Title:

Shallow-Water Piscivore-Prey Dynamics in California's Sacramento-San Joaquin Delta

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Predation is one mechanism that could lead to low native fish abundance in macrophyte dominated shallow-water habitats in the Sacramento-San Joaquin Delta. We used beach seine and gill net sampling to identify and compare the distribution and feeding ecology of three piscivores (striped bass, *Morone saxatilis*, largemouth bass, *Micropterus salmoides*, and Sacramento pikeminnow, *Ptychocheilus grandis*) at five nearshore sites in the Sacramento-San Joaquin Delta. Sampling was conducted March-October 2001 and 2003. We addressed the following questions. What are the spatial and temporal distributions of age-1 and older striped bass, largemouth bass, and Sacramento pikeminnow? What prey are eaten by these predators? What is the relative importance of predator size versus seasonal prey availability on incidence of piscivory for these predators? What is the likely per capita impact of each piscivore on prey fishes, particularly native fishes? All 76 of our individual station visits yielded at least one of the three species, suggesting that piscivorous fishes frequently occur in Delta shallow-water habitats. All three piscivores had diverse diets. There were noticeable seasonal shifts in prey fish for each of the three piscivores. In general, most native fish were consumed during spring (March-May) and the highest prey species richness occurred during summer (June-August). Largemouth bass likely have the highest per capita impact on nearshore fishes, including native fishes. Largemouth bass preyed on a greater diversity of native fishes than the other two piscivores and consumed native fishes farther into the season (July versus May). Based on binomial generalized additive models, incidence of piscivory was predominantly a function of size for largemouth bass and

Sacramento pikeminnow. Largemouth bass became predominantly piscivorous at smaller sizes than Sacramento pikeminnow; about 115 mm versus about 190 mm respectively. In contrast, incidence of piscivory was predominantly a function of season for striped bass. Striped bass were typically most piscivorous during summer and fall regardless of size. We conclude that shallow-water piscivores are widespread in the Delta and generally respond in a density-dependent manner to seasonal changes in prey availability.

Nobriga and Feyrer: Shallow-Water Piscivore-Prey Dynamics in California's Sacramento-San J...

MAY 2007

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ABSTRACT

Predation is one mechanism that could lead to low native fish abundance in macrophyte dominated shallow-water habitats in the Sacramento-San Joaquin Delta. We used beach seine and gill net sampling to identify and compare the distribution and feeding ecology of three piscivores (striped bass, *Morone saxatilis*, largemouth bass, *Micropterus salmoides*, and Sacramento pikeminnow, *Ptychocheilus grandis*) at five nearshore sites in the Sacramento-San Joaquin Delta. Sampling was conducted March-October 2001 and 2003. We addressed the following questions. What are the spatial and temporal distributions of age-1 and older striped bass, largemouth bass, and Sacramento pikeminnow? What prey are eaten by these predators? What is the relative importance of predator size versus seasonal prey availability on incidence of piscivory for these predators? What is the likely per capita impact of each piscivore on prey fishes, particularly native fishes? All 76 of our individual station visits yielded at least one of the three species, suggesting that piscivorous fishes frequently occur in Delta shallow-water habitats. All three piscivores had diverse diets comprised of numerous invertebrate and fish taxa. There were noticeable seasonal shifts in prey fish for each of the three piscivores. In general, most native fish were consumed during spring (March-May) and the highest prey species richness occurred during summer (June-August). Largemouth bass likely have the highest per capita impact on nearshore fishes, including native fishes. Largemouth bass preyed on a greater diversity of native fishes than the other two piscivores and consumed native fishes farther into the season (July versus May). Based on binomial generalized additive models, incidence of piscivory was predominantly a function of size for largemouth bass and Sacramento pikeminnow. Largemouth bass became predominantly piscivorous at smaller sizes than Sacramento pikeminnow; about 115 mm versus about 190 mm respectively. In contrast, incidence of piscivory was predominantly a function of season for striped bass. Striped bass were typically most piscivorous during summer and fall regardless of size. We conclude that shallow-water piscivores are widespread in the Delta and generally respond in a density-dependent manner to seasonal changes in prey availability.

SAN FRANCISCO ESTUARY & WATERSHED SCIENCE

KEYWORDS

SUGGESTED CITATION

INTRODUCTION

The relative effects of predation in tidal rivers and their estuaries are controlled by a complex interaction of factors that directly and indirectly influence prey encounter and capture probabilities. These probabilities can be highly species-specific, location-specific, and strongly influenced by ecosystem change. Piscivorous fishes typically pass through a series of well-described diet shifts as they grow (Mittelbach and Persson 1998) and as prey availability changes (Hartman and Margraf 1992; Buckel et al. 1999). At large spatial scales, piscivore-prey dynamics can be regulated by flow patterns (Meffe 1984) and turbidity (Rodríguez and Lewis 1994; Gregory and Levings 1998), both of which are often changed substantially by dam construction (de Merona et al. 2001; Osmundson et al. 2002; Quist et al. 2004). In tidal river estuaries, river flow affects the overlap of suitable water quality and suitable habitat structures (Manderson et al. 2002; Peterson 2003), which can influence piscivore-prey dynamics (Manderson et al. 1999) that ultimately influence fish nursery habitat quality and recruitment.

