

ARTICLE

Habitat Alterations and a Nonnative Predator, the Striped Bass, Increase Native Chinook Salmon Mortality in the Central Valley, California

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Abstract

Anthropogenic stressors are the leading causes of species and biodiversity declines, driving wide-scale ecosystem changes. Additionally, synergistic effects of multiple anthropogenic modifications, including species introductions and habitat alterations, can have complex outcomes for native species. We assessed how a nonnative predator (the Striped Bass *Morone saxatilis*) and habitat alterations (a small diversion dam and other altered habitats) interacted to influence mortality of native juvenile Chinook Salmon *Oncorhynchus tshawytscha* during their emigration from the lower Mokelumne River, California. Relative abundance and diet surveys across natural and human-altered habitats were used to assess Striped Bass functional and aggregative responses. Per capita consumption (PCC) of juvenile salmon and behavioral aggregation (CPUE) by Striped Bass at a small diversion dam (Woodbridge Irrigation District Dam [WIDD]) were elevated in comparison with those at other altered and natural habitats (WIDD: PCC = 3.54 juvenile salmon, CPUE = 0.189 Striped Bass/s of electrofishing; other altered habitats: PCC = 0 juvenile salmon, CPUE = 0.0024 Striped Bass/s; natural habitats: PCC = not estimable, CPUE = 0.0003 Striped Bass/s). Increased aggregative and functional predator responses created a localized area of heightened predation at WIDD. At this predation hot spot, we used three approaches (experimental Striped Bass removals, diet energetic analysis, and before–after impact assessment) to estimate Striped Bass consumption at 8–29% of the emigrating juvenile salmon population. Striped Bass PCC rates for juvenile salmon as determined by the three approaches were 0.92% (predator removals), 0.71–1.20% (diet energetic analysis), and 0.96–1.11% (before–after impact assessment). Our results (1) illustrate how the synergistic effect of habitat modification and a nonnative predator can exacerbate the mortality of native juvenile salmon during their emigration and (2) highlight the importance of considering interactions among stressors when planning local management strategies and assessing population-level impacts on salmon.

Populations of Pacific salmon *Oncorhynchus* spp. are integral ecological links between terrestrial, freshwater, and marine ecosystems (Merz and Moyle 2006). Salmon also have

tremendous economic value—hundreds of millions of dollars annually. In California, recent salmon population declines have made these species the focus of management and

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restoration (Katz et al. 2012). Juvenile Chinook Salmon *O. tshawytscha* experience high mortality rates during emigration to the sea (Buchanan et al. 2013). Various anthropogenic stressors in the Sacramento–San Joaquin River system, including altered water flows, drought, loss of habitat, and nonnative predators, make it difficult to decipher the major cause of juvenile salmon mortality. Without an understanding of the factors that drive salmon mortality, it is challenging to develop effective management strategies.

Ubiquitous to many aquatic ecosystems, anthropogenic stressors may result in native species endangerment and ecosystem change (Vitousek et al. 1997; Dudgeon et al. 2005; Brook et al. 2008). Two potential threats to juvenile Chinook Salmon include habitat alterations from human infrastructure and the presence of nonnative piscivores. In the Sacramento–San Joaquin Delta, these two threats have the potential to interact and impact juvenile salmon during their emigration. Juvenile salmon pass through various anthropogenically altered habitats, such as dams, water diversions, regulated flows, marinas, and rip-rap channels. Such habitat alterations may cause salmon mortality through entrainment (Deng et al. 2010) or poor habitat quality (Saiki et al. 1992; Baker et al. 1995). Furthermore, managed flows have been shown to decrease juvenile salmon survival (Zeug et al. 2014), and reductions in available floodplain habitat may cause reduced growth (Sommer et al. 2001).

Within the Sacramento–San Joaquin Delta, emigrating juvenile salmon also encounter multiple nonnative piscivores, including the Striped Bass *Morone saxatilis*. Beginning in 1879, Striped Bass from the East Coast were introduced as desirable game fish, and they were actively managed and stocked until 2001, when concern arose over their potential predation on endangered native juvenile salmon (Good et al. 2005). Despite inconclusive predation and diet studies, Striped Bass are considered a potential threat to juvenile salmon due to their high energetic demands (Lindley and Mohr 2002; Nobriga and Feyrer 2008; Loboschefskey et al. 2012). Striped Bass in the Sacramento–San Joaquin Delta are also desirable as recreational game fish and have experienced their own population declines in recent years, thus requiring management intervention to stabilize their numbers for angling. However, because Striped Bass are introduced predators that threaten native salmon populations, they could also be managed to reduce predation impacts. These conflicting interests (recreational fishery versus native species conservation) complicate decisions on how best to manage Striped Bass. Furthermore, uncertainty exists in the importance of various factors that influence salmon mortality, thus posing challenges for management efforts to restore salmon populations.

Typically, species impacts from anthropogenic stressors are studied independently, although evidence suggests that multiple stressors can interact. For example, habitat alterations can alter predator–prey overlap (Kempf et al. 2013; Peters et al. 2013), the success of invading species (Marchetti et al. 2004),

prey vulnerability (Weber and Brown 2012), and predator foraging success (Bartholomew et al. 2000). Through these indirect pathways, habitat alterations can alter predator responses to exacerbate net mortality (Belarde and Railsback 2016). There are two types of predator response: (1) an aggregative response wherein increased predator abundance exerts greater net mortality on a prey population; and (2) a functional response in which increased per capita prey consumption (PCC) relative to density results in higher net predation despite a constant predator abundance (Holling 1959; Murdoch and Stewart-Oaten 1989). An increase in both types of predator response results in an exponential increase in prey consumption—also referred to as a synergistic or functionally moderated interaction (Didham et al. 2007). Additive impacts from multiple stressors may intensify the negative consequences for prey and create artificially inflated predation hot spots, yet they may also allow for spatially focused management strategies. Therefore, scientific studies should assess the interactive effects of human-induced stressors, including habitat alterations and nonnative predators, on juvenile salmon mortality (Grossman et al. 2013). A mechanistic understanding of how stressors impact juvenile salmon and the context dependence of interactions will allow for more ecologically aware and effective management strategies.

