SAN FRANCISCO ESTUARY & WATERSHED SCIENCE
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RESEARCH

Habitat-Specific Foraging by Striped Bass (*Morone saxatilis*) in the San Francisco Estuary, California: Implications for Tidal Restoration

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ABSTRACT

Non-native predatory fish strongly affect aquatic communities, and anthropogenic habitat alterations can exacerbate their effects. Loss of natural habitat, and restoration actions that reverse habitat loss, can modify relationships between non-native predators and prey. Predicting how these relationships will change is often difficult because insufficient information exists on the habitat-specific feeding ecology of non-native predators. To address this information gap, we examined diets of non-native Striped Bass (*Morone saxatilis*; 63 to 671 mm standard length; estimated age 1 to 5 yrs) in the San Francisco Estuary during spring and summer in three habitat types—marsh, shoal, and channel—with the marsh habitat type serving as a model for ongoing and future restoration. Based on a prey-specific index of relative importance, Striped Bass diets were dominated by macroinvertebrates in spring and summer (amphipods in spring, decapods and isopods in summer). In spring, diets were relatively consistent across habitats. In summer, marsh diets were dominated by sphaeromatid isopods and shoal/channel diets by idoteid amphipods and decapods. Striped Bass consumed a variety of native and non-native fishes, primarily Prickly Sculpin (*Cottus asper*) and Gobiidae. The highest importance of fish prey was in the marsh in spring (~40% prey weight), and fish prey comprised less than 25% prey weight in all other season/habitat combinations. Linear discriminant analyses suggested that marsh foraging was prevalent in Striped Bass collected in other habitats, mostly because of the predominance of marsh-associated invertebrates found in the stomachs of individual Striped Bass collected outside the marsh. Striped Bass diets differ across habitats, with marsh foraging important to Striped Bass regardless of collection location. This information can be used to forecast the potential utilization of restored habitats by this non-native piscivore.

SFEWS Volume 20 | Issue 3 | Article 4
https://doi.org/10.15447/sfews.2022v20iss3art4

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KEY WORDS

non-native species, tidal marsh, diet, habitat gradients

INTRODUCTION

Non-native piscine predators, particularly predatory sportfish, can have myriad effects on native communities through consumption, competition, and other interactions (summarized in Moyle 1999; Clarkson et al. 2005; Cucherousset and Olden 2011). The magnitude of these effects is often exacerbated by other anthropogenic environmental changes (Facon et al. 2006), including pollution (McKenzie et al. 2012), climate change (Milazzo et al. 2013), and habitat loss (Didham et al. 2007; Moyle et al. 2010; Sabal et al. 2019). Habitat types—particularly those exhibiting different structural qualities (e.g., littoral versus pelagic zones of lakes, reef versus open water)—mediate interactions between predatory fish and their prey. For example, habitat structure can modify predation effects by impeding predator movement (Savino and Stein 1982), limiting visual range (e.g., physical structure or water clarity; Carter et al. 2010; Ferrari et al. 2014), providing refuge for prey (Persson and Eklov 1995; Warfe and Barmuta 2004), or providing contact points for predators (Lehman et al. 2019). Modifications to habitat structure are often concurrent with increased abundances of non-native species, thereby compounding harm to native communities.

Although many aquatic habitats have been modified by humans, estuaries are particularly affected as a result of habitat loss, water diversions, and species introductions (Cloern and Jassby 2012). These negative effects are widely recognized, and amelioration strategies such as restoration of key habitats or ecosystem functions are increasingly prioritized. However, ostensibly beneficial habitat restoration can unexpectedly benefit non-natives at the expense of native species (Zedler 2000; Korsu et al. 2010). Non-native effects must therefore be considered when assessing restoration success (Bond and Lake 2003; Herbold et al. 2014). For example, within the San Francisco Estuary (estuary), introductions of non-native fish, macroinvertebrate, zooplankton, and plant species (Cohen and Carlton 1998)—as well as physical habitat changes tied to marsh reclamation and water diversions—have resulted in major alterations to nearly all components of the system (Nichols et al. 1986; Cloern and Jassby 2012; Whipple et al. 2012). Historical tidal marsh habitats have seen a dramatic decline in the estuary; upward of 90% of tidal marsh area has been lost to reclamation and water diversions, while open-water habitats have increased (Whipple et al. 2012; Robinson et al. 2014). Although tidal marshes are being restored in an attempt to remedy these losses, substantial uncertainty remains about how the restored habitats may support non-native fishes (Brown 2003; Herbold et al. 2014).

Striped Bass (*Morone saxatilis*), a large-bodied and anadromous piscivore, was introduced into the estuary in 1879 (Moyle 2002) and quickly became abundant enough to support an extensive commercial fishery that persisted until 1935. Striped Bass remains a popular target of recreational anglers and is the most widespread piscivore within the estuary, potentially exerting substantial predation pressure on native fishes (Lindley and Mohr 2003; Loboschefsky et al. 2012; Nobriga and Smith 2020). Throughout its range, Striped Bass occupies many habitats, including bays, surf zones, marshes, shoals, and large rivers. Because of its mobility, size, and use of diverse habitat types, Striped Bass consume a wide variety of prey (Manooch 1973; Nobriga and Feyrer 2007; Grossman 2016), with high seasonal and regional variability (Feyrer et al. 2003; Nobriga and Feyrer 2008; Ferry and Mather 2012). For example, Striped Bass in coastal New England consume invertebrates in higher proportion than Striped Bass in the coastal mid-Atlantic Ocean (Nelson et al. 2003; Overton et al. 2009), and within-region diets are related to seasons and habitats (Nobriga and Feyrer 2007; Ferry and Mather 2012; Baker et al. 2016).

Despite numerous diet studies on Striped Bass in the estuary (Stevens 1966; Thomas 1967; Nobriga and Feyrer 2007; Zeug et al. 2017; Colombano et al. 2021, among others), information about its habitat-specific feeding ecology remains insufficient to evaluate tidal marsh use compared to other estuary habitat types. Shifts in prey community have altered Striped Bass diets (Feyrer et al. 2003), and changes in prey behavior, size, or availability may result in the differential consumption of prey taxa in dissimilar habitat types (Nelson et al. 2006; Overton et al. 2008). A nuanced understanding of habitat-specific foraging by predators such as Striped Bass is a necessary step in forecasting the potential function of restored habitats. To address this information gap, we examined the diets of Striped Bass across three habitat types—marsh, shoal, and channel—with the following objectives: (1) quantify Striped Bass stomach fullness across habitats, (2) characterize Striped Bass diet composition across habitats, and (3) evaluate the potential for habitat-specific foraging by Striped Bass by comparing capture and expected foraging habitats. The habitats in this study represent primary physical habitat types present in the north-central San Francisco Estuary, including habitats generated by future restoration projects, and it is expected that Striped Bass diet and foraging ecology will differ considerably across habitat types.

