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ARTICLE

Enumerating Predation on Chinook Salmon, Delta Smelt, and Other San Francisco Estuary Fishes Using Genetics

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Abstract

The establishment of nonnative predatory fish species is a worldwide phenomenon often having adverse effects on native species. Trophic interactions are complex, and uncertainty is a common theme in discussions of nonnative predator management. Several fishes of the San Francisco Estuary have experienced significant declines in recent decades due to multiple factors, including habitat alteration and predation. The role of predation as a direct cause of mortality remains an open question, as does whether habitat conditions play a role in promoting predation on species of concern. Recent studies using visual identification of prey have found little to no evidence of predation on species listed under the Endangered Species Act such as Delta Smelt *Hypomesus transpacificus* and juvenile Chinook Salmon *Oncorhynchus tshawytscha*. To increase the likelihood of detecting predation, this study employed a genetic approach. We combined this technique with habitat and water quality data to investigate the role that habitat may be playing on incidence of predation. This study focused on detection of predation on Chinook Salmon and Delta Smelt, six other native fish species, and six nonnative fish species by Striped Bass *Morone saxatilis* and other piscivores. Unlike previous studies in the region, the proportion of predators with no prey detected in their gut contents was high (47–81%). The study detected Delta Smelt in 1.3% of Striped Bass—considerably higher than other contemporary predation studies in the Sacramento–San Joaquin Delta. In April 2014, 6.6% of Striped Bass were positive for

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Chinook Salmon—substantially higher than observed in recent visual diet studies. Interestingly, native species comprised a relatively high proportion of Striped Bass prey (60%). Water temperature and conductivity were identified as significant predictors of Chinook Salmon presence in Striped Bass gut contents. This research also suggests that predation on soft-bodied prey may be an overlooked segment of the diets of piscivores.

The establishment of nonnative predatory fish species is a worldwide phenomenon with adverse effects on native species (Rahel and Olden 2008). The effects of these introduced species are complex and highly variable (Best and Arcese 2009), and how to manage them remains the subject of continuous debate (Gozlan 2008; Cucherousset and Olden 2011). The effects of introduced predators are not limited to their prey; they may alter multiple trophic levels through cascading effects with unpredictable results due to indirect, nonadditive, and interactive effects (Bruno and Cardinale 2008). A number of management strategies have been used in different locations with variable success. Examples in North America include predator removal efforts in the Colombia River to reduce predation on outmigrating salmonids (Friesen and Ward 1999) and stocking nonnative sport fish (Chinook Salmon *Oncorhynchus tshawytscha*) to control Alewife *Alosa pseudoharengus* in the Great Lakes after the extinction of Lake Trout *Salvelinus namaycush,* the native top predator (Fenichel et al. 2010).

In California, the Sacramento–San Joaquin Delta (Delta) has also undergone significant changes in its fish assemblages, yet the role of introduced predators remains murky. This study aims to expand the knowledge of predation by nonnative predators as part of a conservation strategy for native fishes.

The Delta is a vast network of tidally influenced marsh, channel, and open-water areas receiving freshwater from the Sacramento and San Joaquin rivers and flowing to San Francisco Bay. Several Delta fishes, including native resident species as well as anadromous fishes, have experienced significant declines (Lindley and Mohr 2003; Newman and Brandes 2010). The decline of these species is due to multiple factors, though it is likely that predation is the most common proximate cause of mortality in the Delta (IEP MAST 2015; Grossman 2016). The role of predation as a direct cause of mortality and the habitat factors that may contribute to current predation patterns—such as water diversions, delayed migrations, predator friendly structures—are not fully understood (IEP MAST 2015).

The role of predation in the decline of Delta fishes remains unclear despite several studies of piscivore diets in the Delta (Stevens 1966; Nobriga and Feyrer 2007, 2008; Baerwald et al. 2012; Schreier et al. 2016; Weinersmith et al. 2019). Nearly all previous piscivore diet studies have used visual identification techniques (but see Schreier et al. 2016 and Michel et al. 2018 for examples of genetic studies) to describe stomach contents, a method with known limitations for positive identification of prey (Kim and DeVries 2001). As a result, few of these studies have found evidence of predation on rare species like Delta Smelt *Hypomesus transpacificus* and juvenile Chinook Salmon, two state and federally protected species (the listing status of California Central Valley Chinook Salmon varies by run, with the spring run listed as federally threatened, winter run as federally endangered, and fall and late-fall runs as species of concern). These two species are of significant management interest because their habitat and migration corridors overlap with major water diversions in the Delta and the water supply for millions of California residents (Service 2007). Thus, a description of piscivore diets, spatial distributions of predation detections, and the habitats associated with the detection of predation are critical to shaping resource management strategies aimed at diminishing predation on protected fishes.

An alternative to previous visual identification approaches is genetic identification of prey, which can improve detection probability, particularly for soft-tissue and early life-stage fish. Studies have shown that eggs and larvae are visually unidentifiable within 30 to 60 min of ingestion (Schooley et al. 2008; Legler et al. 2010). On the other hand, juvenile Chinook Salmon were detectable in 100% of Striped Bass *Morone saxatilis* tested in a controlled feeding experiment after 36 h using genetics (Brandl et al. 2016). By increasing the prey detection window, the genetic approach increases the likelihood of detecting predation on rare prey (Carreon-Martinez et al. 2011), such as some of the native fish in the Delta. Therefore, the use of genetic methods can provide a more complete picture of the taxonomic composition of predator diets, which is critical to quantifying predator–prey dynamics with rare prey of high management concern.