We examined how the combined effects of habitat alterations and a nonnative predator, the Striped Bass, influenced the mortality of emigrating native juvenile Chinook Salmon. We asked three primary questions: (1) “Is the PCC of juvenile salmon by Striped Bass greater at anthropogenically altered habitats?”; (2) “Do Striped Bass aggregate at these habitats?”; and (3) “Within an area of high predation, what is the population-level impact of Striped Bass on an emigrating salmon population?” The present results advance our understanding of interactive effects between stressors and their cumulative impacts on juvenile salmon.

METHODS

Study Site

The Mokelumne River in the eastern Sacramento–San Joaquin Delta of California drains approximately 1,624 km² of the central Sierra Nevada Mountains. The lower Mokelumne River extends 54 km between Camanche Dam and the confluence with the San Joaquin River and serves as the uppermost extent of habitat available to anadromous fishes, including Chinook Salmon and Striped Bass (Figure 1). River flows are highly regulated, with peak flows typically occurring between December and July (Pasternack et al. 2004). Our study sites were located below the Woodbridge Irrigation District Dam (WIDD), which is approximately 50 m wide and 8.5 m high, creating a relatively deep pool of water immediately downstream. A fish ladder at WIDD allows diadromous fishes to access river habitat above the dam. The WIDD area is distinct from other habitats, which

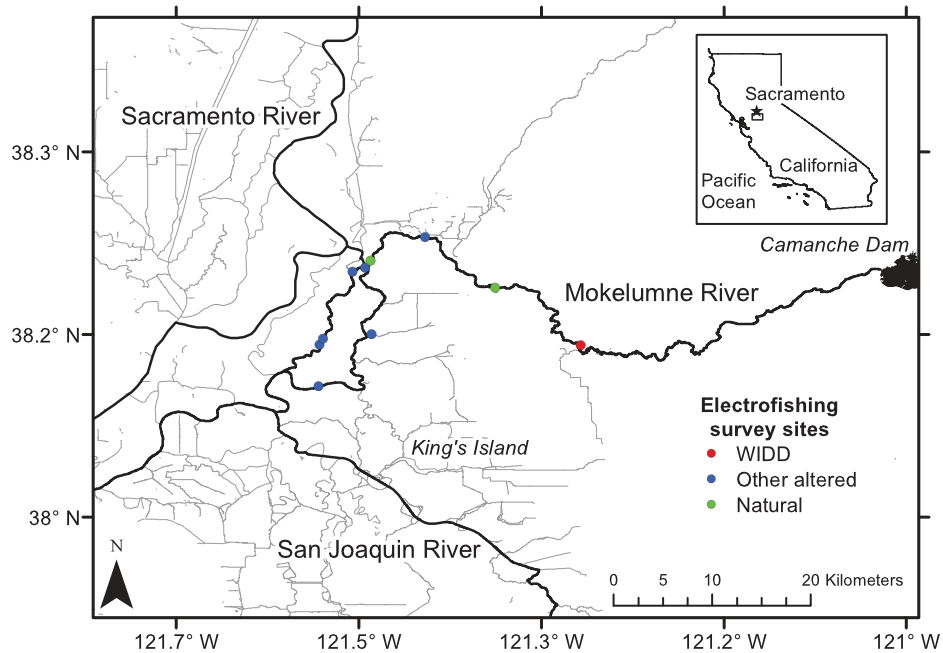


FIGURE 1. Map of the study area on the lower Mokelumne River, California, including electrofishing survey sites (colors represent the three habitat types sampled; WIDD = Woodbridge Irrigation District Dam).

include glides and pools bordered by a mix of natural vegetation, levees, and rip-rap banks (Merz and Setka 2004). The river reach below WIDD is tidally influenced, has an average river gradient of 0.17 m/km, and has substrate consisting of sand and mud.

Over 38 fish species inhabit the lower Mokelumne River, including nonnative Striped Bass and a naturally spawning native population of Chinook Salmon. Striped Bass abundances in the lower Mokelumne River peak during May and June in accordance with annual upstream migrations into freshwater (Moyle 2002). Upon encountering WIDD, the majority of Striped Bass refuse to use the fish ladder blocking their upstream migration, a behavior that has been observed in other Striped Bass populations (Beasley and Hightower 2000; Gephard and McMenemy 2004). Chinook Salmon parr and smolts (~80–110 mm FL) emigrating annually from the headwaters pass WIDD during May and June (Merz et al. 2013). The Mokelumne River Fish Hatchery releases juvenile Chinook Salmon downstream of our study sites, so hatchery fish were not a pertinent part of the fish community we studied. Since 1990, the East Bay Municipal Utility District (EBMUD) has been estimating the annual population of emigrating juvenile Chinook Salmon by using rotary screw traps (2.4 m in diameter; E.G. Solutions, Inc.) to catch juvenile salmon daily during December–July (Volkhardt et al. 2007; Bilski et al. 2011). Estimates of emigrating juvenile Chinook Salmon populations vary annually, but between 20,000 and 1.2 million fish were estimated to have passed WIDD during 2000–2013. The upstream migration of adult Striped Bass

and the downstream migration of juvenile Chinook Salmon co-occur in the spring; therefore, the overlap of predators and prey creates the potential for significant predation to occur in the lower Mokelumne River.

Per Capita Consumption of Juvenile Salmon by Striped Bass in Altered and Natural Habitat Types

To test the hypothesis that habitat alterations affect Striped Bass consumption of juvenile Chinook Salmon, we combined Striped Bass relative abundance surveys with diet analysis to compare rates of salmon predation across different habitat types. Because structures such as dams and water diversions may disorient juvenile salmon and increase predator foraging efficiency (Davis et al. 2012), we predicted that the highest PCC of juvenile salmon by Striped Bass would occur at WIDD, followed by other altered habitats and then natural habitats. We surveyed 10 sites as a part of EBMUD seasonal electrofishing surveys, and we retrospectively assigned each site to one of three habitat categories: diversion dam (WIDD; $n = 1$ site), other altered ($n = 7$ sites), and natural ($n = 2$ sites). The WIDD significantly altered the physical and hydrodynamic environment and was distinct from all other sites. Other altered habitat sites included rip-rap channels and man-made structures (e.g., docks and bridges). These hardened structures modified the river (Hester and Doyle 2011; Jacobson 2011) but to a lesser extent than WIDD. Natural sites lacked hardened structures; although these sites were influenced by management impacts (e.g., flow regulation, historic dredging, etc.), they were bordered by natural vegetation,