MATERIALS AND METHODS

Study Area

Our study site was Ryer Island (38°05'N, 122°01'W; Figure 1), a brackish tidal marsh in the north-central estuary, a region with marine and freshwater influences and diverse habitats that support a wide array of estuarine fishes and macroinvertebrates (Hobbs et al. 2006; Moyle

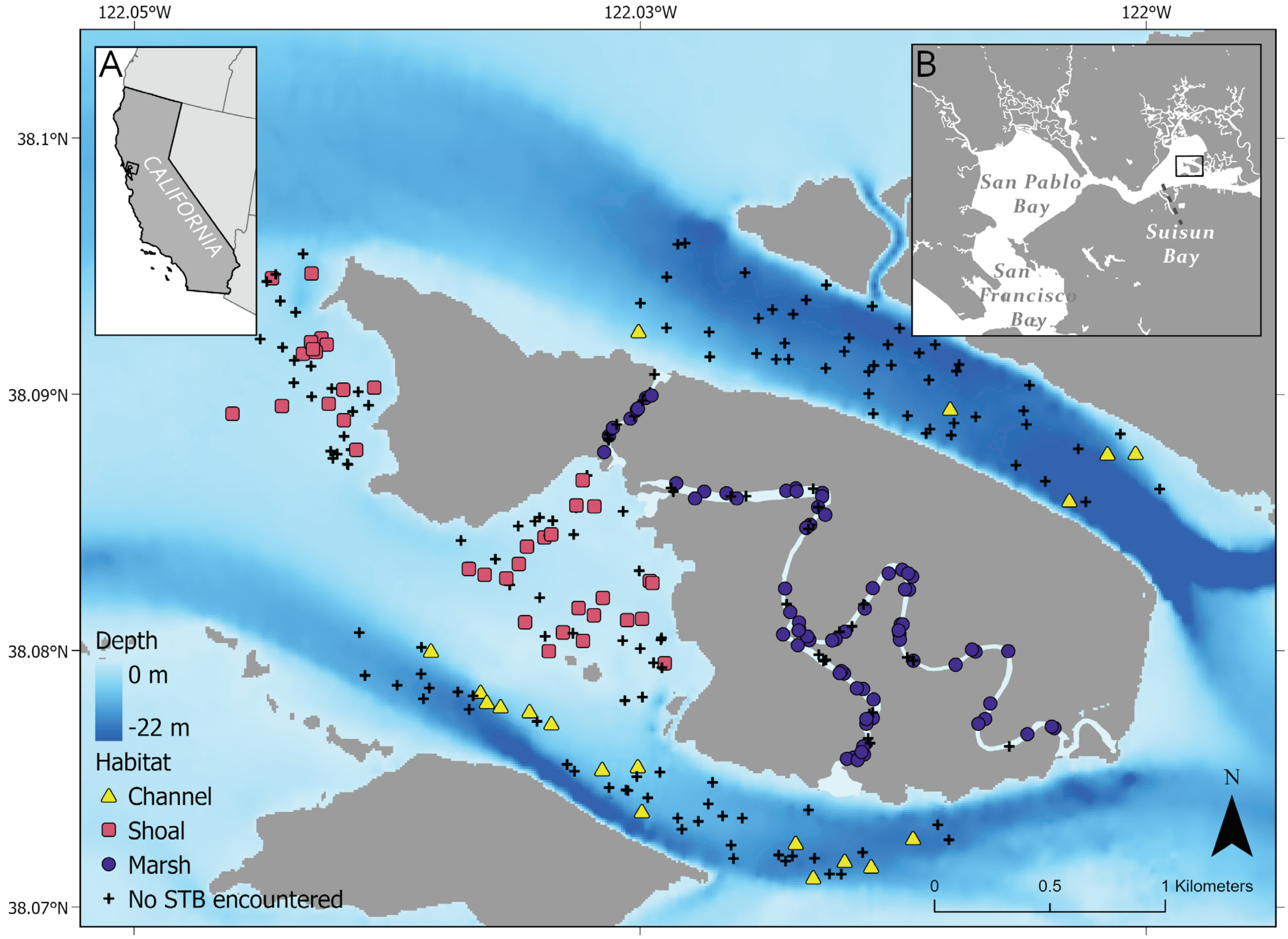

Figure 1 Study area (*main panel*) located within California (**A**) and the San Francisco Estuary (**B**). Sampling locations are noted, with *color* and *symbol* denoting habitat. Locations sampled with no Striped Bass (STB) encountered are shown as *black crosses*. Bathymetry is represented by the *blue gradient* and bathymetry data were obtained from Fregoso et al. 2017.

et al. 2010) and a high density of Striped Bass in channel, shoal, and marsh habitats (Feyrer et al. 2021). The Ryer Island tidal marsh is 347 ha of emergent tidal marsh and dendritic channels approximately 2 m deep that are inundated daily by semidiurnal tides. Within the marsh, meandering dendritic tidal channels are patchily vegetated with sago pondweed (*Stuckenia pectinata*), while channel margins and the marsh plain are covered with emergent vegetation, such as common reed (*Phragmites australis*), California bulrush (*Schoenoplectus californicus*), and cattails (*Typha* spp.). The marsh, encompassing tidal channels and vegetated marsh plain covered with mostly native vegetation, represents a potential target endpoint for tidal marsh restoration projects. Approximately 80 ha of shallow shoals (approximate depth 2 m) adjacent to Ryer Island are sparsely vegetated seasonally by sago pondweed (Borgnis and Boyer 2016). Deep channels (approximate depth 8 m) border Ryer Island to the north and south and are unvegetated.

Field and Laboratory Methods

We collected Striped Bass in spring (March 26–April 5) and summer (July 9–July 18) 2018 under a stratified random sampling design. We sampled day and night using two gear types (gill nets and otter trawls) to minimize time-of-day and size bias. We divided the waters within and around Ryer Island into the three habitats described above (marsh, shoal, and channel) and we generated random sampling sites within them using ArcGIS software (ESRI, Redlands, California, USA). We set gill nets for approximately 60 minutes and measured 1.8 m in height x 45.7 m in length, with five equal-length panels of stretch mesh that measured 38, 51, 64, 76, and 89 mm, consistent with other studies in the region (Zeug et al. 2017; Feyrer et al. 2021; Wulff et al. 2022). We also sampled fish using a four-seam otter trawl 1.5 m high, 4.3 m wide, and 5.3 m long, towed at approximately 4 km/hr. The trawl mesh was 35-mm stretch and lined with a 6-mm stretch cod-end. Before we deployed each sampling gear, we recorded temperature, specific conductivity, turbidity, and dissolved oxygen with a Yellow Springs Instruments (YSI) EXO2 Sonde multimeter. Spring had lower temperature (degrees Celsius; spring: mean 14.3, standard deviation 1; summer: 21.4 ± 1) and specific conductance (µS cm^{-1}; spring: 389 ± 143; summer: 13701 ± 2317) and higher turbidity (Formazin Turbidity Units; spring: 40.1 ± 12; summer: 25.6 ± 16) and dissolved oxygen (mg L^{-1}; spring: 9.5 ± 0.4; summer: 8.3 ± 0.6). For each captured individual, we measured standard length (SL) to the nearest millimeter (mm), and weight to the nearest gram (g). We removed stomach contents by gastric lavage with a modified Seaburg sampler (Seaburg 1957; Hartleb and Moring 1995) and preserved contents of individual stomachs in 10% formalin. All fish were implanted with a T-bar anchor tag (FLOY brand, size FD-94) to evaluate the potential for recapture of fish used for diet analyses.

