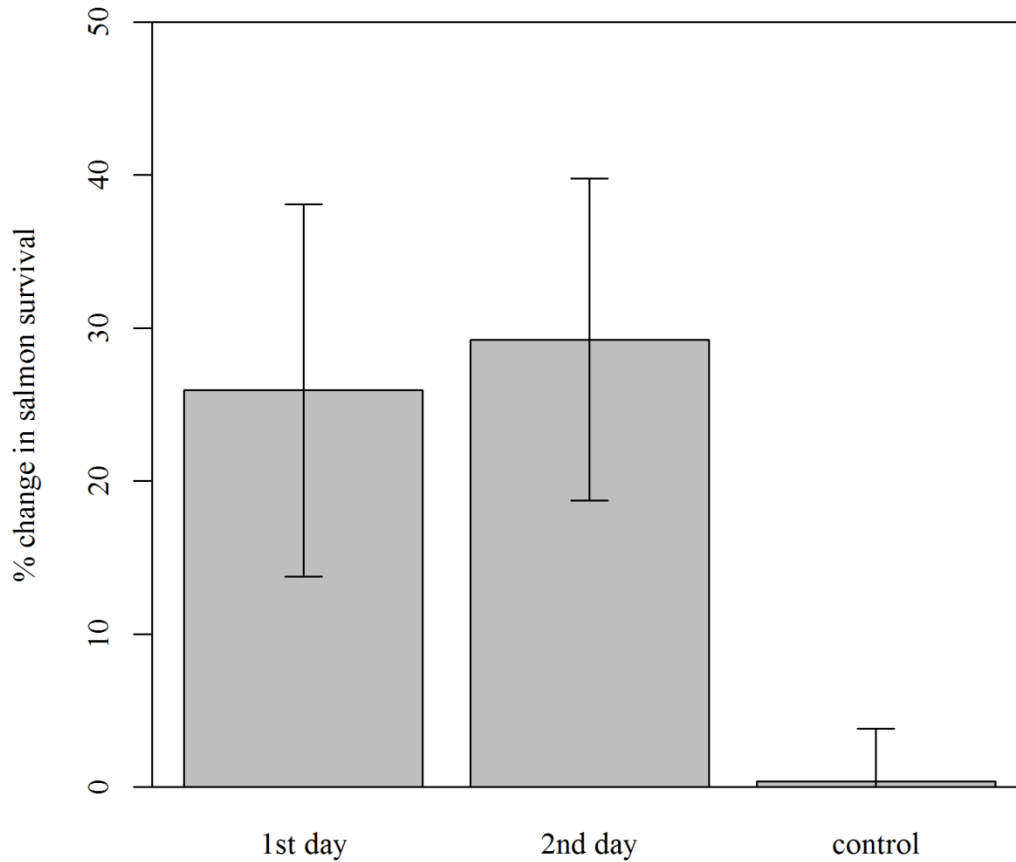


Figure 4. BACI metrics for predator removal treatments, using both 1st and 2nd day after removal and control treatment. + or - 1 SE. Two sample t test comparing treatments with control: 1st day (mean= 25.9%, t= -2.022, df= 10.52, p= 0.069), 2nd day (mean=29.2%, t= -2.605, df= 11.05, p= 0.024).