suggesting fewer disturbances. Striped Bass were captured at the 10 lower Mokolumne River sites by using single-pass boat electrofishing (Smith-Root Model SR-18EH electrofisher) in accordance with the methods of Meador et al. (1993). Each site was surveyed three different times during the juvenile Chinook Salmon emigration period between April 23 and May 24, 2013. Each site contained three fixed transects (~150 m in length) that were parallel to the shoreline and one transect in the mid-channel. Striped Bass relative abundance (CPUE) was calculated as the number of individuals caught per second of electrofishing. Striped Bass were counted, measured (mm FL), and weighed (g). Diet samples were collected from Striped Bass by using nonlethal gastric lavage and were preserved in a 95% solution of ethanol (Hakala and Johnson 2004). Striped Bass are gape limited and switch to piscivory at around 250 mm FL; therefore, only Striped Bass larger than 250 mm FL were considered to be potential predators of juvenile salmon. All analyses reported here only included Striped Bass exceeding 250 mm (Nobriga and Feyrer 2007).

Diet samples from Striped Bass were processed in the laboratory to characterize diet composition and to quantify consumption of juvenile salmon. We identified prey items to the lowest possible taxonomic level, and we enumerated, measured, and weighed each prey group. We used diagnostic bones to distinguish between commonly digested prey species (Hansel et al. 1988; Frost 2000). To determine whether the consumption of juvenile salmon was related to Striped Bass size, we used both a linear relationship and a second-degree polynomial relationship to compare the number of juvenile salmon found in the stomach contents against predator FL (mm). To describe consumption of juvenile salmon in the different habitat types, we compared the percent frequency of occurrence (FO) of identifiable prey types (Baker et al. 2014) and the PCC of juvenile salmon. Only one Striped Bass was caught at a natural site, and its stomach was empty; therefore, the natural habitat category was not included in diet comparisons. Multivariate methods using PRIMER version 6 were used to compare Striped Bass diet composition between the remaining two habitat types (WIDD habitat and other altered habitats). We computed a similarity matrix by using Bray-Curtis distances on square-root-transformed weights (g) of prey categories for each Striped Bass. Distance-based permutation multivariate ANOVA (PERMANOVA; Anderson 2001) was used to test the null hypothesis that there was no difference in Striped Bass diet composition between the two habitat types ($\alpha = 0.05$). Analyses were based on 999 unrestricted permutations of raw data.

Striped Bass Aggregation in Altered and Natural Habitat Types

We used long-term monitoring data collected at a range of habitat types to examine patterns of Striped Bass abundance. We hypothesized that Striped Bass would aggregate in areas

where salmon predation rates were greatest. Thus, we predicted that (1) Striped Bass would aggregate at manmade structures and (2) the largest Striped Bass aggregation would be observed at WIDD, followed by other altered habitats and then natural habitats. Structure may increase prey vulnerability during emigration and may increase predator foraging success, creating profitable feeding locations. We compared Striped Bass CPUE among the habitat categories (WIDD, other altered habitats, and natural habitats); the CPUE data were taken from long-term spring fish community surveys conducted by EBMUD from 1998 to 2013. These data were collected by using the same single-pass electrofishing methods described in the previous section. One-way ANOVA and Tukey's honestly significant difference (HSD) test were used to compare mean Striped Bass CPUE among the WIDD, other altered habitat, and natural habitat types. We performed a square-root transformation on CPUE data to meet statistical assumptions. Pearson's chi-square test was used to compare differences in frequency of Striped Bass caught across sampling events in each habitat type.

Impact on the Population of Out-Migrating Juvenile Salmon

To further assess the potential impact of Striped Bass predation on the population of emigrating juvenile salmon at an area of potentially high interaction (i.e., WIDD), we used three independent approaches: (1) a Striped Bass removal-salmon survival experiment, (2) a diet energetic analysis, and (3) a before-after impact assessment (Figure 2).

Striped Bass removal-salmon survival experiment.—To evaluate how Striped Bass removal would affect juvenile Chinook Salmon survival, we marked and recaptured paired groups of juvenile salmon that were released before and after Striped Bass removal. We hypothesized that there would be a greater percentage of experimental Chinook Salmon recaptures (i.e., greater survival) after Striped Bass removal. The experiment was conducted twice during the out-migration period in 2013 (May 6–10 and May 20–24). However, during the second experiment, we were unsuccessful in removing Striped Bass; therefore, we only consider the first experiment when reporting the results for the Striped Bass removal-salmon survival and diet energetic analyses.

To remove Striped Bass, we conducted four sequential electrofishing passes to cumulatively deplete predators at WIDD. A block net enclosed the study area to prevent predator escapement; this satisfied the assumption of a closed population, which is required for applying the recapture method of estimating predator abundance. We 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, we used a pulsed current and kept the total seconds of electrofishing consistent between passes (Raleigh and Short 1981). Captured fish were held in a live well and were transferred