At smaller spatial scales, piscivore-prey interactions also can be affected by local habitat features (Werner et al. 1983; Greenberg et al. 1995). One important structural aspect of estuarine habitat is water depth. One of many functions that shallow estuarine habitats may serve is that of predation refuge for small fishes; in effect they may reduce predator encounter and capture probabilities. Paterson and Whitfield (2000) concluded the shallow marsh creek system in a South African estuary was a predation refuge for young fishes because large predatory species were rarely collected. McIvor and Odum (1988) found there were fewer attacks on tethered fish in depositional tidal creek habitats than in nearby deeper erosional habitats.

However, the hypothesis that shallow estuarine habitats can be generalized as predation refuges has been questioned (Sheaves 2001). First, not all small estuarine fishes are adapted to use shallow habitats like marsh creeks; many species or early life stages of species are pelagic and thus frequent the deeper habitats often used by large piscivores (Laprise and Dodson 1989; Hagan and Able 2003). These pelagic species/life stages may use turbidity, rather than water depth, as a form of cover from predators (Abrahams and Kattenfeld 1997; Utne-Palm 2002). Second, not all estuarine piscivores are large. Piscivore-prey dynamics typically are strongly size-structured (Reimchen 1990), and many juvenile predators (i.e., < 100 mm or so) can be both abundant and fairly piscivorous in estuarine shallows (Baker and Sheaves 2005). Small fishes recruiting to these nurseries may be readily preyed upon by small predators, so some shallow-water piscivores may have higher per capita impacts on shallow-water fishes than others. For instance, age-0 bluefish *Pomatomus saltatrix*, impart substantial predatory mortality on age-0 striped bass *Morone saxatilis*, in nearshore habitats of the U.S. Atlantic coast (Buckel et al. 1999).

The restoration of shallow-water habitats (SWH) has been considered an important ecosystem rehabilitation tool in California's San Francisco Estuary (Brown 2003). Because the Estuary has lost many of its historical marsh habitats to various reclamation activities, resource managers have expressed hope that SWH could contribute to increased production of declining native and sport fishes. Breaching levees of agricultural 'islands' in the Sacramento-San Joaquin Delta was conceived as a relatively inexpensive way to restore shallow areas to tidal inundation, However, subsequent studies of several breached-levee flooded islands showed they were variably productive (Lucas et al. 2002), structurally simple, and overwhelmingly colonized by Brazilian waterweed

Nobriga and Feyrer: Shallow-Water Piscivore-Prey Dynamics in California's Sacramento-San J...

MAY 2007

Egeria densa and other submerged macrophytes (Brown 2003). Macrophyte-dominated shorelines are primarily inhabited by non-native fishes adapted to use these littoral habitats (Feyrer and Healey 2003; Grimaldo et al. 2004; Nobriga et al. 2005). We recently hypothesized that the interaction of hydrologic regulation of the San Francisco Estuary watershed and local habitat features facilitated the proliferation of exotic macrophytes (Nobriga et al. 2005). The macrophytes influence fish community composition, possibly including the relative importance of biotic structuring mechanisms like competition and predation.
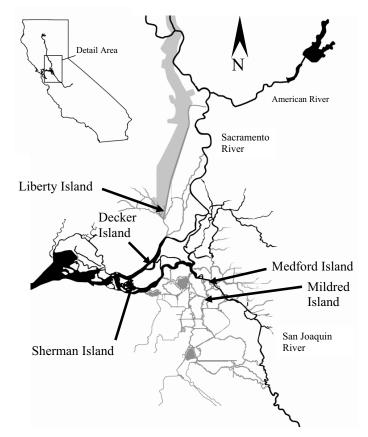
Here, we describe and compare the distribution and feeding ecology of three piscivores that frequent nearshore habitats in the Sacramento-San Joaquin Delta: striped bass, *Morone saxatilis*, largemouth bass, *Micropterus salmoides*, and Sacramento pikeminnow, *Ptychocheilus grandis*. There is considerable management interest in the feeding ecology of piscivorous fishes in the Delta. Elevated predation rates are considered a potential 'indirect effect' of water diversion operations (Brown et al. 1996) and a potential hinderance to shallow-water habitat restoration (Brown 2003). We addressed the following questions. What are the spatial and temporal distributions of age-1 and older striped bass, largemouth bass, and Sacramento pikeminnow? What prey are eaten by these predators? What is the relative importance of predator size versus seasonal prey availability on incidence of piscivory for these predators? For the latter two questions, we hypothesized that native fish prey use would peak during spring, and total incidence of piscivory would peak during summer. Our primary goal was to integrate empirical piscivore-prey data into emerging conceptual models of ecological processes operating in shallow habitats of the Sacramento-San Joaquin Delta (e.g., Brown 2003; Grimaldo et al. 2004; Nobriga et al. 2005). This is a necessary precursor to the development of quantitative predator-prey or ecosystem models, and the design and implementation of successful habitat restoration projects. We also sought to provide insight into the impacts of these piscivores on prey fishes, particularly native fishes.