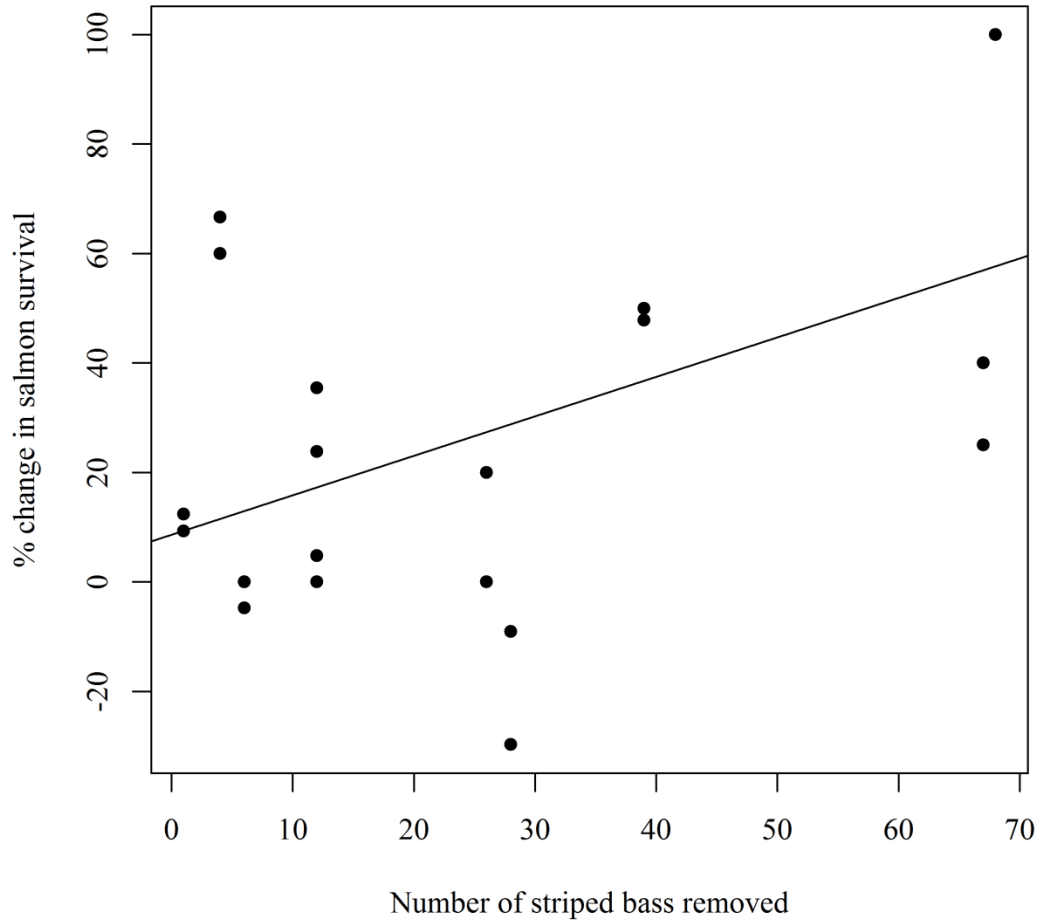