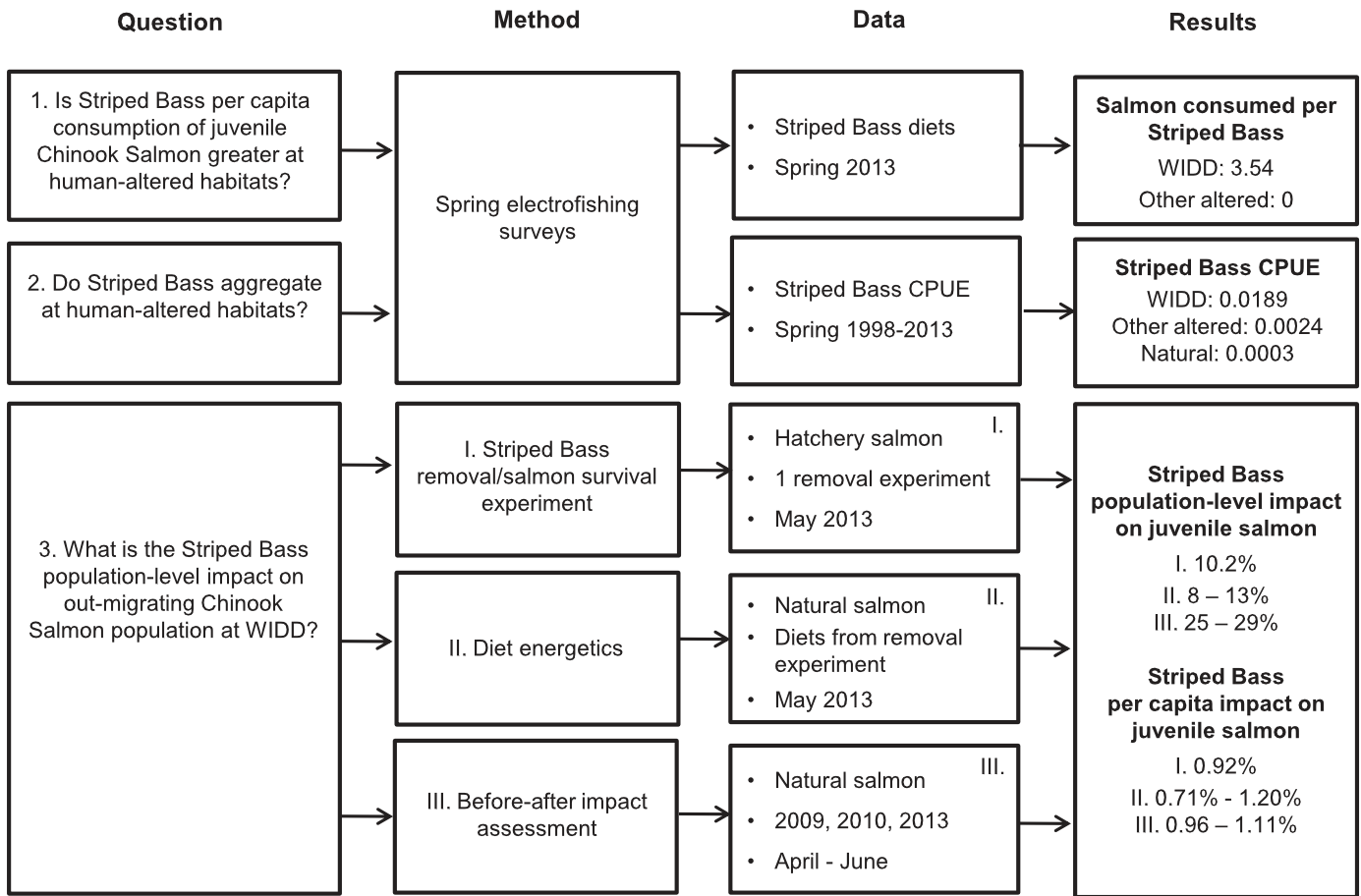


FIGURE 2. Flow chart describing the methods, data, and main results that were used to address each of the main questions in this study (WIDD = Woodbridge Irrigation District Dam).

to holding tanks until we achieved depletion. We counted, weighed (g), and measured (FL, mm) the Striped Bass and collected diet samples via gastric lavage. After depletion passes were completed, Striped Bass were transported and released at an alternative location (King’s Island; Figure 1), whereas all other fish species collected were released back into the study area. We calculated each experiment’s percent depletion by comparing the number of Striped Bass removed to the total Striped Bass population estimates. Total population estimates were determined from multiple-pass depletion electrofishing by using least-squares linear regression of Striped Bass CPUE against the cumulative catch lagged for one unit of effort (Maccina et al. 1995; Cavallo et al. 2012).

To estimate survival of juvenile Chinook Salmon, we conducted an experiment with paired releases of juveniles obtained from the Mokelumne River Fish Hatchery. Each release group (one released before Striped Bass removal and one released after removal) was marked with a unique external visible implant elastomer tag. These tags have high retention rates, are easily detected, and have no observed effect on

survival and growth of juvenile salmon. Therefore, we did not account for tag loss in our survival estimates (Hale and Gray 1998; Bilski et al. 2011; Leblanc and Noakes 2012). During the experiment, water temperature was 17.0°C, and water flow was 4.56 m³/s.

Chinook Salmon from the release groups were slightly smaller (mean = 79 mm FL) than fish in the natural population (mean = 87 mm FL; $t = -10.7$, $df = 145$, $P < 0.01$). To mimic natural salmon emigration, the first release of juveniles ($n = 1,000$) was performed in the evening 2 d prior to Striped Bass removal at the base of the dam (Chapman et al. 2012). A rotary screw trap that operated approximately 200 m downstream of WIDD was checked every morning, and recaptures of juvenile Chinook Salmon were recorded (Volkhardt et al. 2007). The second release of juveniles ($n = 1,000$) was performed at the same location during the evening after Striped Bass removal. Recapture rate was calculated from the number of tagged fish that were recaptured in the screw trap (extrapolated to the total river volume) divided by the total number of tagged fish that were released. Both release and recapture

estimates were divided by the corresponding daily flow (provided by EBMUD) to standardize recaptures based on the volume of water sampled. We examined the difference between the proportion of juveniles recaptured before Striped Bass removal and after removal. After the final recaptures of juvenile Chinook Salmon were recorded, we conducted a single pass of electrofishing to assess whether Striped Bass removal had been maintained over the duration of the experiment. This approach consisted of one experiment in which we removed Striped Bass and measured the change in hatchery Chinook Salmon survival.

Diet energetic analysis.—To determine whether the change in survival observed in the Striped Bass removal–salmon survival experiment was due to predation, we also performed diet analysis of the same predators so as to calculate the percentage of juvenile Chinook Salmon that were consumed. The median number of salmon consumed per Striped Bass removed during the removal experiment was calculated, and a range of fast (13.0 h; 0.54 d) and slow (21.6 h; 0.90 d) gastric evacuation rates was used to extrapolate to daily individual consumption (Elliott and Persson 1978; TID and MID 1992). Gastric evacuation rates were estimated from the average complete evacuation time of tagged juvenile salmon through Striped Bass (Schultz et al. 2015), adjusted to the time until salmon prey become unrecognizable (Elliott and Persson 1978; TID and MID 1992). Individual daily consumption rates were multiplied by the number of Striped Bass removed to calculate daily population-level consumption. To estimate the number of naturally spawned juvenile Chinook Salmon passing WIDD, we used the known number of experimental juveniles released at WIDD and the ratio of the known number of experimental salmon recaptures to the number of naturally spawned juveniles caught in the screw trap. To calculate the juvenile Chinook Salmon populations at WIDD for the day of Striped Bass removal, we assumed that the ratio of naturally spawned salmon caught in the screw trap to the total number of juveniles passing WIDD was constant. The percentage of juvenile Chinook Salmon consumed by Striped Bass was calculated by using the daily population-level consumption rate relative to the estimated number of juveniles that passed WIDD. Furthermore, we examined the amount of naturally spawned juveniles in the diets of Striped Bass from the removal experiment, and we used diet energetics to estimate the population-level impact of Striped Bass predation.