METHODS

Study Area

The Sacramento-San Joaquin Delta is the landward edge of the San Francisco Estuary and a water supply nexus for much of California's population (Figure 1; Arthur et al. 1996; Kimmerer 2002). The Delta receives freshwater runoff from approximately 100,000 km$_2$ (40%) of California's surface area. Most natural runoff occurs during winter and spring (December-May), but significant proportions of natural runoff are captured in numerous reservoirs located throughout the watershed. Managed reservoir releases support regional agriculture and freshwater exports for agriculture and urban users in comparatively arid regions to the south

Figure 1. Map of the Sacramento-San Joaquin Delta showing locations of sampling sites. Primary river channels and embayments are depicted in black. The Yolo Bypass floodplain and Delta sloughs and flooded islands are depicted in gray.

and west. Primarily during the latter half of the nineteenth century and the first half of the twentieth century, the Sacramento-San Joaquin Delta was converted from a seasonally brackish marsh into a network of leveed channels conveying freshwater year-around; the Delta channels surround tracts of land drained to support agriculture (Nichols et al. 1986).

Species Background

Striped bass were introduced to San Francisco Estuary in 1879 (Dill and Cordone 1997). They thrived and supported a commercial fishery until 1935. They still support a recreational fishery despite a steady decline in juvenile production since the 1970s (Kimmerer et al. 2000). The striped bass is the San Francisco Estuary's most broadly distributed and abundant large piscivorous fish (Moyle 2002). Striped bass spawn in large, non-tidal tributaries to the Estuary. Its eggs and larvae are transported to the Estuary low-salinity zone by river currents. Age-1 and older striped bass occur throughout the Estuary and in adjacent freshwater and marine habitats.

Unlike striped bass, largemouth bass are primarily a freshwater fish that cannot successfully reproduce in brackish water (Moyle 2002). Largemouth bass also were introduced to the San Francisco Estuary watershed in the latter 19th Century (Dill and Cordone 1997), although their numbers in the Delta have increased only recently (Brown and Michniuk 2007). This increase was associated with increasing water clarity and submerged macrophyte abundance in the Delta. The increase in abundance has also been apparent based on fishing patterns; largemouth bass abundance has increased sufficiently to support a significant sport fishery (Lee 2000).

The native Sacramento pikeminnow is also a freshwater fish, most often associated with lotic habitats (Moyle 2002). Long-term trends in Sacramento pikeminnow abundance are unknown, but it is common in the Sacramento River basin (May and Brown 2002). Sacramento pikeminnow spawn in non-tidal streams and rivers; they often complete their life cycle within these habitats (Brown 1990). However, some age-1 and older individuals are transported into the Delta by winter-spring flow pulses and likely remain

resident until maturity (Nobriga et al. 2006). Sacramento pikeminnow is not targeted by a sport fishery in the Delta, although it has been harvested for bounty in the upper Sacramento River to reduce presumed predatory effects on emigrating salmonid fishes (Moyle 2002).

Field Methods

We sampled monthly for fishes at five sites using beach seines in wadable-depth habitats, and using gill nets in deeper habitats adjacent to the beach seine sites (Nobriga et al. 2005; Figure 1). The primary purpose of our sampling design was to capture potentially piscivorous fishes from a variety of nearshore habitats for stomach content analysis. Sampling occurred during two piscivore growing seasons, March-October of 2001 and 2003. Two sites (Decker Island and Medford Island) were low velocity areas at the edges of channels. The other sites (Sherman Island, Liberty Island and Mildred Island) were shallow habitats along the internal remnant levees of flooded islands, a local term for former agricultural tracts that were flooded and not reclaimed. We deployed a 30 m x 1.8 m, 3.2 mm mesh beach seine via small, shallow-draft boats. We conducted 2-8 beach seine hauls per site per month (mean = 4). One site was sampled per day, so five days were needed to complete each month's sampling. Samples were collected afternoon through dusk, usually during a flood tide. Water depth at initiation of seine hauls averaged about 1 m at all sites, but varied from 0.4-1.5 m in individual hauls. All fishes collected in the beach seine were identified to species, and subsets of abundant species were measured for total length (TL) or fork length (FL) to the nearest mm. We conducted 158 beach seine hauls in 2001 and 141 beach seine hauls in 2003.