In the laboratory, we identified stomach contents with a dissecting microscope to the lowest feasible taxonomic level using diagnostic keys or bones as necessary (e.g., invertebrates: Kozloff and Price 1987; Carlton 2007; fish: Morris 1981; Hansel et al. 1988; Parrish et al. 2006; Traynor et al. 2010). We enumerated individual diet items, placed them on a blotting towel for 30 s, and recorded wet weights to the nearest 0.0001 g. Large prey items (> 0.01 g) were weighed individually; small items (< 0.01 g) were weighed in aggregate according to taxonomic group.

Data Analysis

Striped Bass Size and Stomach Fullness

We used analysis of variance (ANOVA) to test for differences in fish size and stomach fullness across seasons and habitats. If we found significant differences across habitat based on the ANOVA, we used Tukey's Honestly Significant Difference (HSD) test to identify pairwise differences among habitats. For pairwise tests, we adjusted baseline significance thresholds of 0.05 using a Bonferroni correction to account for multiple tests and family-wise error rate. We calculated an index of stomach fullness as the ratio of food weight to body weight following Smyly (1952):

$$\text{Fullness index} = \frac{\text{Weight of stomach contents}}{\text{Weight of fish without stomach contents}} * 100$$

We used a Kruskall–Wallis chi-square to test whether the number of fish with empty stomachs varied across habitats within each season. We used R software for all statistical analyses (R Core Team 2020).

Sample Size and Taxonomic Resolution

We used prey diversity rarefaction curves (Figures A1 and A2 in Appendix A) to determine if we collected enough samples to accurately characterize the diets of fish for each season (Heck et al. 1975). This step was necessary to identify the level of taxonomic resolution at which we could analyze the data. A rarefaction curve for diets at the finest taxonomic level of resolution (typically genus or species) did not reach an asymptote (as defined by the slope of the last four samples in the species accumulation curve; slope = 0.102), indicating that sample sizes were insufficient to evaluate diets at the finest possible taxonomic resolution. A rarefaction curve of grouping prey items based on broader taxonomic relationships reached an asymptote (slope < 0.01), indicating that sample sizes were sufficient for further analysis based on these prey groupings, identified in Table 3.

Striped Bass Diet Differences and Composition Across Sizes, Habitats, and Seasons

Because Striped Bass diets are known to change across size (Moyle 2002), we conducted permutational multivariate analysis of variance (PERMANOVA; Anderson 2001) on counts of items within prey groupings to test for diet differences across "large" (> 250 mm SL) and "small" (< 250 mm SL) Striped Bass, with habitat (channel, shoal, marsh) and season (spring, summer) as blocking variables. Fish greater than 250 mm SL (large) represent the sub-adult life stage, and fish smaller than 250 mm represent the late juvenile life stage (Moyle 2002). If Striped Bass diets did not differ based on size class, we then consolidated both size classes for all other habitat/season combinations. We used pairwise PERMANOVA to test for differences in diet composition across all three habitats, with season as a blocking variable. Data were permutated 999 times to determine the p-value based on Bray–Curtis distance dissimilarities using log(x+1)-transformed prey category count data. We performed all PERMANOVA analyses using the 'vegan' package (Oksanen et al. 2019) for R software (R Core Team 2020). We adjusted baseline significance thresholds of 0.05 using a Bonferroni correction to account for multiple tests and family-wise error rate.

To identify Striped Bass diet composition across habitats and seasons, we calculated the percent Prey-Specific Index of Relative Importance (% PSIRI; Brown et al. 2012):

$$\%PSIRI = \frac{\%FO_i \times (\%PN_i + \%PW_i}{2}$$

where $\%FO$ equals the frequency of occurrence in fish stomachs of prey species i; and $\%PN_i$ and $\%PW_i$ are the percent prey-specific abundances by number and weight, respectively. The percent prey-specific abundances are the average percent abundance of prey category i by number ($\%PN_i$) or weight ($\%PW_i$). The $\%PSIRI$ is preferable over the conventional IRI because (1) it does not over-emphasize abundant prey items; and (2), it is additive over taxonomic levels (Brown et al. 2012). Therefore, the $\%PSIRI$ of a prey category will be equivalent to the sum of the $\%PSIRI$ of the species within that category.

Striped Bass Capture vs. Foraging Habitat

We used linear discriminant analysis (LDA) to classify individual Striped Bass collection locations based on counts of prey within prey categories. With this analysis, we classified collection location for a subset of individuals based on their collection location and diets, and then predicted collection location for the remainder based on their diets. Misclassifications (e.g., a fish caught in the marsh but predicted to have been caught elsewhere based on its diet) identify the potential for fish collected in each habitat to have foraged elsewhere. We used 75% of the available diet data in each season to generate a linear discriminant model using the package

'MASS' for R software (Ripley et al. 2020). We then used this model to classify habitat for the remaining 25% of the available data. We repeated this procedure for 1000 bootstrapped data sets, and summarized comparisons between predicted and actual habitat classifications.

DATA AVAILABILITY

Data collected in support of this study can be accessed from Steinke et al. (2019; *https://doi.org/10.5066/P9YGG46K*).

RESULTS

Fish Size and Stomach Fullness

We collected 269 Striped Bass across both seasons (spring and summer). Of those, 235 individual fish had diet items in their stomachs, and 34 individuals had empty stomachs (Table 1). The marsh yielded the greatest number of individuals during both spring and summer; the channel yielded the least. Striped Bass ranged in size from 63 to 671 mm standard length (SL), corresponding to estimated ages of 1–5 y (Moyle 2002). Fish sizes differed across sampled habitats in both seasons (ANOVA, spring – $F_{2,\,115} = 11.01$, $p < 0.001$; summer – $F_{2,\,113} = 7.16$, $p = 0.001$). A post-hoc Tukey HSD test for the spring showed that fish captured from the shoal were significantly shorter than fish captured from the channel and marsh habitats ($p = 0.007$ and $p < 0.001$, respectively), while the length of fish captured from the marsh and channel were not significantly different from each other ($p = 0.99$). In summer, fish captured from the shoal were significantly smaller than fish captured from the marsh habitat ($p < 0.001$), but we found no other statistically significant differences across habitats (channel-shoal $p = 0.07$; marsh-channel $p = 0.85$). Notably, although the difference in Striped Bass size between channel and shoal in summer was not significant at a 0.05 threshold, it was close, suggesting that channel fish were still larger than shoal fish. No fish were recaptured during this study.