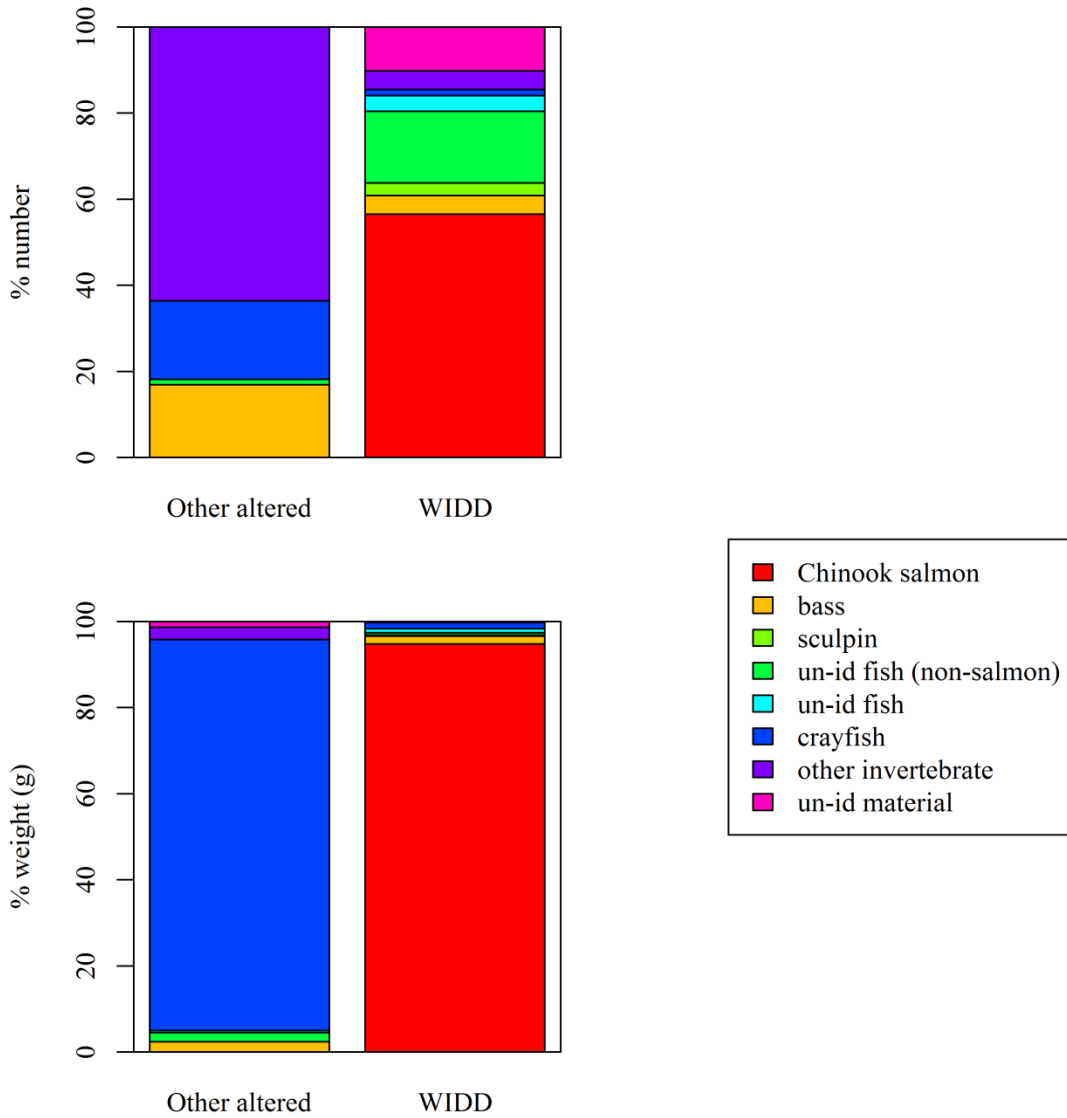