This study is a survey of predation by nonnative piscivores on native species with the aim to investigate predation patterns and the habitat conditions associated with these predation events. The sampling focused on the northern Delta, a region that possesses habitat most resembling the historic native habitats of the region. We sampled six species of predators: Striped Bass, Sacramento Pikeminnow *Ptychocheilus grandis*, Largemouth Bass *Micropterus salmoides*, Smallmouth Bass *Micropterus dolomieu*, Channel Catfish *Ictalurus punctatus*, and White Catfish *Ameiurus catus*. The primary target predator,

nonnative Striped Bass, are hypothesized to be the primary predator consuming Delta Smelt in open water habitats (Nobriga and Smith 2020) and are among the most abundant predator in pelagic habitats, which are typically occupied by prey species of interest. Sacramento Pikeminnow serves as a comparative native piscivore targeting similarly sized prey (Moyle 2002). Smallmouth Bass were included because their abundances have increased in recent decades (Brown and Michniuk 2007), and little data exist on their diets in the Delta. Likewise, Largemouth Bass have experienced a similar increase in abundance, but their diets have been studied (Nobriga and Feyrer 2007; Weinersmith et al. 2019). Incidentally sampled Channel Catfish and White Catfish were also included as predators for a cursory assessment of their diets in the region.

Many native fishes utilize the northern Delta's habitats for migration, spawning, rearing, or foraging. The native fish community investigated in this study includes Chinook Salmon, Delta Smelt, Splittail *Pogonichthys macrolepidotus*, Longfin Smelt *Spirinchus thaleichthys*, steelhead *Oncorhynchus mykiss*, Green Sturgeon *Acipenser medirostris*, and White Sturgeon *Acipenser transmontanus*. To provide a basis for comparison, common nonnative prey species were surveyed as well, including Threadfin Shad *Dorosoma petenense*, Wakasagi *Hypomesus nipponensis*, and Mississippi Silverside *Menidia audens*.

In a broader context, this study provides an overview of the prey species complex (which may include larval fishes) during a period of severe drought. By sampling along migration routes as well as spawning and rearing habitat, we aimed to present a sampling of predation on a broad spatial scale, linking predation with water quality and other environmental parameters to explore the relationships between predation and habitat and water quality. The study investigated (1) patterns of piscivore catch and prey detection across the northern Delta, (2) spatial and temporal patterns in Striped Bass prey composition, and (3) habitat attributes associated with Striped Bass consumption of two key native fishes of concern (Chinook Salmon and Delta Smelt).

METHODS

Study location.—Predators were sampled across the northern Delta, along three potential migration corridors for out-migrating Chinook Salmon—Steamboat Slough, Miner/Sutter Slough, and the Sacramento River (Figure 1A)—as well as potential rearing areas for Delta Smelt and other native species—Liberty Island and the Sacramento Deep Water Ship Channel. This region is dominated by strong tidal flows, although net flows are enhanced in the migration corridors during high flow periods (winter and spring). Finally, predators were collected from the lower Sacramento River downstream of the confluence of Steamboat Slough near Rio Vista, California. This latter sampling region represents an area downstream (seaward) of the inputs of all the other sampling regions. We sampled here to provide a reference point where all migratory prey species transiting the northern Delta would have to pass, providing an opportunity for all prey fish migrating during the sample period to be detected. There

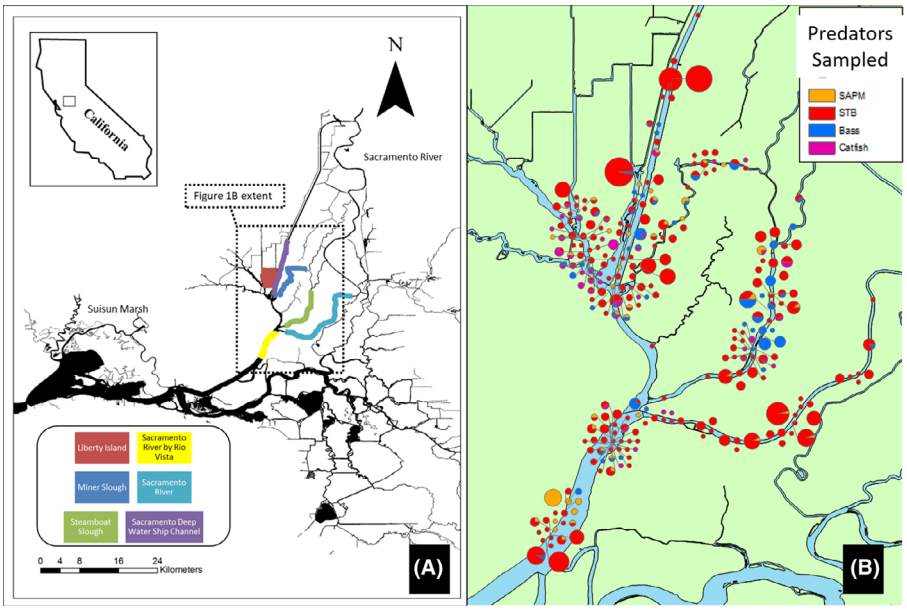

FIGURE 1. **(A)** The six sampling regions for examining diets of predatory fishes in the northern Sacramento–San Joaquin Delta with **(B)** spatial distribution of predators collected.

were short periods during the June samplings when the Delta cross channel gates were open, permitting flow from the Sacramento River into the central Delta. During these periods, the lower Sacramento river does not represent all the flow from all the sampled regions.

Predator sampling.—The primary target of sampling was Striped Bass, the apex pelagic predator in the Delta (Moyle 2002). Other piscivorous fish species—Largemouth Bass, Smallmouth Bass, White Catfish, Channel Catfish, and the native Sacramento Pikeminnow—were opportunistically collected and saved for analysis. As the targets of this sampling were predators consuming native fish greater than 50 mm FL, our sampling focused on predators greater than 200 mm FL (Nobriga and Smith 2020).