The incidence of empty stomachs observed in the spring ($n = 23$; 19.5%) was double the frequency of empty stomachs observed in the summer ($n = 11$; 9.5%, Table 2). However, based on Kruskal–Wallis chi-square analysis, season had no statistically significant association with empty stomachs (although it was *nearly* significant, $p = 0.06$), nor did habitat during either the spring ($p = 0.47$) or summer ($p = 0.88$) seasons. Seasonally, fish captured during the summer had stomach fullness values higher than fish collected during the spring ($F_{1,257} = 21.21$, $p < 0.001$; Table 1). In spring, stomach fullness was significantly lower in the channel than in the other two habitats ($F_{3,134} = 4.29$, $p = 0.006$), but there were no significant differences across habitats in the summer.

Striped Bass Diet Differences and Composition Across Habitats and Seasons

A total of 9,989 prey items representing 46 prey taxa were identified from 235 Striped Bass stomach samples (Table 3). Diets were diverse but largely dominated by invertebrates. The sphaeromatid isopod *Gnorimosphaeroma oregonensis* and the corophiid amphipod *Americorophium spinicorne* were the most dominant diet items by count. Striped Bass diets only differed by fish size class (small, large) in the marsh in spring (Pseudo-$F_{1,63} = p < 0.001$; Table 2). Fish size classes were therefore separated for the marsh in spring and consolidated for all other season–habitat combinations. Abundance of dominant prey categories relative to fish size can be found in Appendix A (Figure A3).

There were significant diet differences across habitats in both spring (Pseudo-$F_{2,110} = 3.15$, $p = 0.002$) and summer (Pseudo-$F_{2,107} = 23.12$, $p = 0.001$). Although pairwise PERMANOVA tests resulted in p values below 0.05 in spring (Table 2), results were not significant after correction for multiple tests, suggesting weak diet differences. Pairwise PERMANOVA tests indicated diet differences across summer habitats, with the marsh significantly different from the channel (Pseudo-$F_{1,84} = 14.01$, $p = 0.001$) and the shoal (Pseudo-$F_{1,96} = 40.77$, $p = 0.001$); the channel and shoal were not statistically different from each other.

Table 1 Number of individual Striped Bass collected, number of Striped Bass with empty stomachs, number of Striped Bass in small (< 250 mm) and large (> 250 mm) size categories, fish standard length (mean ± standard deviation, minimum, maximum), weight (mean ± standard deviation, minimum, maximum), and stomach fullness index

Season	Spring			Summer		
Habitat	Channel	Shoal	Marsh	Channel	Shoal	Marsh
n Striped Bass	21	45	76	16	27	84
n empty	5	8	10	1	2	8
n </≥ 250 mm SL	6/9	29/4	38/27	8/5	21/4	28/44
SL (mm)	279 ± 13 (193, 421)	207 ± 10 (63, 352)	282 ± 10 (107, 671)	265 ± 13 (189, 373)	211 ± 8 (139, 292)	269 ± 9 (136, 512)
Wt (g)	421 ± 53 (140, 1120)	213 ± 29 (5, 810)	503 ± 68 (22, 4500)	384 ± 57 (197, 905)	194 ± 20 (54, 475)	418 ± 41 (47, 2120)
Stomach Fullness Index	0.26 ± 0.2	0.83 ± 0.2	0.83 ± 0.2	1.53 ± 0.5	2.52 ± 0.5	2.17 ± 0.4

Table 2 PERMANOVA results (*p*-values) for Striped Bass diet comparisons across size classes (denoted with "L" for large and "S" for small) within habitat and season, and pairwise habitat comparisons within a season. *Underlined* values denote *p* values less than 0.05, while *bold and underlined* denote statistical significance after correcting for multiple tests.

Test	Habitat	Spring	Summer
Size	Channel	0.962	0.748
	Shoal	0.164	0.829
	Marsh	**0.001**	0.159
Habitat Comparison	Channel - Shoal	0.071	0.141
	Channel - Marsh (L)	0.060	**0.001**
	Channel - Marsh (S)	0.033	
	Marsh (L) -Shoal	0.251	**0.001**
	Marsh (S) -Shoal	0.062	

Seasonal variation in diet composition was indicated by the PSIRI (Table 4, Figure 2). Crustaceans (primarily amphipods and isopods) dominated spring diets in all habitats, comprising greater than 60% PSIRI in each. Fish were the only other prey category that contributed more than 10% PSIRI in spring. Spring diet differences across habitat were largely driven by changes in the crustaceans consumed; sphaeromatid isopods had higher % PSIRI in the marsh, and decapods and mollusks had higher % PSIRI in the channel. In the spring, large Striped Bass in the marsh consumed more fish than in other habitats. The contents of summer diets were also dominated by crustaceans in the shoal and marsh (80% and 57% PSIRI, respectively), but decapods, mysid shrimp, and fish were more important in the channel and in summer generally. Idoteid isopods dominated shoal diets; sphaeromatid isopods were abundant in marsh diets. Although never contributing more than 10% PSIRI, other diet groups (insects, mollusks, worms, and other) were occasionally found in more than 10% of stomachs (Table 4).

In total, 89 individual fish were collected from stomach samples, that represented 14 identifiable fish categories (either species or families; Table 3). Gobies (Gobiidae) and Prickly Sculpin (*Cottus asper*) accounted for 35% of the individual fish found in diets and were collected from all three habitats. The marsh-inhabiting Tule Perch (*Hysterocarpus traskii*) was solely found in diets collected from the marsh (5% of sampled stomachs), and Threespine Stickleback (*Gasterosteus aculeatus*) were found in diets from the channel (3%) and the marsh (4%). The remaining fish species were less important for Striped Bass diets from any habitat, occurring in five or fewer stomachs in total; however, 21% of the fish diet items could not be positively identified as a result of extensive digestion.

Striped Bass Capture vs. Foraging Habitat

In spring, LDA models correctly classified habitat based on diet 40% of the time (Appendix A; Tables A1 and A2). The LDA model correctly classified the habitat of small Striped Bass

Table 3 Total count of all prey taxa collected from Striped Bass stomachs and their frequency of occurrence in each habitat and season. Categories below Decapods are organized by total prey count.