Deeper water (2-4 m) adjacent to the beach seine sites was sampled using gill nets (60 m x 2.4 m; randomized panels of 51-102 mm stretch mesh). The gill nets were set parallel to shore for 20-40 minutes, 2-6 times per visit (mean = 0.9 hr sampled per visit). Gill net effort was concentrated around sunset to target actively foraging fishes moving toward or from the wadable habitats. All fishes collected in the gill net were identified to species and measured for TL or FL to the nearest mm.

We examined the stomach contents of age-1 and older striped bass (n = 570; 63-776 mm) and largemouth bass (n = 320; 58-569 mm), and the foregut contents of Sacramento pikeminnow (n = 282; 65-504 mm). For each species, up to ten individuals per gear per day were retained for stomach contents evaluation. Fishes were chosen haphazardly from the available size ranges. Whole fish up to 306 mm were preserved in the field in 10% formaldehyde. In the laboratory, these fish were re-measured and weighed to the nearest 0.01 g using an electronic balance. Their stomachs/foreguts were then removed and all contents were identified to the lowest practicable taxon and summarized as frequencies of occurrence. For fish larger than 306 mm, stomachs /foreguts were removed in the field and preserved as above. The field dissection of stomachs from fishes > 306 mm precluded laboratory weight measurements. However, the stomach /foregut contents of field-dissected stomachs also were examined in the laboratory using the methods described above.

Data Analysis

For the first study question (piscivore distribution), we evaluated nearshore piscivore persistence at our sampling sites by combining the beach seine and gill net catches for use in a semi-quantitative, presence-absence analysis because both beach seine and gill net capture efficiencies changed during the sampling seasons. In general, beach seine capture efficiency decreased with increasing piscivore length, whereas gill net capture efficiency increased with increasing piscivore length (Nobriga et al. 2006), impairing the accuracy of among-site and among-month comparisons of catch per unit effort. However, our gear choices reliably detected the presence of nearshore piscivores, hence our use of them for collecting fish for stomach contents. For the analysis, we calculated the percentage of sampling days that each predator species was collected by either beach seine or gill net at each site, each year. Then, we summed these percentages to develop 'persistence indices.' These indices had a potential maximum value of 1000 (100% x 5 sites x 2 years). We assume that differences in the indices reflect the breadth of nearshore piscivore distribution, both spatially and seasonally.

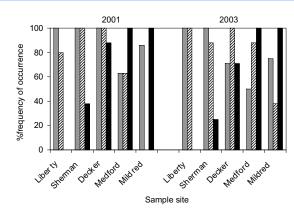We used stomach content data to answer study questions two and three. In the upper estuary there are persistent seasonal trends in the relative densities of young fish that we predicted would influence prey fish occurrence in piscivore diets. Most native fishes spawn from February-June, prior to most established non-native fishes, which tend to spawn during May-August (Matern et al. 2002; Feyrer 2004; Grimaldo et al. 2004). The exact timing of reproduction and the relative densities of native and nonnative fishes are affected by interannual differences in water temperature and flow magnitude, but native species relative abundance is always highest during spring before most of the nonnative species have spawned. Further, total young-of-year fish densities reach their annual peak during summer after most nonnative species also have spawned. We hypothesized that: 1) native fish prey use would peak during spring because this is the time of year that native fishes have their highest relative abundance in the Delta; and 2) total incidence of piscivory would peak during summer because that is the time of year that young fish densities are highest.

We tested these hypotheses using a two-step approach. To evaluate whether native species were most commonly eaten during spring, we summarized the monthly mixes of native and non-native prey fishes and qualitatively evaluated the mixes. We combined data for both years for this analysis. To test the hypothesis that total piscivory was highest during summer, we used a binomial generalized additive modeling (GAM) approach (logit link function) to test the relative importance of size and season on incidence of piscivory. For the purpose of the analysis, we defined "piscivory" as the presence of fish prey in the stomach/foregut and used this as our response variable. We used Julian day (January 1 = day 1) as a surrogate for prey fish relative density based on the seasonal trends we described above. By basing the analysis on the Julian day of each season, both years could be evaluated together. Each piscivore was modeled separately. We used predator fork length, Julian day, and their interaction term as explanatory variables. Explanatory variables were considered statistically significant predictors of incidence of piscivory if the *P*-value of their chi-square statistic was ≤ 0.05. The model fits were evaluated by comparing the difference between the null and residual deviance in the models. The null deviance is akin to the total variance

in linear regression. The residual deviance is the amount of variability left unexplained after the model is fit. The difference between null and residual deviance is analogous to the r-squared statistic in linear regression.

RESULTS

Age-1 and older piscivores were consistently collected across stations and sampling days. All 76 of our individual station visits yielded at least one of the three species, and usually more than one (Figure 2). Striped bass were collected at every site in both years, and were collected from Liberty and Sherman islands during every visit. Sacramento pikeminnow also were collected from all five sites, though they were not collected from Mildred Island in 2001. The only site that always yielded Sacramento pikeminnow was Decker Island. Largemouth bass were always collected from Medford and Mildred islands, but were not collected at Liberty Island in either year. The persistence index was highest for striped bass (845), followed by Sacramento pikeminnow (757), and by largemouth bass (622). This suggests striped bass had the broadest spatio-temporal distribution and largemouth bass the narrowest.