Within each of the six sampling areas, a minimum of ten sampling events (net sets) were conducted over the course of a sampling day. All sampling areas were sampled 4–5 d per sampling month. Depending on logistics, permitting, and crew safety considerations, sampling events were either conducted during the dawn/day (0600–1600 hours) or at dusk/night (1900–0300 hours). Sampling was conducted in the months of December, April, and June over the course of 2 years (December 2012 to June 2014) which coincided with a period of prolonged drought. These months were chosen to encompass the critical periods of native fish migration while minimizing the risk of incidentally sampling large-bodied listed species.

Predators were sampled using anchored gill nets (60 × 2 m; randomized panels with stretch mesh sizes of 63.5, 76.2, 88.9, 101.6, 127, and 152.4 mm). During the initial sampling period in December 2012, trammel nets were used to minimize harm to listed species. Trammel nets were, however, were found to be less effective at catching target species, so gill nets were used for the remainder of the project. Sampling effort was reduced during April 2013 due to this transition (Table 1). Gill nets were set for 30–60 min depending on debris and permit requirements. The orientation of the net to shore was randomized between perpendicular (70% of sets) and parallel (30% of sets) to effectively sample all targeted predator species. In addition to gill-net sampling, piscivorous fish were collected opportunistically using rod-and-reel sampling. This sampling was conducted using lures to not confound later stomach content analyses. All predators collected with rod and reel were included in summary data but omitted from statistical analyses to prevent introducing potential biases due to habitat differences and the hunger status of predators sampled by the two methods.

All fishes collected were identified to species and their FL (mm) measured, with listed species being processed immediately upon being found in the net. Water quality parameters were recorded using a Yellow Springs Instruments 6600 multi-parameter sonde and included temperature (°C), pH, electrical conductivity (μS/cm), turbidity (formazin nephelometric units [FNU]), and dissolved oxygen (mg/L). Additionally, Secchi depth (cm), water depth at the start and end of the net (m), GPS coordinates, and tide/current conditions were recorded at each set.

Predator processing and dissections.—All predator stomachs and gut contents were preserved in situ on the boat for later genetic analysis. After euthanasia, predator stomachs were injected with 5–10 mL of 95% ethanol through the esophagus using a sterile serological pipette with a rubber bulb. Predators were then individually bagged and placed on wet ice until the end of the sampling day when they were transferred to a −20°C freezer for later dissection. For each predator, the crew used new nitrile gloves and new pipettes to prevent contamination. Pipette bulbs, measuring boards, and critical boat surfaces were sterilized using a 15% bleach solution after each net set. For a detailed assessment of various gut contents preservation methods, see Brandl et al. (2016).

To determine the overall risk of contamination introduced from predator capture through final dissection, we conducted an experiment during normal sampling using a surrogate predator with no prior exposure to ambient target DNA. For this experiment, mackerel *Scomber* spp. were purchased from a bait shop, prepackaged and frozen, so as to have the least likelihood of being exposed to DNA from any target species. The experiment was conducted after a standard night of gill-net sampling during which three catfish and four Striped Bass were sampled. Thawed mackerel were vigorously exposed to gill nets and the deck of the sampling vessel for 60 s, after which they were processed identically to other predators. Back at the lab, the mackerel were dissected and analyzed per the standard protocol (below).

In a laboratory, preserved fish were removed from −20°C and thawed in warm water. Upon thawing, each predator was removed from its bag, and an initial incision was made in the body wall using sterilized scissors. Separate sterilized instruments were used once the body cavity was opened to prevent contaminating the inner cavity of the fish with DNA from the outside of the fish. Care was taken to use one gloved hand for handling the outside of the fish and the other gloved hand for inside the fish. After the entire gastrointestinal tract was removed, gloves were changed and the gastrointestinal tract was emptied by squeezing the contents into a petri dish. From the petri dish, the gut contents were moved to a 50-mL conical tube containing 4.5 mL of buffer ATL and 500 μL of proteinase K (Qiagen, Valencia, California). An additional 5 mL of buffer mix was added if the volume of gut contents was more than 15 mL. Gut fullness and volume (mL) were recorded for every dissection. Gut fullness was a qualitative assessment of the presence of material in the gut consisting of a categorical ranking from 0 (completely empty) to 4 (distended). At times a viscous, homogenous liquid

TABLE 1. Temporal distribution of predator fish species captured for investigation of fish predation in the northern Sacramento–San Joaquin Delta.

Sampling month	Diel sampling period	Primary gear type	Number of net sets	Predator species						Total predator samples
				Channel Catfish	Largemouth Bass	Sacramento Pikeminnow	Smallmouth Bass	Striped Bass	White Catfish	
December 2012	Day	Trammel	106	1	8	2	3	18	3	35
April 2013	Day	Trammel/gill	93	2	14	3	2	15	15	51
June 2013	Night	Gill	108	7	8	12	9	68	6	110
December 2013	Day	Gill	170	0	12	26	1	32	0	71
April 2014	Night	Gill	118	1	7	15	6	391	6	426
June 2014	Night	Gill	150	9	18	6	21	94	6	154
Total			745	20	67	64	42	618	36	847
Mean FL (mm)				428	318	463	284	453	319	
FL range (mm)				325–559	220–563	230–593	205–382	197–895	237–435	

was found in the gastrointestinal tract. These guts were classified as a 1, though in results that reference visual analyses, stomachs rated as 0 or 1 were considered "empty," as it was unclear to what extent the homogenous liquid was digested food. Tools were washed with soap and hot water, then sterilized in a 20% bleach solution for a minimum of 10 min, rinsed with water, and finally rinsed with 95% ethanol. New bench paper was used for every dissection.