				Spring			Summer	
Prey category	**Prey taxa**	**Count**	**Channel**	**Shoal**	**Marsh**	**Channel**	**Shoal**	**Marsh**
Fish	Gobiidae	16	6.3%	2.8%	9.1%	6.7%	0.0%	5.3%
Fish	Prickly Sculpin *Cottus asper*	15	0.0%	5.6%	9.1%	0.0%	4.0%	3.9%
Fish	Threespine stickleback *Gasterosteus aculeatus*	8	0.0%	0.0%	3.0%	6.7%	0.0%	3.9%
Fish	Tule Perch *Hysterocarpus traskii*	7	0.0%	0.0%	1.5%	0.0%	0.0%	7.9%
Fish	Mississippi Silverside *Menidia audens*	5	6.3%	0.0%	0.0%	6.7%	0.0%	3.9%
Fish	River Lamprey *Lampetra ayresi*	4	12.5%	2.8%	0.0%	0.0%	0.0%	0.0%
Fish	Sacramento Splittail *Pogonichthys macrolepidotus*	4	0.0%	0.0%	0.0%	0.0%	0.0%	3.9%
Fish	Common Carp *Cyprinus carpio*	2	0.0%	0.0%	0.0%	0.0%	0.0%	2.6%
Fish	Striped Bass *Morone saxatilis*	2	0.0%	2.8%	0.0%	0.0%	0.0%	1.3%
Fish	Centrarchidae	2	0.0%	2.8%	1.5%	0.0%	0.0%	0.0%
Fish	Cyprinidae	2	0.0%	0.0%	1.5%	0.0%	0.0%	1.3%
Fish	American Shad *Alosa sapidissima*	1	0.0%	0.0%	0.0%	6.7%	0.0%	0.0%
Fish	Chinook Salmon *Oncorhynchus tshawytscha*	1	0.0%	0.0%	1.5%	0.0%	0.0%	0.0%
Fish	Sacramento Blackfish *Orthododon microlepidotus*	1	0.0%	0.0%	0.0%	0.0%	0.0%	1.3%
Fish	Unid. Fish	19	6.3%	11.1%	9.1%	13.3%	8.0%	5.3%
Decapods	*Crangon franciscorum*	176	12.5%	16.7%	10.6%	53.3%	96.0%	13.2%
Decapods	*Palaemon macrodactylus*	2	0.0%	0.0%	0.0%	0.0%	0.0%	1.3%
Decapods	*Palaemon modestus*	1	0.0%	0.0%	0.0%	0.0%	0.0%	1.3%
Decapods	Unid. Decapoda	3	0.0%	0.0%	1.5%	0.0%	4.0%	0.0%
Sphaeromatidae	*Gnorimosphaeroma oregonensis*	5547	12.5%	16.7%	53.0%	6.7%	12.0%	67.1%
Sphaeromatidae	Unid. Sphaeromatidae	219	0.0%	8.3%	7.6%	6.7%	4.0%	14.5%
Gammaroidea	*Gammarus daiberi*	923	56.3%	47.2%	50.0%	6.7%	24.0%	23.7%
Gammaroidea	*Grandidierella japonica*	49	0.0%	22.2%	12.1%	0.0%	0.0%	1.3%
Gammaroidea	Unid. Gammaroidea	683	6.3%	41.7%	28.8%	20.0%	32.0%	34.2%
Corophiidae	*Americorophium spinicorne*	1227	18.8%	47.2%	62.1%	13.3%	8.0%	61.8%
Corophiidae	*Americorophium stimpsoni*	42	6.3%	11.1%	15.2%	0.0%	0.0%	0.0%
Corophiidae	Unid. Corophium	60	0.0%	16.7%	9.1%	0.0%	0.0%	1.3%
Mysidacea	Mysidacea	440	0.0%	8.3%	3.0%	33.3%	12.0%	3.9%
Idoteidae	Synidotea sp.	401	0.0%	16.7%	10.6%	53.3%	76.0%	5.3%
Idoteidae	Idotea sp.	2	0.0%	0.0%	1.5%	6.7%	0.0%	0.0%
Insects	Corixidae	30	0.0%	0.0%	3.0%	0.0%	0.0%	15.8%
Insects	Diptera	6	0.0%	8.3%	4.5%	0.0%	0.0%	0.0%
Insects	Odonata	5	0.0%	0.0%	6.1%	0.0%	0.0%	1.3%
Insects	Lepidoptera	2	0.0%	0.0%	0.0%	0.0%	0.0%	1.3%
Insects	Coleoptera	1	0.0%	0.0%	0.0%	0.0%	0.0%	1.3%
Insects	Ephemeroptera	1	0.0%	0.0%	0.0%	0.0%	0.0%	1.3%
Worms & Other	Nematoda	13	0.0%	2.8%	1.5%	6.7%	0.0%	5.3%
Worms & Other	Polychaete	13	6.3%	5.6%	6.1%	0.0%	0.0%	7.9%
Worms & Other	Cestoda	4	0.0%	2.8%	0.0%	0.0%	0.0%	3.9%
Worms & Other	Unid. Egg	2	0.0%	0.0%	1.5%	0.0%	0.0%	1.3%
Worms & Other	Hirudinea	1	0.0%	0.0%	1.5%	0.0%	0.0%	0.0%
Molluscs	Gastropoda	18	0.0%	2.8%	0.0%	0.0%	0.0%	9.2%
Molluscs	*Potamocorbula amurensis*	8	12.5%	8.3%	0.0%	6.7%	4.0%	0.0%
Molluscs	*Corbicula fluminea*	2	6.3%	0.0%	1.5%	0.0%	0.0%	0.0%
Other Crustacea	*Nippoleucon hinumensis*	19	0.0%	5.6%	0.0%	0.0%	0.0%	0.0%
Detritus	Detritus	7	6.3%	0.0%	1.5%	0.0%	0.0%	2.6%