Before–after impact assessment.—We used a before–after impact assessment (Table 1) based on existing EBMUD data to retrospectively determine (1) whether Striped Bass removal affected the survival of natural Chinook Salmon populations in the Mokelumne River and (2) whether the magnitude of impact was related to the number of Striped Bass removed. The rotary screw trap below WIDD captured emigrating juvenile salmon each day. Because the catches were highly autocorrelated, we hypothesized that the catch of juvenile Chinook Salmon would

TABLE 1. Summary of 10 predator removal events used for the before–after impact assessment of Striped Bass predation effects on juvenile Chinook Salmon survival at the Woodbridge Irrigation District Dam on the lower Mokelumne River, California. Effects were calculated between the day before predator removal and the first or second day after removal.

Removal date	Number of Striped Bass removed	Striped Bass mean FL (mm)	Day after removal	Change in juvenile salmon survival
2009 Removal events				
Apr 8	6	602	1	–0.047
			2	0.000
May 21	12	432	1	0.000
			2	0.238
Jun 3	26	476	1	0.200
			2	0.000
Jun 16	19	350	1	–0.297
			2	–0.090
2010 Removal events				
Apr 23	4	457	1	0.666
			2	0.600
May 18	37	372	1	0.500
			2	0.478
Jun 3	55	286	1	1.00
			2	1.00
Jun 15	64	338	1	0.400
			2	0.250
2013 Removal events				
May 8	12	479	1	0.047
			2	0.354
May 22	2	248	1	0.123
			2	0.093

increase on the day after a predator removal event and that the magnitude of that catch would increase with increasing numbers of Striped Bass removed. We tested this prediction by calculating the percent change in Chinook Salmon survival ($100 \times \{[\text{After} - \text{Before}] / [\text{After} + \text{Before}]\}$) by using juvenile salmon catches in the screw trap on the day before and the day after an impact (i.e., a predator removal event) and control (i.e., no predator removal). This value scales from 100% to –100%, with zero indicating that catches before and after removal are identical, positive values indicating an increase in juvenile salmon catch after removal, and negative values indicating a decrease in juvenile salmon catch after removal.

Additional predator removals were conducted by EBMUD in 2009 and 2010; boat electrofishing was used to catch, deplete, and remove Striped Bass, Largemouth Bass *Micropterus salmoides*, and Spotted Bass *Micropterus punctulatus* (all nonnative species) from the vicinity of WIDD. Multiple passes were not separated, and there was no block net in place. The impact treatment included 10 total predator

removal events that occurred in 2009 ($n = 4$), 2010 ($n = 4$), and 2013 ($n = 2$; Table 1). Because electrofishing during predator removal can injure or cause mortality to Chinook Salmon, the catch of juvenile salmon in the screw trap on the first day after removal might have been diminished (Schreer et al. 2004). For this reason, we calculated the percent change in salmon survival in two ways: (1) between the day before removal and the first day after removal and (2) between the day before removal and the second day after removal. For the control (no predator removal), we calculated the percent change in Chinook Salmon survival for all pairs of days for which there was no predator removal event ($n = 139$ pairs in 2009, 2010, and 2013). We also excluded days during which debris prevented the rotary screw trap from fishing properly. We used Welch's two-sample t -tests to compare mean percent change in salmon survival between days without a predator removal (control) and between days with a predator removal (impact). To assess whether the percent change in juvenile Chinook Salmon survival was correlated with the numbers of Striped Bass removed, we conducted a linear mixed-effects regression analysis using (1) the percent change in salmon survival as the response variable, (2) the number of Striped Bass removed and the mean size of Striped Bass as predictor variables, and (3) period (the first or second day after removal) as a random effect. This approach utilized 10 predator removal events occurring over 3 years to examine whether the survival of naturally spawned Chinook Salmon changed due to Striped Bass predation.

RESULTS

Per Capita Consumption of Juvenile Salmon by Striped Bass in Each Habitat Type

Striped Bass diet composition, including consumption of juvenile Chinook Salmon, differed markedly between WIDD habitat and other altered habitats during 2013 (Figure 3). Striped Bass ranged from 250 to 925 mm FL, with an average size of 553 mm at WIDD ($n = 21$ fish) and an average size of 439 mm at all other sites ($n = 29$ fish; $t = 3.08$, $df = 10.18$, $P = 0.003$). Diet data showed that Striped Bass consumption of juvenile salmon was not significantly size dependent based on examination of either a linear relationship ($R^2 = 0.00$, $P = 0.572$) or a second-degree polynomial relationship ($R^2 = 0.057$, $P = 0.219$); therefore, diets to be used for energetic analysis were not separated based on predator size-classes. The PERMANOVA detected significant differences in Striped Bass diets between WIDD habitat and other altered habitats (pseudo- $F = 17.3$, $df = 1$, $P = 0.001$). Juvenile Chinook Salmon were the dominant prey type consumed by Striped Bass caught at WIDD (FO = 72.73%), whereas juvenile salmon did not occur in the diets of Striped Bass from any other altered locations. Striped Bass consumed primarily crayfish (Decapoda) at the other locations (FO = 50%; Figure 3). High juvenile salmon content in Striped Bass diets at WIDD is in accordance with previous diet studies conducted at