All three piscivores had diverse diet compositions comprised of numerous invertebrate and fish taxa (Table 1). Corophiid and gammarid amphipods were frequently consumed by all three predators. All three predators also consumed annelids, but more frequently in 2003 than 2001. Striped bass were the most frequent consumer of mysids and decapod shrimp. Largemouth bass were the most frequent consumer of most insect taxa and the only preda-

Figure 2. Frequencies of occurrence of age-1 and older piscivores based on the combined beach seine and gill net sampling for each sampling location and year. The gray bars are for striped bass, the bars with diagonal lines are for Sacramento pikeminnow, and the black bars are for largemouth bass.

Table 1. Diet composition of striped bass *Morone saxatilis*, largemouth bass *Micropterus salmoides*, and Sacramento pikeminnow *Ptychocheilus grandis*, collected from nearshore habitats in the Sacramento-San Joaquin Delta during March-October of 2001 and 2003.

	Striped bass		Largemouth bass		Sacramento pikeminnow	
	2001	2003	2001	2003	2001	2003
Number of stomachs with food	131	114	104	113	48	98
Annelids[a]	< 1	12	0	9	4	21
Bivalves	2	2	0	0	0	0
Insects						
Diptera	5	3	12	10	8	2
Heteroptera	0	0	8	12	4	2
Odonata	2	0	28	20	4	0
Other	2	0	1	3	28	5
Crustaceans						
Amphipods						
Corophiidae	31	49	13	22	20	60
Gammaridae	18	23	28	30	12	4
Isopods	2	4	0	4	8	5
Mysids	38	21	2	2	0	0
Copepods/cladocera	0	2	8	4	0	1
Decapods						
Eriocheir sinensis	1	0	0	0	0	0
Decapod shrimp[b]	11	17	5	10	0	1
Crayfish	1	0	3	2	2	1
Native fishes						
Chinook salmon	1	0	1	1	0	0
Prickly sculpin	1	0	10	12	2	1
Sacramento pikeminnow	0	0	0	1	0	0
Splittail	1	0	0	2	0	0
Starry flounder	0	1	0	0	0	0
Tule perch	0	1	2	4	0	1
Non-native fishes						
American shad	0	2	0	0	0	1
Threadfin shad	10	11	1	1	2	0
Unspecified shad	4	8	5	0	4	0
Bigscale logperch	0	0	0	1	2	0
Golden shiner	0	0	1	0	0	0
Inland silverside	3	4	7	9	6	4
Largemouth bass	1	0	3	4	0	0
Lepomis spp.	0	0	0	7	0	0
Rainwater killifish	0	0	2	1	0	0
Striped bass	3	1	2	0	2	1
Tridentiger spp.	0	4	1	3	0	2
Western mosquitofish	0	0	0	1	0	0
Yellowfin goby	10	4	17	9	10	2
Unspecified goby	0	1	0	3	0	0
Unspecified cyprinodontiform	1	0	0	2	0	0
Unspecified fish	20	12	20	12	10	4
Other vertebrates						
Bullfrog tadpole	0	0	1	0	0	0
Muscidae	0	0	1	0	0	0

[a]Most identifiable specimens were the nereid polychaete *Neanthes limnicola*   [b]Most identifiable specimens were *Exopalaemon modestus*

Nobriga and Feyrer: Shallow-Water Piscivore-Prey Dynamics in California's Sacramento-San J...

MAY 2007

tor found to occasionally prey on vertebrates other than fish.

We identified 15 prey fish species, and two additional genera (*Lepomis* and *Tridentiger*); hence, a total of at least 17 species were consumed during our study (Table 1). Sixteen of the 17 taxa were eaten by largemouth bass, 12 of 17 by striped bass, and 10 of 17 by Sacramento pikeminnow. Two native fishes (prickly sculpin, *Cottus asper*, and tule perch, *Hysterocarpus traski*) and five nonnative fish taxa (threadfin shad, *Dorosoma petenense*, inland silverside, *Menidia beryllina*, striped bass, yellowfin goby, *Acanthogobius flavimanus*, and *Tridentiger* spp.) were preyed on by all three piscivores. Note that unidentified fish remains were common, so all of these results should be considered minimum estimates.