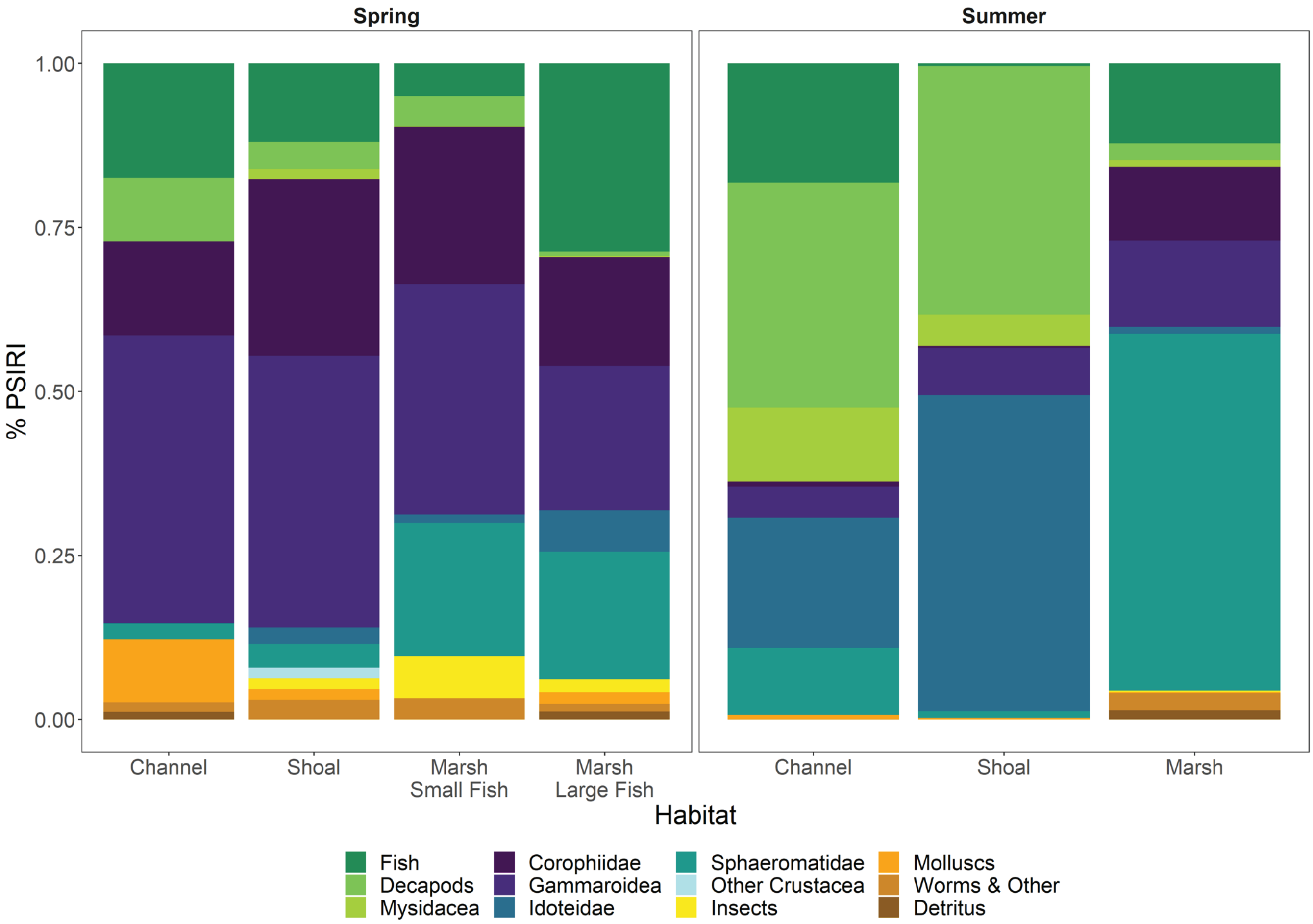

Figure 2 Percentages of major diet item groups of Striped Bass by season, habitat, and size class, expressed as percent prey-specific index of relative importance (% PSIRI)

from the marsh most frequently (58%); fish from the shoal were classified correctly only 31% of the time and were often misclassified as marsh (~60%). Fish from the channel were rarely classified correctly (7%) and instead were classified as shoal (55%) or marsh (38%). In summer, LDA models were more in agreement with known capture locations (~79%), with 97% accuracy for marsh fish. Fish from the shoal were classified correctly 51% of the time; channel fish were only classified correctly 18% of the time. Marsh classification was largely correct, with a distinct marsh diet profile suggesting that fish collected from the channel or shoal classified as marsh fish foraged in the marsh. Striped Bass collected in the channel were often classified as shoal or marsh in both seasons, and Striped Bass diets reflect marsh foraging in summer more than expected from capture location (Figure 3).

DISCUSSION

Striped Bass consume a wide variety of prey items throughout the estuary and its broader range (Grossman 2016). This study demonstrated that Striped Bass diets were measurably different across seasons and dominant habitat types in the north-central stuary, with demersal fish and macroinvertebrates largely dominating diets across all samples. High importance of demersal prey is generally consistent with contemporary studies of Striped Bass diets in the estuary and other regions (Zeug et al. 2017; Colombano et al. 2021), although that differs from historical Striped Bass diets in the estuary (Stevens 1966;

Table 4 Metrics summarizing diets of Striped Bass. All values are expressed as percentages (percent prey-specific index of relative importance (% PSIRI), total percent count, and total percent weight). Note, counts and weights are across the entire dataset of non-empty stomachs, and not the values used for calculation of % PSIRI (see "Materials and Methods").

				Diet Group											
					Crustacea										
							Amphipoda		Isopoda						
Metric	**Season**	**Habitat**	**Fish Size**	**Fish**	**Decapods**	**Mysidacea**	**Corophiidae**	**Gammaroidea**	**Idoteidae**	**Sphaeromatidae**	**Other Crustacea**	**Insects**	**Molluscs**	**Worms & Other**	**Detritus**
% PSIRI	Spring	Channel	All	17.4	9.7	0.0	14.3	43.9	0.0	2.5	0.0	0.0	9.5	1.5	1.1
		Shoal	All	12.0	4.1	1.6	26.9	41.4	2.5	3.7	1.5	1.7	1.6	3.0	0.0
		Marsh	Small	5.0	4.7	0.0	24.0	35.2	1.2	20.3	0.0	6.5	0.0	3.2	0.0
			Large	28.7	0.7	0.1	16.7	21.9	6.4	19.4	0.0	2.0	1.8	1.2	1.2
	Summer	Channel	All	18.2	34.3	11.3	0.8	4.8	19.8	10.2	0.0	0.0	0.7	0.0	0.0
		Shoal	All	0.4	37.8	4.9	0.2	7.2	48.2	1.0	0.0	0.0	0.2	0.0	0.0
		Marsh	All	12.2	2.6	1.0	11.3	13.2	1.1	54.4	0.0	0.2	0.1	2.7	1.4
Frequency of Occurrence (%)	Spring	Channel	All	25.0	12.5	0.0	25.0	62.5	0.0	12.5	0.0	0.0	18.8	6.3	6.3
		Shoal	All	25.0	16.7	8.3	61.1	72.2	16.7	25.0	5.6	8.3	11.1	11.1	0.0
		Marsh	Small	18.4	15.8	2.6	81.6	81.6	10.5	57.9	0.0	13.2	0.0	10.5	0.0
			Large	57.1	3.6	3.6	60.7	57.1	14.3	57.1	0.0	7.1	3.6	7.1	3.6
	Summer	Channel	All	40.0	46.7	33.3	13.3	26.7	53.3	13.3	0.0	0.0	6.7	6.7	0.0
		Shoal	All	12.0	80.0	12.0	8.0	48.0	76.0	16.0	0.0	0.0	4.0	0.0	0.0
		Marsh	All	34.2	14.5	3.9	61.8	53.9	5.3	80.3	0.0	19.7	9.2	14.5	2.6
Count (%)	Spring	Channel	All	40.2	66.7	0.0	63.9	76.0	0.0	30.6	0.0	0.0	48.1	11.1	33.3
		Shoal	All	34.0	15.5	17.8	41.8	37.6	10.7	13.5	47.9	26.0	7.4	22.7	0.0
		Marsh	Small	15.9	17.9	3.0	32.0	30.7	13.2	31.8	0.0	25.9	0.0	18.0	0.0
			Large	28.5	11.1	4.0	35.9	38.6	36.5	35.3	0.0	27.2	33.3	18.8	50.0
	Summer	Channel	All	44.3	57.5	46.3	11.7	18.3	29.6	82.4	0.0	0.0	14.3	0.4	0.0
		Shoal	All	5.6	36.2	46.7	5.9	18.5	59.0	9.4	0.0	0.0	9.1	0.0	0.0
		Marsh	All	12.5	12.8	37.1	23.3	26.6	15.1	69.0	0.0	1.7	2.6	15.2	19.6
Weight (%)	Spring	Channel	All	71.5	88.0	0.0	50.9	64.4	0.0	9.4	0.0	0.0	53.5	36.7	2.9
		Shoal	All	52.3	33.4	20.8	30.0	36.9	19.4	15.9	7.7	15.2	21.8	31.0	0.0
		Marsh	Small	38.1	32.6	0.4	17.2	33.0	10.2	32.3	0.0	44.2	0.0	31.3	0.0
			Large	66.0	25.6	4.1	10.7	29.6	52.6	32.6	0.0	28.9	67.1	14.3	16.7
	Summer	Channel	All	46.6	70.9	21.6	0.2	17.3	36.4	71.1	0.0	0.0	5.3	0.1	0.0
		Shoal	All	1.1	39.5	34.3	0.4	7.4	67.8	2.9	0.0	0.0	3.2	0.0	0.0
		Marsh	All	47.3	20.1	11.7	12.4	17.9	25.0	64.3	0.0	0.5	0.5	13.7	83.3