Genetic detection.— Gut contents were incubated at 55°C for 2 d to dissolve the tissues. To avoid clogging the DNA extraction columns, samples were centrifuged at $1{,}000 \times g$ for 15 min, and 100 µL of the supernatant was diluted with 100 µL lysis buffer and the mixture was loaded onto 96-well blocks for extraction on a Qiagen BioRobot using a Qiagen DNeasy Blood and Tissue kit according to the manufacturer's instructions. Sample DNA was preamplified in a primer-limited environment for 14 cycles using primers from previously developed species-specific assays (Baerwald et al. 2011; Brandl et al. 2015), and high-throughput quantitative PCR was performed on the Biomark system (Fluidigm, South San Francisco, California) using the species-specific primers with corresponding hydrolysis probe. A positive detection was defined as logarithmic amplification of target DNA in three of six technical replicates after ambiguous amplifications were removed (Brandl et al. 2015). Due to a lack of assay specificity, Largemouth Bass and Smallmouth Bass detections were combined and treated as a single entity (*Micropterus* spp.) for this study.

Analysis of patterns of piscivore catch and prey detection.— Summary data and spatial distribution for target predator and prey species were compiled for the 6 months of sampling. All catch was included except for predators from whom their own DNA did not amplify—an indication there was a problem during the DNA extraction or amplification process. Channel and White catfish were an exception because we did not develop assays for these species, so all sampled catfish were included. These data included fish caught by rod-and-reel sampling in addition to the primary net sampling.

Analysis of spatial and temporal patterns in Striped Bass prey composition.— Data from all captured Striped Bass were utilized, regardless of capture method, with the implicit assumption that dietary composition was independent of sampling effort or efficiency. Due to high temporal variability in Striped Bass catch, each sampling month was analyzed separately, resulting in 36 location–month pairings (6 months × 6 locations). Ordination of prey composition was performed using nonmetric multidimensional scaling conducted in R (R Core Team 2017) using the vegan package (Oksanen et al. 2016). Vectors were included to indicate when detection of a prey species had a significant correlation with a grouping of location–months. To compare the variation in species abundance and composition among sampling units, beta diversity was calculated using a nonparametric analysis of similarity (Clarke 1993) with the null hypothesis that there was no difference in Striped Bass diet between regions or months.

Analysis of habitat attributes associated with consumption of Chinook Salmon and Delta Smelt.— The study detected eight instances of predation on Delta Smelt by Striped Bass, including two detections in the lower Sacramento River in December; five detections in Miner Slough, Steamboat Slough, and Liberty Island in April; and one detection in Liberty Island in June. Delta Smelt were not detected in the gut contents of Striped Bass in sufficient numbers for reliable examination of habitat attribute associations. Therefore, our methods and results focused exclusively on Striped Bass predation of Chinook Salmon. A binomial response generalized linear model (logistic regression) was created in R to examine the effect of habitat attributes (water temperature, electrical conductivity, and turbidity) and Striped Bass FL on Chinook Salmon presence–absence in the gut contents of Striped Bass. To avoid confounding factors associated with seasonal effects, extreme catch variability among our sampling months, and other factors, this analysis was confined to April 2014. Striped Bass FL was included to test for ontogenetic effects of predator size. Collinearity among covariates was tested by calculating variance inflation factor scores in R (threshold value of 3). Iterative model testing was conducted, and model fit was assessed using Akaike information criterion for small sample sizes (AIC_c), calculated using the AICcmodavg package in R (Mazerolle and Mazerolle 2017). A ΔAIC_c threshold of 2.0 was used to rank models and determine the best model. Models that ranked better than the null are reported. The 95% confidence intervals (CI) for model parameters were also calculated in R (R Core Team 2017) to assess whether coefficients were significantly different from zero.

RESULTS

A total of 745 net sets were conducted over 88 d of sampling (Table 1). Of the 2,196 fish sampled, a total of 847 target predators in the target size range were saved for genetic diet analysis. Predators were mainly captured using gill nets ($n = 746$), with relatively minor contributions from rod and reel ($n = 63$) and trammel nets ($n = 38$). Sampling effort was not evenly distributed across all sampling regions, with the Deep Water Ship Channel ($n = 296$ sets) receiving the most and Liberty Island ($n = 82$) receiving the least effort. Striped Bass comprised the majority (73%) of the predators sampled (Table 1). The proportion of total catch for the other five predator species varied between 2% and 8%.

The five control mackerel were treated in June 2014. Sample extraction and genetic processing were successful, and no target DNA amplified from the mackerel gut contents indicating that contamination from sampling, vessel processing, and lab dissection was not detected.

Patterns of Piscivore Catch and Prey Detection

Catch patterns.— Striped Bass catch was the most variable across the 6-month sampling period as compared with other predator species, with 63% of all Striped Bass catch occurring in April of 2014 (Table 1; Figure 1B). Among all predators (excluding conspecifics), the most common nonnative prey were Striped Bass (17%) and Mississippi Silverside (9%), whereas the most frequently detected native prey were Sacramento Pikeminnow (16%) and Chinook Salmon (13%) (Table 2). Among the other prey species of special management concern, Delta and Longfin smelt accounted for 4% and 6% of the prey detected, respectively. White Sturgeon, Green Sturgeon, and steelhead were rarely detected, with three, zero, and two detections, respectively.

Empty guts.— Overall, the quantity of predators with no prey detected in their gut contents was high (47–81%, depending on species). In Striped Bass, we were unable to genetically detect prey in 74% of samples, while visually, 76% of samples had empty or nearly empty guts (qualitative fullness of 0 or 1). Taken together, 62% of Striped Bass had no prey detected in either visual or genetic analyses, indicating partial concordance between the detection methods. Other predators had somewhat higher, though still low levels of prey detection by genetic methods (Table 2).

Piscivores as prey.— Also noteworthy was the proportion of piscivores detected as prey throughout the study. Striped Bass and Sacramento Pikeminnow were the most frequently detected prey in the gut contents of other predators (Table 2). Collectively, predators accounted for 47% of prey detections, not including either catfish species (no assays were developed for the catfishes) or the potential for cannibalism.