There were noticeable seasonal shifts in prey fish consumed by all three piscivores (Table 2). Collectively, most native fish use occurred during spring (March-May) and the highest prey species richness occurred during summer (June-August). Largemouth bass preyed on a greater number of native fish than the other two piscivores and consumed native fish farther into the season (July) than the other two piscivores (May).
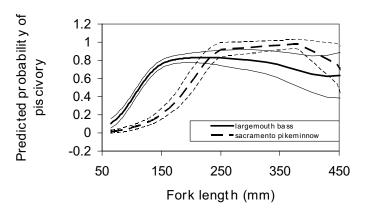
Largemouth bass piscivory was significantly influenced by fork length (chi-square = 12.3; P = 0.005), but not season (chi-square = 2.10; P = 0.52). The fork length X season interaction also was not significant (chi-square = 3.46; P = 0.30). The percentage of null deviance explained by largemouth bass fork length was 18%. Sacramento pikeminnow piscivory also was affected by fork length (chi-square = 13.3; P = 0.003), but not season (chi-square = 4.02; P = 0.25), and with no significant interaction (chi-square = 4.57; P = 0.19). The percentage of the null deviance explained by Sacramento pikeminnow fork length was 33%. Largemouth bass became piscivorous at smaller sizes than Sacramento pikeminnow (Figure 3). The GAMs predicted that 50% of largemouth bass were piscivorous at about 115 mm, whereas Sacramento pikeminnow were about 190 mm before 50% of individuals were piscivorous. In contrast to largemouth bass and Sacramento pikeminnow, striped bass piscivory was significantly affected by season (chi-square = 24.6; P = 0.00002), but not fork length (chi-square = 7.37; P = 0.06). The fork length x season interaction also was not significant (chi-square = 4.42; P = 0.22). The season-only model explained 31% of the null deviance in striped bass piscivory. Striped bass typically only exceeded the 50% piscivory threshold during summer and fall regardless of size (Figure 4).

Table 2. Seasonal occurrence of prey fish species in piscivore stomachs from nearshore habitats of the Sacramento-San Joaquin Delta. Data for 2001 and 2003 are combined. Prey species are coded as follows: AmeSha = American shad *Alosa sapidissima*, BigLog = Bigscale logperch *Percina macrolepida*, ChiSal = Chinook salmon *Oncorhyncus tschawytscha*, GolShi = Golden shiner *Notemigonus crysoleucas*, InlSil = Inland silverside *Menidia beryllina*, LarBas = Largemouth bass *Micropterus salmoides*, Lepomi = *Lepomis* spp., PriScu = Prickly sculpin *Cottus asper*, RaiKil = Rainwater killifish *Lucania parva*, SacPik = Sacramento pikeminnow *Ptychocheilus grandis*, Splitt = Splittail *Pogonichthys macrolepidotus*, StaFlo = Starry flounder *Platyichthys stellatus*, StrBas = Striped bass *Morone saxatilis*, ThrSha = Threadfin shad *Dorosoma petenense*, Triden = *Tridentiger* spp., TulPer = Tule perch *Hysterocarpus traski*, YelGob = Yellowfin goby *Acanthogobius flavimanus*.
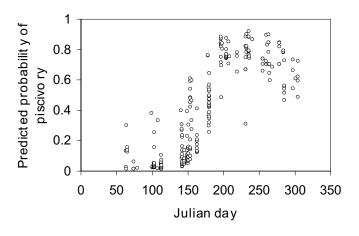
Predator Species	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct
Largemouth bass	ChiSal[a]	PriScu[a]	Lepomi	ChiSal[a]	InlSil	GolShi	InlSil	BigLog
	InlSil	TulPer[a]	PriScu[a]	InlSil	LarBas	InlSil	LarBas	InlSil
	PriScu[a]		TulPer[a]	LarBas	Lepomi	LarBas	Lepomi	YelGob
			WesMos	PriScu[a]	PriScu[a]	Lepomi	Triden	
			YelGob	RaiKil	SacPik[a]	RaiKil	YelGob	
				Splitt[a]	ThrSha	ThrSha		
				StrBas	Triden	Triden		
				YelGob	YelGob	YelGob		
Sacramento pikeminnow	InlSil	PriScu[a]	BigLog	InlSil	InlSil	YelGob	InlSil	AmeSha
		Triden	PriScu[a]	StrBas	StrBas		YelGob	InlSil
		YelGob	TulPer[a]	ThrSha	Triden			YelGob
				YelGob				
Striped bass	ChiSal[a]	PriScu[a]	StaFlo[a]	InlSil	InlSil	AmeSha	AmeSha	InlSil
		Splitt[a]	Triden	StrBas	StrBas	InlSil	LarBas	ThrSha
			TulPer[a]	ThrSha	ThrSha	StrBas	ThrSha	Triden
			YelGob	YelGob	YelGob	ThrSha	YelGob	YelGob
						Triden		
						YelGob		

[a]Native species

Figure 3. Predicted relationships between size (fork length) and incidence of piscivory (presence of fish prey in guts or stomachs) based on binomial generalized additive modeling for largemouth bass and Sacramento pikeminnow. The bold lines are the predicted response; finer lines are ± 1 standard error.

Figure 4. Predicted relationship between season (indexed as Julian day; January 1 = day 1) and incidence of piscivory (presence of fish prey in guts or stomachs) in age-1 and older striped bass. The results are based on binomial generalized additive modeling. The scatter in the probabilities of piscivory show the statistically marginal ($P = 0.06$) influence of striped bass fork length.