Figure 5. Mixed linear regression. BACI metric increases with increasing number of striped bass removed ($t= 2.426$, $df= 17$, $p= 0.026$).

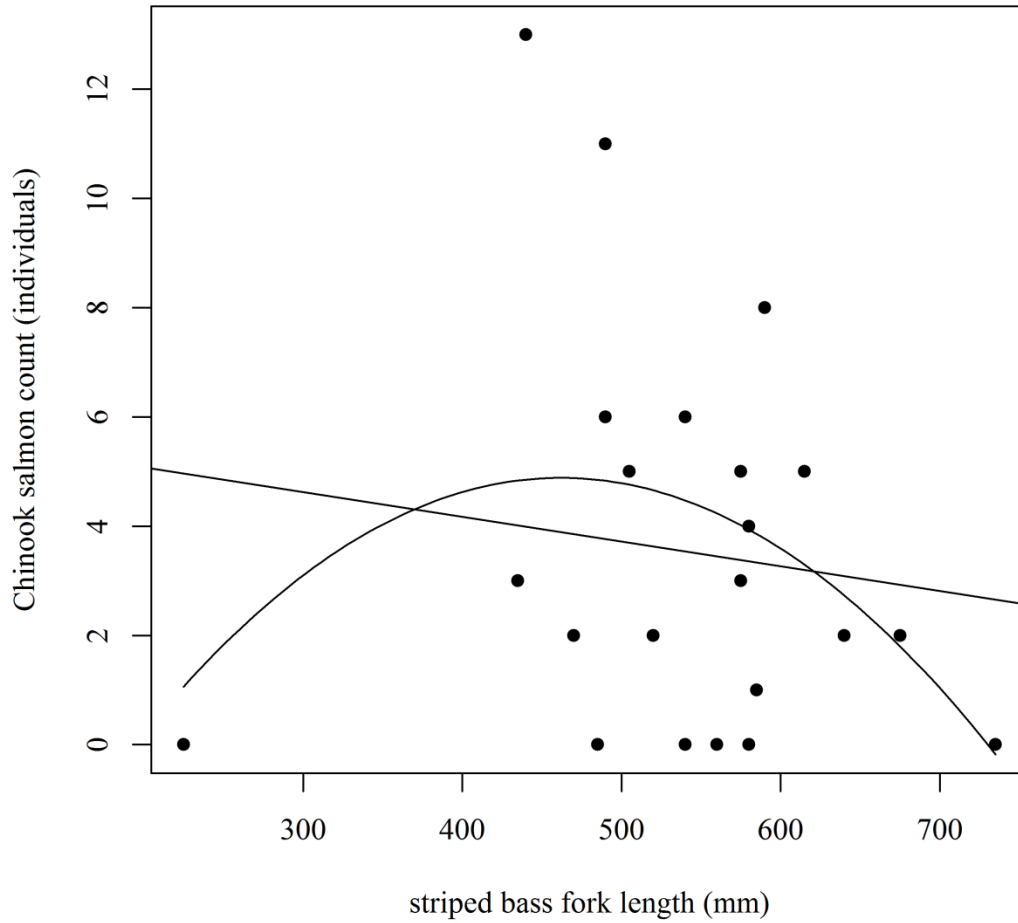
Appendices

prey category	Striped bass Other altered n=30			Striped bass WIDD n=22			Black bass WIDD n=42		
	% FO	% number	% weight	% FO	% number	% weight	% FO	% number	% weight
Chinook salmon	0.00	0.00	0.00	72.73	56.52	94.82	7.14	9.68	48.70
Bass spp.	10.00	16.88	2.33	9.09	4.35	1.83	2.38	3.23	3.41
sculpin	0.00	0.00	0.00	13.64	2.90	0.16	7.14	22.58	13.01
Fish non-salmon	3.33	1.30	2.20	13.64	16.67	0.56	11.90	22.58	6.84
Un-id fish	3.33	0.00	0.43	22.73	3.62	0.94	11.90	12.90	5.98
crayfish	50.00	18.18	90.87	13.64	1.45	1.48	21.43	16.13	19.59
Other invertebrate	13.33	63.64	2.86	18.18	4.35	0.00	7.14	9.68	0.04
Un-id material	3.33	0.00	1.32	18.18	10.14	0.20	9.52	3.23	2.43

Appendix 1. Total table of diet composition including percent frequency of occurrence (FO), percent number and percent weight.

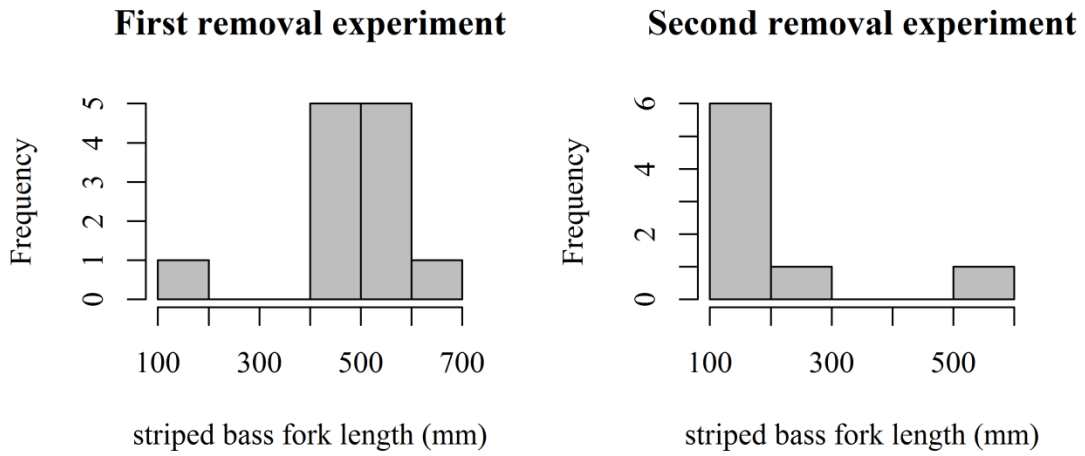


Appendix 2. Percent number and percent weight of diet items from striped bass caught at other altered sites and WIDD. Only one striped bass was caught at natural sites and it was empty, so is not shown in this figure.