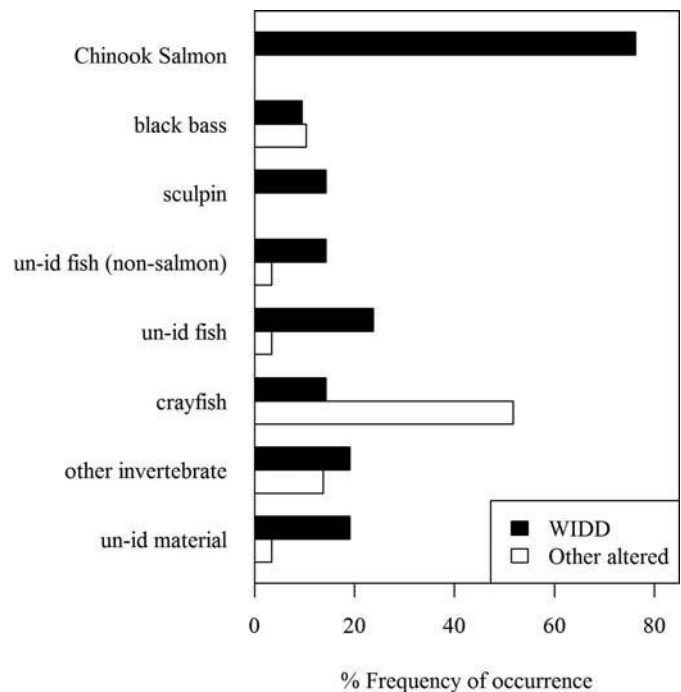


FIGURE 3. Composition of the diets for Striped Bass captured at the Woodbridge Irrigation District Dam (WIDD; black bars) and other altered habitats (white bars) in the lower Mokelumne River. Diets are expressed as percent frequency of occurrence for positively identifiable prey items (un-id = unidentifiable; black bass = *Micropterus* spp.).

the dam (Boyd and Merz 2006). The PCC of juvenile Chinook Salmon by Striped Bass was 3.54 at WIDD and 0 at the other altered habitats.

Striped Bass Aggregation in Altered and Natural Habitat Types

Striped Bass aggregated at WIDD, with an eightfold increase in CPUE at WIDD (mean CPUE = 0.0189 Striped Bass/s of electrofishing) relative to other altered habitats (mean CPUE = 0.0024 Striped Bass/s) and a 60-fold increase in CPUE relative to natural habitats (mean CPUE = 0.0003 Striped Bass/s; Figure 4). One-way ANOVA and Tukey's HSD test indicated significant differences in CPUE between all pairs of habitat types: WIDD and other altered habitats ($P < 0.001$), WIDD and natural habitats ($P < 0.001$), and other altered and natural habitats ($P = 0.03$). Striped Bass were caught during 13 (86.6%) of 15 surveys at WIDD; 37 (37.0%) of 100 surveys in other altered habitats; and 6 (28.6%) of 21 surveys in natural habitats (Pearson's chi-square test: $df = 4$, $P = 0.0048$). Striped Bass ranged from 256 to 904 mm FL at WIDD (mean = 537 mm; $n = 138$ fish), from 258 to 705 mm FL at other altered habitats (mean = 420 mm; $n = 177$ fish), and from 409 to 510 mm FL at natural habitats (mean = 456 mm; $n = 36$ fish; ANOVA: $P < 0.001$).

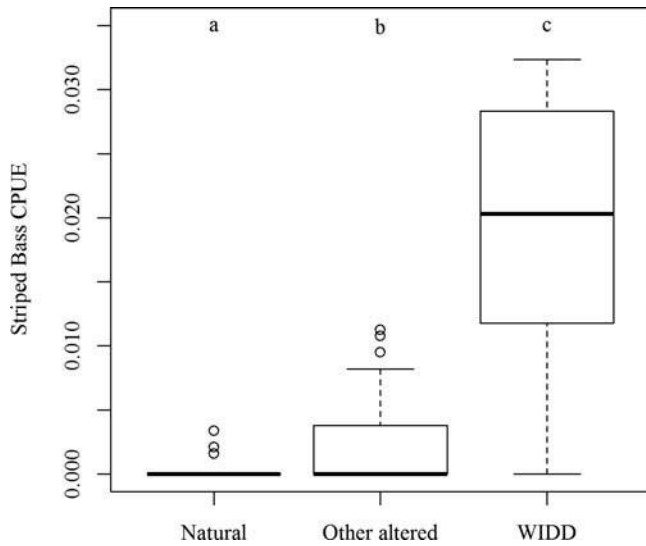


FIGURE 4. Striped Bass aggregation, measured as the CPUE (Striped Bass/s of electrofishing) at natural habitats, other altered habitats, and the Woodbridge Irrigation District Dam (WIDD). Box plot shows the median (bold black line), 25th and 75th percentiles (ends of box), the range in the most extreme data points (ends of whiskers), and outliers (open circles). All pair combinations were significantly different (ANOVA and Tukey’s honestly significant difference test; natural versus other altered: $P = 0.03$; natural versus WIDD: $P < 0.001$; other altered versus WIDD: $P < 0.001$).

Impact on the Population of Out-Migrating Juvenile Salmon

Striped Bass removal–salmon survival experiment.—Estimated Chinook Salmon survival increased by 10.21% after the removal of 11 Striped Bass (per capita impact = 0.92%; Table 2). We depleted 78.4% of the total Striped Bass population (including all sizes), and removed 11 predatory Striped Bass that were capable of consuming juvenile salmon. Greater than 99% of the tagged juvenile Chinook Salmon were recaptured in the screw trap during the morning after their release, suggesting that juveniles were migrating through the basin immediately and that the first release group had moved past the screw trap by the time the second group was released. After the removal experiment

was completed, single-pass electrofishing indicated that Striped Bass removal was maintained, as we caught no additional Striped Bass.

Diet energetic analysis.—Based on diet samples from Striped Bass that were caught during the removal experiment, we calculated that a median of five juvenile salmon were consumed per predator. Gastric evacuation rates (slow and fast) generated individual daily consumption rates of 5.5–9.2 juvenile salmon/d. Using the 11 Striped Bass that were removed, we scaled individual consumption to a daily population-level consumption of 61–101 juvenile salmon/d. The mark–recapture estimate of Chinook Salmon population size was 770 juveniles; therefore, the 11 Striped Bass removed were estimated to have consumed between 7.9% (slow evacuation) and 13.2% (fast evacuation) of the emigrating juvenile population passing WIDD (per capita impact = 0.71–1.20%; Table 2). A potential concern was that the number of juvenile Chinook Salmon in Striped Bass diets was artificially inflated due to our introduction of tagged hatchery juveniles into the system during the removal experiment. However, because over 99% of experimentally tagged juveniles migrated through the reach within 12 h of release, at least 24 h had elapsed before a diet sample was taken, and a 24-h period is greater than the evacuation time for recognizable prey.