Predation on native prey.— Of the predators that had detectable stomach contents, native prey comprised 60% of the detections in Striped Bass gut contents (Table 3). Lower proportions of native prey were detected in other predators, such as Sacramento Pikeminnow (41%), Smallmouth Bass (36%), White Catfish (33%), Largemouth Bass (23%), and Channel Catfish (14%). Notably, predation on Longfin Smelt was detected in 20% of Sacramento Pikeminnows.

Spatial and Temporal Variation in Striped Bass Prey Composition

Further examination of the high proportion of native prey detections in Striped Bass gut contents showed that the most frequent detections were of Sacramento Pikeminnow ($n = 32$), Chinook Salmon ($n = 29$), and Splittail ($n =$

TABLE 2. Number of prey detections in predator species collected in the northern Sacramento–San Joaquin Delta, with proportions of predators sampled with that prey species in parentheses. Nonnative species are noted with an asterisk (*). Note that the parenthetical proportions may not sum to 1 because multiple species may be detected in a single individual.

	Predator species												
Prey species	Channel Catfish $n = 20$		Largemouth Bass $n = 67$		Sacramento Pikeminnow $n = 64$		Smallmouth Bass $n = 42$		Striped Bass $n = 618$		White Catfish $n = 36$		Total detections
Chinook Salmon	0		0		0		3	(0.07)	29	(0.05)	0		32
Delta Smelt	0		0		0		0		8	(0.01)	1	(0.03)	9
Green Sturgeon	0		0		0		0		0		0		0
Micropterus spp.*	1	(0.05)			1	(0.02)			25	(0.04)	2	(0.06)	29
Longfin Smelt	0		0		13	(0.20)	0		2	(0.01)	0		15
Mississippi Silverside*	2	(0.01)	1	(0.01)	1	(0.02)	0		17	(0.03)	2	(0.06)	23
Sacramento Pikeminnow	1	(0.05)	3	(0.04)			0		32	(0.05)	3	(0.08)	39
Splittail	0		0		1	(0.02)	1	(0.02)	18	(0.03)	1	(0.03)	21
Steelhead	0		0		0	(0.00)	0		2	(0.01)	0		2
Striped Bass*	3	(0.15)	8	(0.12)	17	(0.27)	7	(0.17)			7	(0.19)	42
Threadfin Shad*	0		1	(0.01)	1	(0.02)	0		18	(0.03)	1	(0.03)	21
Wakasagi*	0		0		0		0		2	(0.01)	0		2
White Sturgeon	0		0		0		0		2	(0.01)	1	(0.03)	3
No detections	13	(0.65)	54	(0.81)	30	(0.47)	31	(0.74)	458	(0.74)	18	(0.50)	

18). These prey species were found in all sampling regions, though Steamboat Slough and the downstream Sacramento River locations consistently had the highest detection frequency for these species (Table 4). We used nonmetric multidimensional scaling ordination to examine spatial and temporal patterns of prey detection in Striped Bass gut contents across the 3 months with the highest Striped Bass catch (June 2013, April 2014, and June 2014). The composition of prey detections for each month at each location is depicted in Figure 2. Typically, prey compositions were similar across locations within a given month, indicating a seasonal pattern for prey detections. After the vectors for each assayed species were overlaid, a clear pattern was shown with native species (Chinook Salmon, Splittail, and Sacramento Pikeminnow) as prey in April and the nonnative *Micropterus* spp. in the other months. Species with vectors not included did not show a significant relationship. Analysis of similarity results confirmed that prey composition was significantly different among the three sampling months ($P < 0.01$) but not among sampling regions ($P = 0.97$). The three most abundant native prey, as mentioned previously, were significantly correlated with samples from April 2014 ($\rho > 0.5$, $P < 0.01$).

TABLE 3. Comparison of total native and nonnative prey detections in gut contents of predator species in the northern Sacramento–San Joaquin Delta, with the percent of total detections comprised of native prey.

Predator species	Native prey	Nonnative prey	Total	% native prey
Channel Catfish	1	6	7	14
Largemouth Bass	3	10	13	23
Sacramento Pikeminnow	14	20	34	41
Smallmouth Bass	4	7	11	36
Striped Bass	93	62	155	60
White Catfish	6	12	18	33
Total	121	117	238	51

Habitat Attributes Associated with Striped Bass Consumption of Native Threatened Fishes

Extreme temporal variability in predator catch prevented an analysis that spanned across months, so the analysis was limited to April 2014. Striped Bass consumption of Chinook Salmon was not evenly distributed across our sampling regions (Figure 3A). Striped Bass captured in the three northern Delta migratory routes (upper Sacramento River, Miner Slough, and Steamboat Slough) had significantly more Chinook Salmon DNA detected in their stomach contents compared to other regions (Figure 3A; $\chi^2 = 7.64$, $P = 0.006$). Our generalized linear model analysis resulted in the best model, based on AIC_c score, relating electrical conductivity and water temperature to predation on Chinook Salmon by Striped Bass (Table 5). Each covariate's variance inflation factor score was <2.0, the model had a McFadden's R^2 of 0.10, and 95% CIs for each covariate's coefficient did not overlap with zero. Temperature had a positive coefficient, while conductivity

TABLE 4. Prey detections in all predator species for each sampling region in the northern Sacramento–San Joaquin Delta. Nonnative species are noted with an asterisk (*), and number of net sampling sets per region is included as *n*.