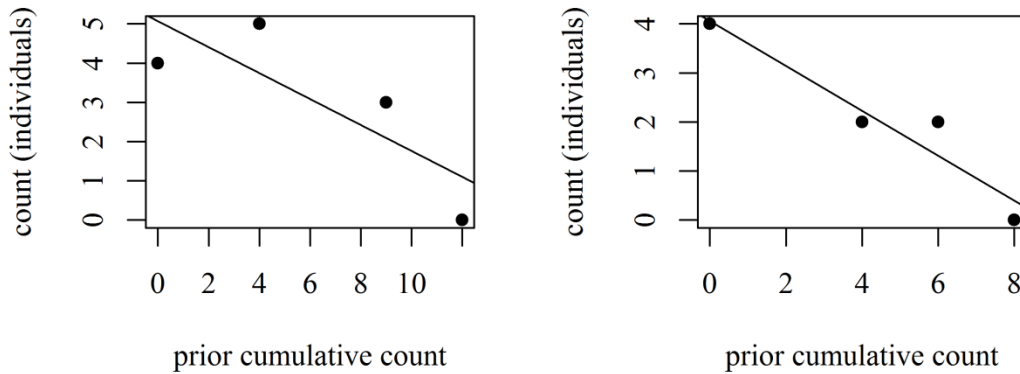


Appendix 3. Striped bass consumption of juvenile salmon by striped bass length.

Linear regression ($R^2 = -0.033$, $p = 0.572$). 2nd degree polynomial ($R^2 = 0.057$, $p = 0.219$).

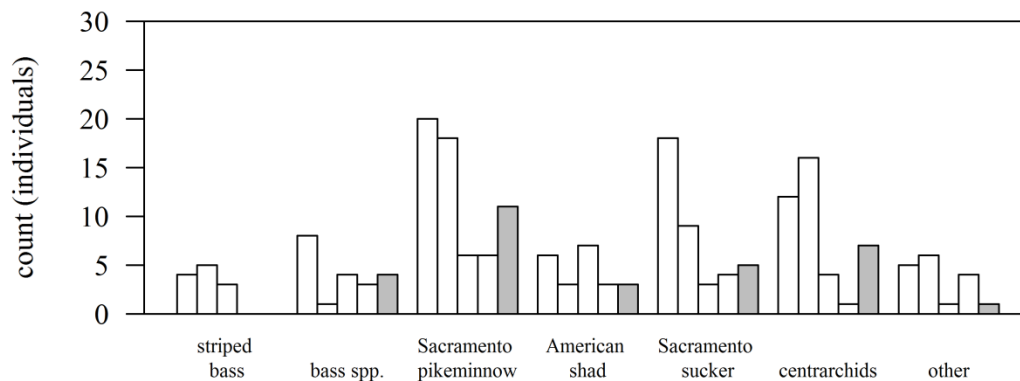


Appendix 4. Length histograms of striped bass removed in first (left) and second (right) removal experiments.

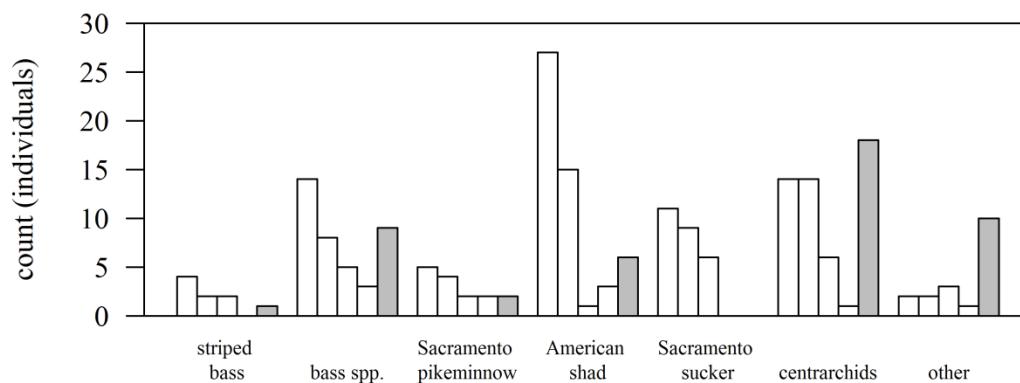


Appendix 5. Logistic regressions estimating striped bass population estimates for first removal experiment ($p=0.187$, $R^2=0.491$, $N_0=15.3$, 78.4% depletion) and second removal experiment ($p=0.0438$, $R^2=0.871$, $N_0=8.87$, 89.9% depletion).