Before–after impact assessment.—The before–after impact assessment indicated that the survival of naturally spawned Chinook Salmon increased by 25–29% after predator removal. Ten removal events occurred between May 7 and June 16 (in 2009, 2010, and 2013), and 1–68 Striped Bass (average = 26.3 individuals) were removed per event (Table 1). For the control, the mean percent change in juvenile salmon survival between pairs of days without predator removal was 0.3%. For the impact treatments, the percent change in juvenile salmon survival was 25.9% between the day before predator removal and the first day after removal ($t = -2.02$, $df = 10.52$, $P = 0.06$) and 29.2% between the day before removal and the second day after removal ($t = -2.61$, $df = 11.05$, $P = 0.02$). Welch’s two-sample t -tests indicated that both of the predator removal treatments showed an increase in the number of juvenile Chinook Salmon caught relative to the control (i.e., no

TABLE 2. Summary of population-level and per capita impacts of Striped Bass predation on juvenile Chinook Salmon, as derived from three independent approaches.

Method	Years	Population-level impact (%)	Striped Bass mean FL (mm)	Number of Striped Bass removed	Per capita impact (%)
Striped Bass removal–salmon survival experiment 1	2013	10.2	492	11	0.92
Diet energetics analysis	2013	7.9–13.2	492	11	0.71–1.20
Before–after impact assessment	2009, 2010, 2013	25, 29	404	26 ^a	0.96–1.11

^aAverage number of Striped Bass removed across multiple replicates.

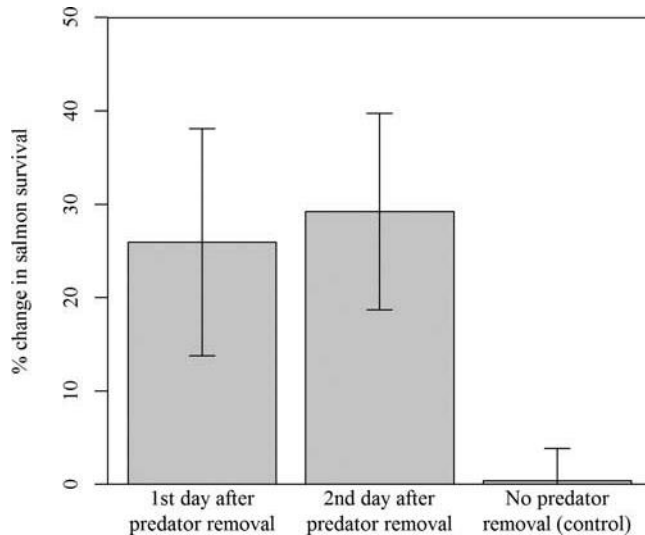


FIGURE 5. Mean (\pm SE) percent change in juvenile Chinook Salmon survival for the impact treatment (Striped Bass [predator] removal) between the day before predator removal and the first or second day after removal and for the control (no predator removal). Results of two-sample t -tests comparing impacts relative to the control were as follows: first day (mean = 25.9%; $t = -2.022$, $df = 10.52$, $P = 0.069$) and second day (mean = 29.2%; $t = -2.605$, $df = 11.05$, $P = 0.024$).

predator removal; Figure 5). Across all removal events, the average number of Striped Bass removed was 26; therefore, the Striped Bass per capita impact was estimated at 0.96% for the first day after removal and 1.11% for the second day after removal (Table 2). Mixed-effects linear regression indicated that the survival of juvenile Chinook Salmon increased with an increasing number of Striped Bass removed ($t = 2.329$, $df = 17$, $P = 0.0324$; Figure 6). We also examined average Striped Bass size as a covariate to the number removed, but we found that size had no significant effect.

DISCUSSION

Multiple stressors can interact, resulting in complex consequences for native species. In this example, a local predation hot spot (WIDD) was associated with increased PCC of juvenile Chinook Salmon by Striped Bass and attracted larger numbers of Striped Bass, thus decreasing the survival of emigrating juvenile salmon by 8–29%. This interaction was synergistic, as habitat increased both the functional and aggregative predator responses.

We found that the diets of Striped Bass collected at WIDD consisted primarily of juvenile Chinook Salmon, and the per capita impact of Striped Bass on juvenile salmon was higher at WIDD than at other altered locations. Alterations at WIDD may create profitable feeding conditions by concentrating prey into higher densities due to a shortened river width or upstream location where salmon densities are greater. Additionally, WIDD may disorient emigrating juvenile salmon due to sudden

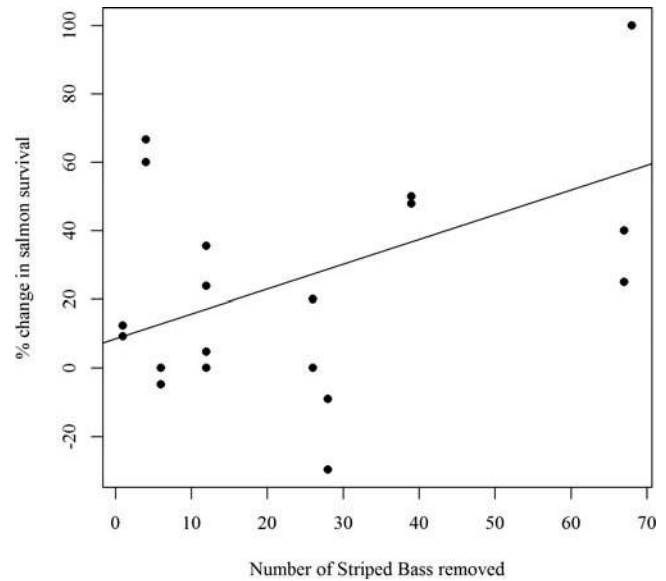


FIGURE 6. Mixed linear regression of the percent change in juvenile Chinook Salmon survival (response variable) against the number of Striped Bass removed (predictor variable), with period (first or second day after predator removal) used as a random effect ($t = 2.329$, $df = 17$, $P = 0.0324$).

changes in water velocity as they pass the dam (Deng et al. 2010); WIDD may also favor visual predators due to reduced turbidity (Gregory and Levings 1998; Horodysky et al. 2010). Increased consumption of juvenile salmon by predatory fish below dam-like structures has been attributed to prey disorientation, increased transit time through study reaches, and predator aggregations (Rieman et al. 1991; Blackwell and Juanes 1998; Tucker et al. 1998).