	Sampling location						
Prey species detected in all predator species	Liberty Island $n = 82$	Miner Slough $n = 115$	Sacramento River (upper) $n = 115$	Sacramento River (lower) $n = 189$	DWSC[a] $n = 107$	Steamboat Slough $n = 137$	Total detections
Chinook Salmon	1	6	9	4	3	9	32
Delta Smelt	3	3	0	2	0	1	9
Green Sturgeon	0	0	0	0	0	0	0
Micropterus spp.*	2	9	2	6	2	8	29
Longfin Smelt	0	0	0	13	2	0	15
Mississippi Silverside*	6	1	2	4	6	4	23
Sacramento Pikeminnow	5	4	7	4	7	12	39
Splittail	1	3	10	1	3	3	21
Steelhead	0	1	1	0	0	0	2
Striped Bass*	8	3	5	10	4	12	42
Threadfin Shad*	8	0	1	5	4	3	21
Wakasagi*	1	1	0	0	0	0	2
White Sturgeon	0	0	0	0	3	0	3

[a]DWSC = Sacramento Deep Water Ship Channel.

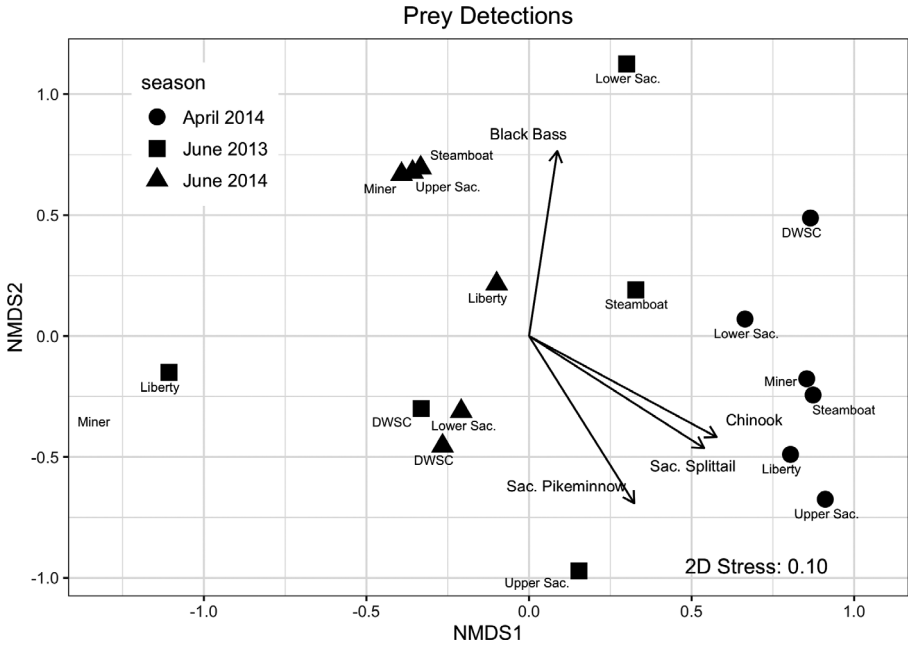

FIGURE 2. Nonmetric multidimensional scaling ordination comparing month–locations of prey detections in Striped Bass. The metric used to compare the assemblages for each month–location was incidence of detection per Striped Bass. Vectors indicate significant correlations between individual prey species and month–location assemblages ($r^2 > 0.50$; $P < 0.01$). The plot shows that the prey assemblages from each month–location are grouped by month rather than location, indicating that prey assemblages vary by season rather than location. Species labels on vectors are Black Bass = *Micropterus* spp., Sac. Pikeminnow = Sacramento Pikeminnow, Sac. Splittail = Splittail, Chinook = Chinook Salmon.

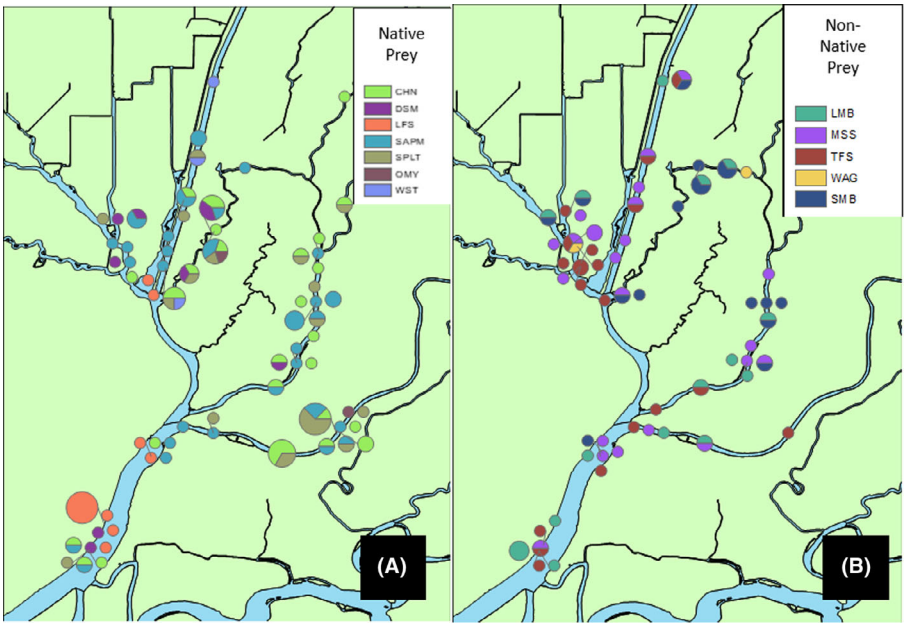

FIGURE 3. Spatial distribution of **(A)** native prey species and (B) nonnative prey species detected in predator gut contents in the northern Sacramento–San Joaquin Delta. The size of the pie charts corresponds to the number caught at a given sampling location.

had a negative coefficient. These results indicate that the detection of Striped Bass predation on Chinook Salmon was higher in habitats with relatively higher temperature and lower conductivity.