DISCUSSION

Striped bass, largemouth bass, and Sacramento pikeminnow are three of the major predators of juvenile and small adult fishes in the Delta. Moreover, they appear to be the dominant piscivores in nearshore habitats, where juvenile striped bass and Sacramento pikeminnow and juvenile-adult largemouth bass can be considered resident fishes (Stevens 1966; Feyrer and Healy 2003; Nobriga et al. 2005; 2006; Brown and Michniuk 2007). Our study indicates that collectively these predators frequently occur in Delta shallow-water habitats (Figure 2). However, we acknowledge that having only five sampling sites limited our ability to generalize about piscivore distributions across the entire Delta. The study also yielded new information about predator-prey dynamics involving these fishes, and provided insight into the relative importance of piscivory on native fishes. These results have management implications for native fishes and the design of shallow water restoration projects.

Does Piscivory in Shallow Water Habitat Follow Predictable Patterns?

There is a large body of literature on the prey choices of piscivorous fishes. Piscivore prey choices are functions of encounter and capture probabilities. Both encounter and capture probabilities are probably affected by prey relative abundance (Buckel et al. 1999). Encounter probabilities also are influenced by environmental factors such as turbidity (Gregory and Levings 1998) and vegetation density (Greenberg et al. 1995; Buckel and Stoner 2000). Capture probabilities also are influenced by prey behavior (Scharf et al. 2003), and morphological features, the most important of which is prey to predator size ratios (Juanes and Conover 1994; Hartman 2000). Differences in piscivore habitat use and foraging strategy also influence prey use. Some piscivores forage most efficiently in open-water (unstructured) environments, whereas others forage most efficiently in structured environments (Greenberg et al. 1995; Buckel and Stoner 2000). In general, striped bass and Sacramento pikeminnow are examples of the former; largemouth bass is an example of the latter (Moyle 2002). These differences were reflected in diet compositions (Table 1). For instance, largemouth bass were the most frequent consumer of *Lepomis* spp. and prickly sculpin, fishes that are common in submerged macrophyte habitats (Grimaldo et al. 2004), and vegetation-oriented invertebrates like insect larvae. In contrast, and as reported previously (Stevens 1966; Feyrer et al. 2003),

striped bass were the most frequent consumer of mysids and clupeid fishes, both of which are common in open-water environments.

Each of the piscivores we examined had diverse and dynamic diets (Tables 1-2), which is consistent with studies from other locations with diverse prey assemblages (Hartman and Brandt 1995; de Almeida et al. 1997). Field observations of changes in piscivore stomach contents through time have indicated that piscivorous fishes exhibit prey switching behavior as predicted by a type-III (density-dependent functional response; Buckel et al. 1999). However, laboratory research does not support this (Buckel and Stoner 2000). Rather, the field-observed pattern may arise as an artifact of predators aggregating in microhabitats that support a transiently available abundant prey, thus 'ignoring' rarer prey occupying different microhabitats. In our study, native fish occurrence in piscivore stomachs was highest in spring, and total piscivory was highest in summer (Table 2; Figures 3-4). This matches the prey switching pattern reported by Buckel et al. (1999). We think that shallow-water piscivores in the Delta generally respond to seasonal changes in prey availability in the same way piscivorous fishes do in other locations, and are thus very predictable. Though piscivores may not invoke density-dependent prey switching, predation mortality is likely density-dependent because high relative abundance translates into more encounters with predators (Buckel and Stoner 2000). In the upper San Francisco Estuary, the intra- and interannual variation in young-of-year fish abundance (and relative abundance) is affected by water temperatures and for some species, river flow variation (Matern et al. 2002; Feyrer 2004; Grimaldo et al. 2004). Therefore, it is likely that these abiotic variables also fundamentally mediate predation mortality.

Are Some Predators Worse Than Others For Native Fishes?

Largemouth bass had the highest per capita predatory influence on nearshore fishes, followed by striped bass, and then Sacramento pikeminnow. This conclusion is supported by two lines of evidence. First, the number of both native fish species and total fish species observed in the stomach/foreguts of each predator varied in the above-mentioned order (Table 2). It is interesting that largemouth bass consumed a greater number of native fish species than striped bass and Sacramento pikeminnow because largemouth bass had lower spatial overlap with most native fishes than the other two predators (Nobriga et al. 2005). Second, largemouth bass switched to piscivory at a smaller size than the other two predators (Figures 3-4). This means juvenile largemouth bass are a particularly effective small, shallow-water piscivore. Thus, largemouth bass predation may be particularly detrimental to native fishes where largemouth bass become established. In the Delta, largemouth bass have become established mainly where submerged macrophytes have proliferated (Nobriga et al. 2005; Brown and Michniuk in press).