Thomas 1967; Feyrer et al. 2003) when pelagic fish and invertebrates were more abundant. This likely reflects changing conditions in the estuary, whereby common pelagic prey (e.g., clupeids, osmerids, mysid shrimp) have declined considerably over the last half century (Sommer et al. 2007; Feyrer et al. 2015; Zeug et al. 2017). This shift away from pelagic prey is not unprecedented, as similar trends have been observed within Striped Bass's native range (Pruell et al. 2003; Walter et al. 2003), although the proportion of pelagic prey fluctuates seasonally. The prey variability observed in this study, coupled with shifts in dominant prey types over

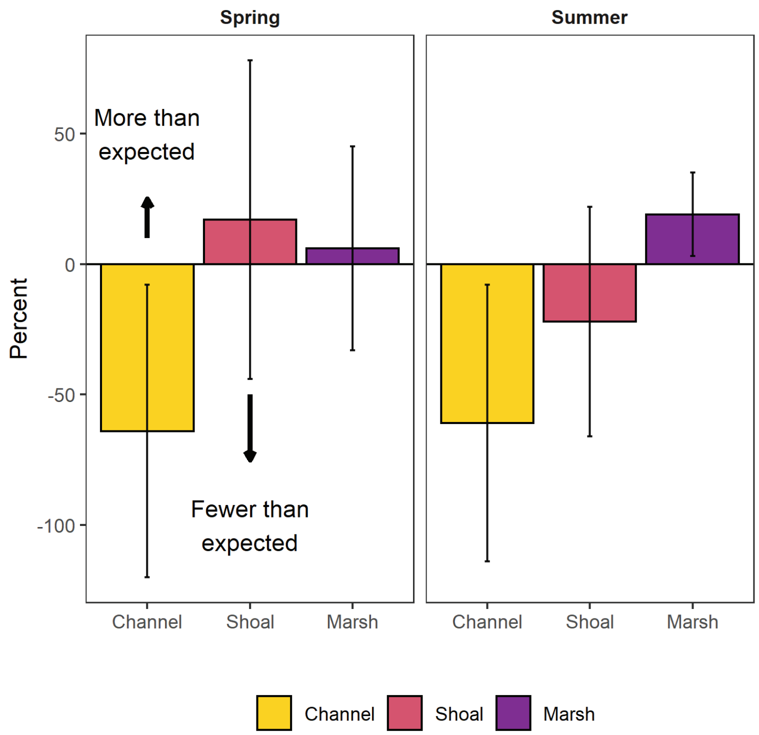

Figure 3 Percent difference between the model-classified number of individuals from a habitat and the number of individuals collected from that habitat. *Error bars* represent standard deviation in predictions from bootstrapped Linear Discriminant Analysis results. Values above zero indicate fish were classified as a habitat more frequently than expected given known capture locations, and values below zero indicate fish were classified as a habitat less frequently than expected.

time in the estuary, indicate that Striped Bass are an adaptable and opportunistic predator able to adjust to changing environmental conditions and prey availability.

Seasonal and Habitat Variability

Seasonal variability in consumption of benthic prey differs regionally, with invertebrate consumption elevated in winter and spring in the coastal mid-Atlantic Ocean (Manooch 1973; Overton et al. 2008) and summer in coastal New England (Ferry and Mather 2012). In this study, total invertebrate consumption was generally consistent across seasons, and variability was instead associated with specific invertebrate categories. Spring diets were largely dominated by mesohaline invertebrates (e.g., corophiid and gammaroid amphipods), which are typically associated with brackish and freshwater habitats in the estuary (Young et al. 2018; Hartman et al. 2019). Summer diets were dominated by more polyhaline taxa, including the California bay shrimp (*Crangon franciscorum*) and idoteid isopods (Gewant and Bollens 2005; Howe et al. 2014). Sphaeromatid isopods were most consumed in the marsh in both seasons. Observed invertebrate taxa in Striped Bass diets were consistent with other local diet studies in tidal marsh habitats (Howe et al. 2014, Colombano et al. 2021). Other than isopods, diets were relatively similar across habitats within spring, although PERMANOVA test results were near significance (-values ranging from 0.06 to 0.07), suggesting weak structure in diets associated with habitat. Summer diets had much stronger differences across habitats, with decapod consumption relatively high in channel and shoal habitats, and the marsh still driven largely by sphaeromatid isopods. Idoteid isopods were abundant in summer shoal diets but not in other habitat/season combinations.

Hydrology is a prominent driver of seasonal conditions in this region of the estuary, including fish and invertebrate communities (Moyle et al. 2010; Feyrer et al. 2015, and others). During this study, we observed riverine outflow reducing salinity to near freshwater (~0.2 PSU) in spring, with higher salinity in summer. This salinity variability is consistent with the abundance of largely freshwater and oligohaline invertebrates in spring diets, and more meso- and polyhaline invertebrates in summer diets. Resident fish prey species from this study are largely tolerant of a wide range of salinities and exhibited less

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seasonal variability. It is possible that Striped Bass diets and habitat-specific foraging will differ in droughts (observed in this study) compared with wet years; however, the low summer–fall freshwater outflow common in California's Mediterranean climate means findings from this study are likely applicable for at least part of the year under all hydrologic conditions.