To test whether our model results were merely an artifact of the geographic differences in detection, we tested for differences between water temperature and conductivity between the upper and lower regions. Both metrics

TABLE 5. Model selection results for generalized linear models that were used to identify habitat variables affecting the detection of Chinook Salmon predation by Striped Bass in samples collected during April 2014 in the northern Sacramento–San Joaquin Delta. Abbreviations are AIC_c = corrected Akaike's information criterion, $\Delta AIC_c = AIC_c$ difference, Turb = turbidity (FNU), Temp = water temperature (°C), FL = fork length (mm), and Cond = electrical conductivity (μS/cm). Parameter coefficients are listed under each covariate, and *P*-values are indicated by asterisks (*$P < 0.05$, **$P < 0.01$). The best model is shown in bold.

				Covariates			
Model	AIC_c	ΔAIC_c	Intercept	Temp	Cond	Turb	FL
Temp + Cond	**173.97**	**0**	**−3.18**	**0.23***	**−0.02****		
Temp + Cond + Turb	173.56	−0.41	−7.29*	0.48*	−0.23**	0.08	
Temp + Cond + Turb + FL	175.60	1.63	−7.16*	0.48*	−0.02**	0.08	<−0.01
Cond	177.36	3.39	0.15		−0.012**		
Turb	186.82	12.85	−1.85**			−0.06	
Null	188.59	14.62	−2.55**				

were significantly different, with upstream regions being fresher ($P < 0.001$) and cooler ($P < 0.001$), indicating that the patterns observed in the model are more nuanced than differences in water quality upstream and downstream averaged over the sampling periods.

DISCUSSION

This study provides a broad survey of predation on species of concern in the northern Delta region. While predator and prey abundances and distribution were not estimated, this study's broad sampling of the northern Delta and sensitive detection methods highlight important temporal and spatial variation in predation. Future study designs would benefit from more specific study questions and a focus on how to best utilize presence–absence data produced using this method.

Contemporary genetic approaches typically allow for more species to be detected than visual identification (Baerwald et al. 2012; Oyafuso et al. 2016), but the method is not without limitations (King et al. 2008; Bowen and Iverson 2012). We acknowledge there are many alternative pathways by which DNA could have entered the stomach contents besides predation. For example, secondary predation, postsampling contamination, scavenging, or environmental DNA contamination could all theoretically lead to detections of prey DNA. Of these, secondary predation is perhaps the most likely to be a confounding factor, as the size of the predators sampled was sufficient to allow for ingestion of prey, which were themselves capable of consuming fish. However, generally low detection rates and an overall paucity of large-bodied prey in predator gut contents indicates that primary predation is the most parsimonious explanation for our detections. Additionally, the experimental control using mackerel indicated that contamination during sampling and processing was unlikely to have introduced many, if any, false positives.

What Patterns of Piscivore Catch and Prey Detection Were Observed across the Northern Delta?

Catch patterns.— Predator sampling was marked by a large catch of Striped Bass in April 2014. It is likely that this catch pattern for Striped Bass was due to our sampling overlapping with the Striped Bass spawning migration period in the Delta, which typically begins in April (Moyle 2002). The diets of Striped Bass showed a large variety of species; all 13 assayed prey taxa were detected in Striped Bass except for Green Sturgeon. The breadth of prey observed is consistent with the hypothesis that Striped Bass are not highly selective in their prey choice, and they have been shown to exhibit considerable trophic adaptability (Nobriga and Feyrer 2008).

Empty guts.— This study contrasts with other diet studies that used visual analyses to identify fish and invertebrate prey. A previous diet study (Zeug et al. 2017) showed that only 18% of Striped Bass guts were empty, whereas this study showed 62% of Striped Bass had no prey detected genetically or visually. The disparity may be due to sampling location differences between the studies. Zeug et al. (2017) focused their sampling in the confluence region of the Sacramento and San Joaquin rivers, downstream of our sampling sites in November and December of 2010 and 2011. When pared down to the overlapping site, the Lower Sacramento sampling station in December, our study observed a similar rate of empty guts to the Zeug study (18%), indicating that Striped Bass did not consume prey as frequently in the upstream sampling locations and/or during the months of spawning migration.

Piscivores as prey.— Another notable finding was the degree to which predatory fish comprised relatively high proportions of the diets of other predatory fish. Striped

Bass consumed other predators at rates comparable to their more traditional prey items like Threadfin Shad and Chinook Salmon. Additionally, 27% of Sacramento Pikeminnow were found to have Striped Bass in their gut contents. This finding may provide insight into the debate surrounding the effectiveness of predator removal as a means of improving survival rates of native species. If there is a high proportion of predators consuming other predators, would predator removal release predation pressure on nontarget predators, thereby increasing their populations and reducing the long-term effectiveness of predator control efforts? It is possible that this mechanism factored into the results of other studies (Cavallo et al. 2013; Michel et al. 2020) in which the catch of some predators increased after an initial predator removal effort —a process called "compensatory immigration" (Lieury et al. 2015; Minnie et al. 2016). Compensatory immigration was also supported by Stompe et al. (2020), who noted the flexibility and overlap of the diets between Striped Bass and Sacramento Pikeminnow, allowing them to fill each other's niche where the population of the other had declined.

Predation on native species.— Longfin Smelt were detected in gut contents of 20% of Sacramento Pikeminnows ($n = 13$). The vast majority of these detections were along the Sacramento River near Rio Vista in December, a key migration period and location for Longfin Smelt as they move upstream to spawn (Moyle 2002). Because this study opted for a broader reach with less fine-scale sampling, the question arises: is this reach of the Sacramento River a hotspot for predation on Longfin Smelt? It would be interesting to evaluate this question further to determine whether Sacramento Pikeminnow are an important predator of Longfin Smelt.