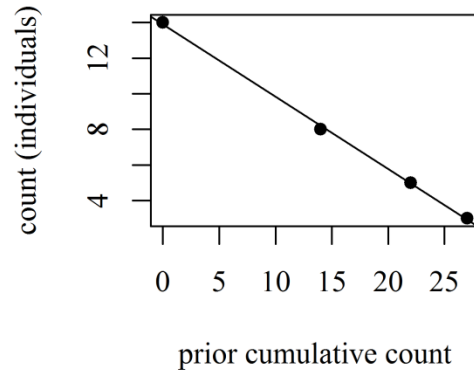
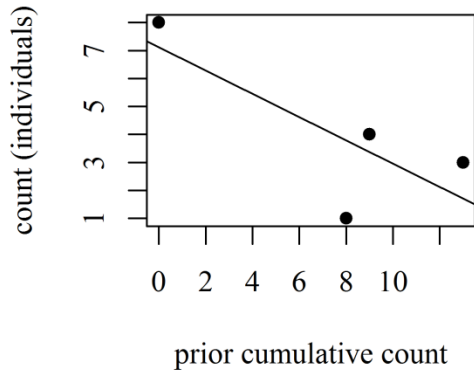
First removal experiment



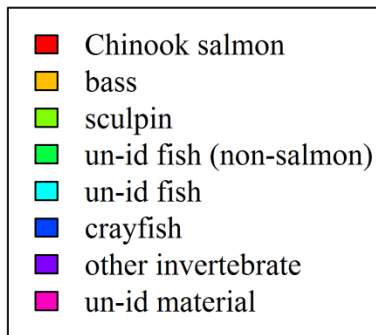
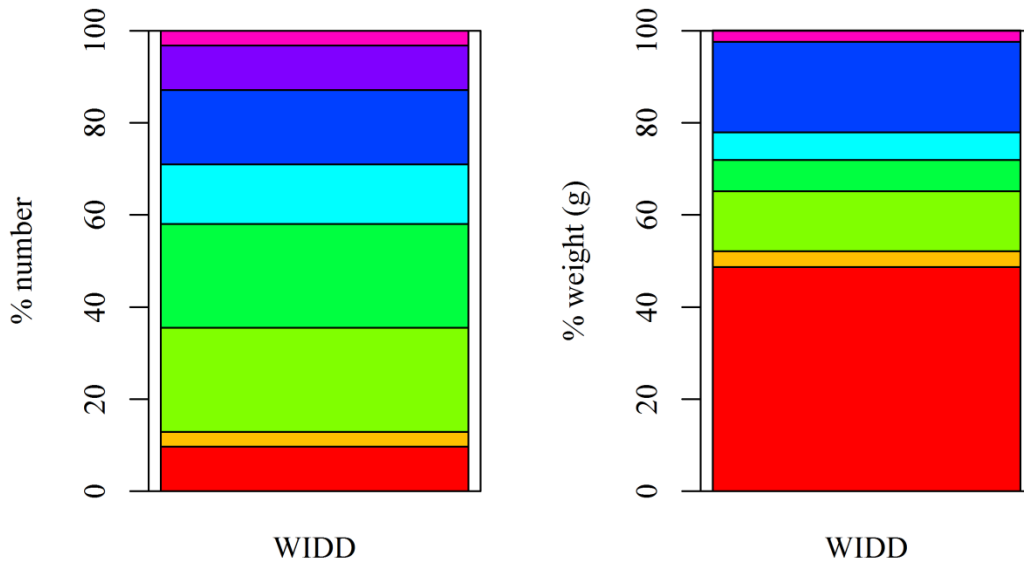
Second removal experiment



Appendix 6. White bars left to right are depletion passes 1, 2, 3, and 4 respectively. Gray bars are single pass conducted two days after depletion after experiment was complete. Bass spp. (*Micropterus* spp.), Sacramento pikeminnow (*Ptychocheilus grandis*), American shad (*Alosa sapidissima*), and Sacramento sucker (*Catostomus occidentalis*). Counts include fish of all sizes.



Appendix 7. Logistic regressions estimating black bass population estimates for first removal experiment ($p= 0.07$, $R^2= 0.6209$, $N_0= 16.54$, 96.9% depletion) and second removal experiment ($p= 0.0004$, $R^2= 0.9987$, $N_0= 34.19$, 80.0% depletion).



Appendix 8. Percent number and percent weight of diet items from black bass caught at WIDD.

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