Fish were only the most important diet item for large Striped Bass in the marsh in spring, and not any other habitat/season combination, consistent with Zeug et al. (2017). The dominant fish diet items were littoral or benthic fish species of least concern, with few pelagic or special status-fishes observed in diets. The natives Prickly Sculpin and Tule Perch were consumed more frequently in the marsh, and the only special-status fish identified (Chinook Salmon, *Oncorhynchus tshawytscha*, run unknown) occurred in a stomach from a fish collected in the marsh. The dominant fish prey items (Gobiidae, Prickly Sculpin, Threespine Stickleback) are locally abundant but generally poorly sampled by existing surveys and studies, including an extensive sampling of the fish community in and around Ryer Island (Feyrer et al. 2021). This makes it difficult to assess relative abundance of prey items in the environment; however, the relative abundance of gobies and sculpins matches what is known from nearby Suisun Marsh (Young et al. 2017; O'Rear et al. 2021).

Many of the fish diet items (21%) could not be positively identified because of extensive digestion. It is possible that special-status fish comprised a greater proportion of fish diet items but could not be identified, but the opportunistic nature of Striped Bass coupled with low abundance of special-status species makes this interpretation unlikely (Nobriga et al. 2013). This possibility could be further addressed by using genetic analysis by using genetic analysis of stomach contents to improve identification of digested fish (Brandl et al. 2015; Schreier et al. 2016; Michel et al. 2018; Stompe et al. 2020). It should be noted that this study focused on relatively small individuals, and main prey that support very large adult Striped Bass (age-5 +) in the estuary are unknown and require further study.

We observed a relatively low proportion of Striped Bass containing no identifiable contents (13%). This is lower than the proportion of empty stomachs found during a previous diet study encompassing the same geographic area (25%; Zeug et al. 2017). Stomach fullness was relatively consistent across habitats, with fullness only low in the channel in spring, indicating the importance of sampled habitats for Striped Bass foraging. Many plausible explanations for variability in stomach fullness and empty stomachs across seasons (generally lower in spring) exist. For example, in spring captured Striped Bass may have been migrating (Sabal et al. 2019), with associated energetic demands, potential reductions in foraging, and more empty stomachs. Another explanation might be that the invertebrates consumed in spring are typically smaller-bodied than those consumed in summer and may have been digested more quickly despite the lower temperatures. Regardless, the relatively low proportion of empty stomachs indicates the value of either this region (Ryer Island) or sampled habitats to Striped Bass foraging. Notably, invertebrate prey that dominate observed Striped Bass diets (based on PSIRI) are lower in caloric content than other principal dietary components of Striped Bass (Loboschefsky et al. 2012), although evaluation of this on fish health and/or condition was not part of this study.

Habitat-Specific Foraging

The association of certain "indicator" invertebrate taxa with particular habitat/season combinations provides some confidence in the relationship between an individual Striped Bass's capture and forage habitats. For example, idoteid isopods were overwhelmingly associated with shoal diets in the summer; it is therefore likely that fish captured in the marsh or channel with high consumption of idoteids may have foraged in the shoal. Similarly, a preponderance of sphaeromatid isopods indicated marsh foraging. This logic contextualizes the summer discriminant analysis results and suggests that many fish captured in the channel were foraging on the shoal or in the marsh. Associations of individual indicator taxa were less clear in the spring; although, based on misclassifications and on sphaeromatid abundance in some diets, it appears possible that at least some fish captured in the shoal and/or channel may have foraged in the marsh. Collectively, these results indicate that Striped Bass forage in shallow-water habitats—both shoal and marsh—in higher frequency than expected from capture location, with significant relevance to habitat management and restoration. This type of habitat-specific foraging is well-documented in Striped Bass (Harding and Mann 2003), because tidal marsh productivity is disproportionately important to Striped Bass in coastal New England (Baker et al. 2016).

Context and Implications

It is important to consider the historical context for habitat-specific foraging by Striped Bass in the estuary, and implications for future restoration. When Striped Bass were introduced to the estuary, the landscape was dominated by tidal marsh habitats (Whipple et al. 2012), which supported a large component of estuary productivity (Cloern et al. 2016, 2021), presumably including Striped Bass. The value of tidal marshes to Striped Bass likely declined as marshes were destroyed in reclamation and levee construction, although remnant marsh habitats still support local consumption (Howe et al. 2014; Schroeter et al. 2015; Young et al. 2021; Colombano et al. 2021). As large-scale habitat restoration proceeds in the future, Striped Bass will likely use restored tidal marshes, potentially in unexpected ways. Findings from this study are particularly relevant to habitat restoration between the confluence of the Sacramento and San Joaquin rivers, and Carquinez Strait. This region is typified by high salinity variability, similar prey community, and is an area of much planned and ongoing habitat restoration.

Although most native prey fish species in this study are locally common, negative effects from Striped Bass on at-risk populations are still possible (Nobriga and Smith 2020). However, it is difficult to predict predator–prey dynamics within these new habitats, based on the limited scope of this and other studies of estuary non-native predators (Grossman 2016; Michel et al. 2018; Wienersmith et al. 2019; Colombano et al. 2021). Any concern over potential effects of Striped Bass in restored tidal habitat needs to be tempered by the recognition that habitat restoration will likely provide a net benefit to native fishes even with increased predation (e.g., through expanded refugia, increased food availability). Striped Bass likely utilized tidal marshes in the historical estuary, they do so in the contemporary estuary, and they are likely to continue to do so as habitat is restored. Further research is needed to understand the dynamics within this changing seascape. Current long-term monitoring programs are not designed to target all prey taxa important to Striped Bass, particularly epibenthic invertebrates (amphipods and isopods) and demersal fishes (gobies and sculpin). These additional data would be a first step in identifying seasonal and spatial effects on macroinvertebrates, littoral fishes, predator–prey dynamics, and how non-native predators will utilize restored tidal marshes and other habitats.

ACKNOWLEDGMENTS

Funding was provided by the U.S. Bureau of Reclamation (Interagency Agreement # R15PG00085). Thanks to the field crews for working under inclement conditions, including David Ayers, Ethan Clark, Justin Clause, Ethan Enos, Mary Jade Farruggia, Brian Gold, Emerson Gusto, Craig Haskell, Jessie Kathan, Veronica Larwood, Oliver Patton, and Matt Sholtis. Special thanks to Christopher Vallee for superb skippering. Comments and feedback from Mark Inc, Ted Sommer, and three anonymous reviewers greatly improved this manuscript. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

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