Also noteworthy was the detection frequency of Chinook Salmon in Smallmouth Bass guts (27%). No previous studies have examined the life history or diets of Smallmouth Bass in the Delta, and little is known about their distribution in the system. Brown and Michniuk (2007) found a slight increase in their occurrence in electrofishing surveys in the early 2000s compared to the 1980s, though their occurrence never exceeded 0.3% of total catch. Thus, predation by Smallmouth Bass may have localized effects on Chinook Salmon not previously acknowledged, warranting further investigation.

How Does Striped Bass Prey Composition Vary Spatially and Temporally across the Northern Delta?

Previous reports of predation on Delta Smelt by Striped Bass in the San Francisco Estuary have shown that 0.4, 0, and 0% of Striped Bass had Delta Smelt visually identifiable in their gut for diet studies conducted in 1963–1964, 2001, and 2003, respectively (Nobriga and Feyrer 2008). These figures include sampling that took place when Delta Smelt were relatively abundant (1963–1964). The current study found that 1.3% of Striped Bass contained Delta Smelt DNA in gut contents. This observation may be attributed to the sensitivity of the genetic method or differences in the season sampled or the sampling region. While these do not represent direct comparisons, our findings indicate that the predator–prey dynamics between these species are not well understood, an idea highlighted by Nobriga and Smith (2020), who posit that the lack of historic data has prevented an understanding of the outsized role that Striped Bass may play as a predator in the estuary. Unfortunately, the small number of detections dispersed over the six sampling months precluded further analyses in this study.

Likewise, this study found 6.6% of Striped Bass positive for Chinook Salmon in the month of highest catch—a number higher than previous local studies of 0.4% and 0.5% (Nobriga and Feyrer 2008)—and similar to Michel et al. (2018), who also used a genetic approach.

Native species comprised a relatively high proportion of Striped Bass prey detections overall (60%), which corresponds to natives being detected in 15% of all Striped Bass sampled. The percentage of native fish detected varied by month, with 29, 82, and 20% of prey detections composed of native species in December, April, and June, respectively. These proportions are representative of the reproductive phenology of the fish of the Delta (Moyle 2002; Nobriga and Feyrer 2007) but are interesting when considering the relative abundance of native species found in monitoring surveys. In the Yolo Bypass (part of the northern Delta) during our study period, surveys showed less than 10% of total catch was comprised of native species (Mahardja 2016), a proportion matched by other monitoring surveys in the northern Delta (Castillo et al. 2018).

Furthermore, visual diet studies have shown that Striped Bass prey consist primarily of invertebrates and invasive fishes (Stevens 1966; Nobriga and Feyrer 2008; Zeug et al. 2017). The high proportion of natives observed here is not due to bias from the relatively low number of assays, since the most common prey observed in the cited studies above were represented in the genetic assays, including the most common forage fishes (i.e., Threadfin Shad and Mississippi Silverside). The observed trend may be explained by the nonselective foraging of Striped Bass and the recruitment patterns of native fishes in the sampling years, or we could speculate that Striped Bass may have a preference for some native fish species.

General patterns observed in the nonmetric multidimensional scaling were confirmed through the analyses of similarity. Prey detections did not differ substantively across locations within a given month, but they were distinct across sampling months, with more native prey observed in April and more nonnative prey in June. This variability may be explained by the relative density of small prey after

spawning—young-of-the-year native fishes are most dense after spawning in April compared to young-of-the-year nonnatives, which reach peak abundance in June (Moyle 2002). However, another phenomenon that may contribute to the observed pattern is the high mobility of Striped Bass (Mather et al. 2010). Striped Bass may be utilizing the same feeding grounds, which vary seasonally, but may be captured in a separate area due to their high mobility. The relatively small project area here may diminish the likelihood that the predation event and capture event took place in the same region.

Are Particular Habitat Attributes Associated with Striped Bass Consumption of Chinook Salmon?

We found a higher proportion of Chinook Salmon DNA present in Striped Bass gut contents from upstream migratory regions (6.8% from Miner Slough, Steamboat Slough, and the upper Sacramento River) compared to downstream (lower Sacramento River; 2.6%) and off-channel (Liberty Island, Deepwater Ship Channel; 1.6%) areas for all months combined. The upper regions of our sampling area are characterized, compared to the lower regions, by increased riprapped banks, narrower channels, lower turbidity, and higher velocities. The lower regions, however, are characterized by greater tidal movement and shallow shoals.

Water quality parameters identified as significant predictors of Chinook Salmon presence in Striped Bass gut contents were temperature and conductivity. The middling goodness of fit metric (McFadden's $R^2 = 0.10$) is likely due to the limited catch and the large number of zeros in the model. We still consider the model useful because the variables are significant and the lower R^2 may be explained by the nature of the data. Previous work utilizing genetic prey identification techniques identified turbidity as a significant predictor of Mississippi Silverside predation on larval Delta Smelt (Schreier et al. 2016). While turbidity was not a significant predictor in this analysis, turbidity was significantly lower in the upper regions, which experienced greater predation. Given this, it remains likely that turbidity influences Striped Bass predation and our sample sizes were insufficient to detect it.

In conclusion, we identified predation patterns and factors that may contribute to predation by sampling predators across a range of habitat types. These results help to fill an information gap in Delta research that has been highlighted by previous syntheses efforts (IEP MAST 2015; Grossman 2016). The broad reach of the study, combined with the more sensitive genetic methods, presents some interesting observations, such as the prevalence of empty guts in the predators of the region and the disproportionate level of native species detected in the stomachs of Striped Bass. More broadly, this research suggests that predation on soft-bodied prey may be an overlooked segment of the diets of piscivores, and genetic studies provide a tool to investigate this aspect of piscivore diets. Second, given the prevalence of predators consuming other predator species, this study provides an interesting perspective for the discussion on predator removal to alleviate predation pressure on federally listed species. This study highlights the usefulness of the genetic approach for predation studies, and it serves as a proof of concept for high-throughput genetic diet studies generally.

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