Striped Bass aggregated at WIDD, exhibiting an eightfold increase in CPUE compared with that at other altered locations and a 60-fold increase in CPUE compared with that at natural locations. The aggregation corresponded to an area where PCC of juvenile Chinook Salmon was also greatest (i.e., at WIDD), suggesting that Striped Bass will aggregate in areas of profitable feeding. Feeding aggregations are common in nature; for example, Striped Bass aggregate behind dams on the U.S. East Coast to feed on migrating Blueback Herring *Alosa aestivalis* (Davis et al. 2012). Alternatively, blockage of upstream migration could account for the observed aggregation of Striped Bass at WIDD because this species is known to avoid using fish ladders (Beasley and Hightower 2000). Regardless of the reason for aggregation, we saw an increase in the abundance of Striped Bass at WIDD, and the interaction of increasing both functional and aggregative predator responses resulted in greater predation on juvenile Chinook Salmon at WIDD relative to other locations.

We used three separate approaches to assess the impact of Striped Bass on the population of emigrating juvenile Chinook Salmon at WIDD, and we generated a range of 8–29% for juvenile salmon mortality. Per capita impacts were used to

compare the three approaches, indicating that a single Striped Bass could consume 0.71–1.20% of the juvenile Chinook Salmon population (Table 2). Despite limitations in each approach, the estimated per capita impacts of Striped Bass on juvenile salmon aligned remarkably well. The first approach was the Striped Bass removal–salmon survival experiment, which showed a 10.2% increase in survival of juvenile Chinook Salmon after 11 Striped Bass were removed, thereby supporting our original hypothesis.

The second approach to estimating the impact of Striped Bass on the emigrating juvenile salmon population included a diet energetic analysis of the Striped Bass that were collected during the removal experiment. Diet energetic analysis demonstrated that 7.9–13.1% of the emigrating juvenile Chinook Salmon were consumed. These results are similar to the 10% increase in juvenile salmon survival from the removal experiment. It is important to note that the diet estimate is only for one sampling instance (i.e., the population of 11 Striped Bass); surveys at WIDD in other years have indicated a Striped Bass population of approximately 60 fish, and thus the magnitude of predation could have been even higher during those years. Diet energetic analysis provides an alternative method to validate the magnitude of predation found in the Striped Bass removal and salmon survival experiment.

The third and most robust approach to estimating the population-level impact was the before–after impact assessment, which detected a 26–29% increase in the survival of juvenile Chinook Salmon after Striped Bass were removed from the WIDD site. This analysis included 10 replicate removal events spanning 3 years, differences in timing throughout the Chinook Salmon emigration period, and variation in environmental conditions. During eight of the removal events, three nonnative species (Striped Bass, Largemouth Bass, and Spotted Bass) were removed from the WIDD area. However, diet data from the Largemouth Bass and Spotted Bass collected at WIDD showed that the consumption of juvenile salmon was less than 1% (M. Sabal, unpublished data), suggesting that the increase in survival was driven primarily by the removal of Striped Bass. Collectively, the three approaches estimated 8–29% mortality of juvenile Chinook Salmon due to Striped Bass predation at WIDD.

The tendency for Striped Bass to aggregate at dams and to show increased consumption of anadromous fish is not unique to WIDD, as studies have documented such occurrences at the Red Bluff Diversion Dam on the Sacramento River, California (Tucker et al. 1998), and at the Essex and Holyoke dams on the East Coast (Blackwell and Juanes 1998; Davis et al. 2012). Furthermore, other predators aggregate at dams to prey on salmon: such predators include other fish species (Rieman et al. 1991), sea birds (Ruggerone 1986; Wiese et al. 2008), and pinnipeds (Yurk and Trites 2000; Keefer et al. 2012). In each of these situations, complex management has been necessary to address the opposing needs of predator and prey species (Harvey and Kareiva 2005). To compare population-

level impacts from the present study with those reported in other studies, McNary Dam on the Columbia River is approximately 15 times longer than WIDD; average population-level consumption of juvenile salmon by three predators (Smallmouth Bass *Micropterus dolomieu*, Walleye *Sander vitreus*, and Northern Pike *Ptychocheilus oregonensis*) in John Day Reservoir (123 km in length; behind McNary Dam) was 14%, and 21% of that loss occurred in the area immediately behind the dam (0.5-km reach; Rieman et al. 1991). On the San Joaquin River, California, Buchanan et al. (2013) found two reaches where juvenile Chinook Salmon mortality was consistently high, ranging from 6% to 17%. Therefore, Striped Bass impacts on juvenile Chinook Salmon at WIDD (8–29% mortality) rival or exceed the impacts observed in high-predation areas of other systems.

There has been some debate about the relative importance of the major drivers of juvenile salmon mortality in the Sacramento–San Joaquin Delta: water exports, habitat loss, water pollution, and nonnative 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 population-level impacts on juvenile salmon and the interactive effects of these different anthropogenic stressors. There is value in local studies that assess population-level impacts and that test the feasibility of management strategies, such as predator removals. Such studies increase our understanding of the ecological mechanisms and context-dependent attributes of predator–prey interactions (Hunsicker et al. 2011; Grossman et al. 2013). We examined nonnative Striped Bass and their interactions with habitat alterations to assess the local impact on a population of out-migrating juvenile Chinook Salmon at a predation hot spot. Our goal was to provide a tool for evaluating predatory impacts on juvenile salmon in specific areas of concern or interest.

Future studies should assess basinwide migration survival after predator removals, as delayed downstream compensatory mortality may eliminate long-term increases in survival. Another area that deserves future research is the functional role of smaller Striped Bass (<250 mm FL) and their potential predatory impacts on juvenile salmon because there is uncertainty in the available gape limitation data. We only examined one predation hot spot (WIDD), whereas many manmade structures exist throughout the Sacramento–San Joaquin Delta, and it will be important to compare findings and determine which common characteristics of such structures create this synergistic interaction. Our findings highlight that habitat features—particularly a small diversion dam—can create a predation hot spot by modifying the functional and aggregative responses of predators. Therefore, it is important to consider habitat alterations and interactive effects when estimating large-scale predation impacts and when planning local management strategies. On a larger scale, widespread global change, including habitat alterations and the introduction of nonnative species across ecosystems and taxa,

increases the probability that interactive effects will influence native prey populations and heightens the importance of studies focusing on these interactions.

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