The population-level impact of largemouth bass on pelagic native fishes and/or their pelagic early life stages may be mitigated by its limited use of open-water (Nobriga et al. 2005) and brackish habitats (Matern et al. 2002). Thus, our finding of a generally high per capita predatory impact may not reflect the cumulative predatory impact of largemouth bass on all potential prey species. For instance, striped bass likely remains the most significant predator of Chinook salmon, *Oncorhyncus tschawytscha* (Lindley and Mohr 2003), and threatened Delta smelt, *Hypomesus transpacificus* (Stevens 1966), due to its ubiquitous distribution in the Estuary and its tendency to aggregate around water diversion structures where these fishes are frequently entrained (Brown et al. 1996).

Are Shallow Water Habitats Predation Refuges?

Our study was not specifically designed to evaluate whether shallow-water habitats in the Delta provide predation refuges because we did not attempt to estimate predation rates across a depth gradient. However, the frequent collection of piscivores from the shallow-water habitats we sampled (Figure 2) suggests these habitats are easily accessed by large and small predators alike. The Delta channels and flooded islands are generally simple habitats lacking extensive marsh development (Brown 2003). Most historical marsh habitats were lost to dredging and levee reinforcement. In much of the Delta, abrupt depth changes occur where narrow shoals abut dredged channels. Several large tidal lakes have formed where levee breaches

have flooded islands because the land subsided during the period it was reclaimed for agriculture (Lucas et al. 2002). The sites we sampled for the present study had wadable shoal widths ranging only from 9-39 meters depending on specific location and tidal stage (Nobriga et al. 2005). Thus, we think our results provide some support for the conclusion of Sheaves (2001) that shallow estuarine habitats cannot be generalized as predation refuges, if only because of limited shallow-water habitat complexity.

How Do Our Results Affect Our Understanding of the San Francisco Estuary?

We found that the dynamics of striped bass piscivory differed from largemouth bass and Sacramento pikeminnow because age-1 and older striped bass piscivory was more strongly affected by season than fork length. This is consistent with the findings of Stevens (1966) who showed an intra-annual waxing and waning of striped bass piscivory superimposed on the gradual increase in piscivory between young-of-year and adults. Thus, it appears that striped bass respond strongly to the seasonal cycle of juvenile fish production in the upper Estuary. This may be relevant to hypothesized juvenile striped bass density-dependence (Kimmerer et al. 2000) given long-term declines in upper estuary pelagic fish abundance (Kimmerer 2006).

The upper San Francisco Estuary is an abiotically-driven ecosystem (Jassby et al. 1995; Matern et al. 2002). Abiotic variation (mainly stemming from climate and river flow variation) can strongly influence when and where piscivory substantially affects fish community structure (e.g., Meffe 1984; Rodríguez and Lewis 1994; Henderson and Corps 1997). Presumably, the relative and increasing success of non-native, summer-spawning fishes reflects the abiotic ecosystem changes that have occurred in the Estuary and its watershed (Matern et al. 2002; Feyrer 2004; Grimaldo et al. 2004; Nobriga et al. 2005). During summer, age-1 largemouth bass and Sacramento pikeminnow reach sizes that allow them to forage more efficiently on fishes (Figure 3), and striped bass of multiple ages also increase their use of fish prey (Figure 4; Feyrer et al. 2003). Thus, the production of piscivore biomass in the upper estuary is linked to this changing fish fauna. This suggests that watershed-scale factors and species

invasions that have changed the upper Estuary fish communities probably also control piscivore production. It would be interesting to explore whether piscivore populations based on nonnative fish production can exert significant long-term, top-down impacts on some or all declining native fishes due to decoupling of native fish production from piscivore production.

What Are The Implications For Habitat Restoration?

There is a growing body of evidence that shallow habitats dominated by submerged macrophytes are generally unsuitable for the Delta's remnant native fish fauna. Grimaldo et al. (2004) found very few native fish larvae in macrophyte-dominated habitats, suggesting they are either rarely used as spawning habitats or native fish larvae suffer high mortality when they use submerged macrophytes for spawning. Brown and Michniuk (2007) reported a long-term decline in native fish abundance relative to nonnative fish abundance in the Delta based on shoreline electrofishing. The native fish decline occurred coincident with the range expansion of submerged macrophytes (principally Brazilian waterweed, Egeria densa) and nonnative centrarchid fishes, including largemouth bass. Previously, we reported evidence of comparatively low native fish relative abundance and stronger biotic control of fish community composition in nearshore habitats dominated by submerged macrophytes (Nobriga et al. 2005). Predation by largemouth bass is one mechanism previously hypothesized to result in low native fish abundance where submerged macrophytes proliferate (Brown 2003; Nobriga et al. 2005). In the present study we have presented evidence that largemouth bass, the dominant piscivore of submerged macrophyte-dominated habitats, has a high per capita predatory influence. This is consistent with our previous finding of biotic structuring in this habitat type (Nobriga et al. 2005). We strongly suggest that restoration projects in the Delta need to discourage submerged macrophyte domination regardless of what mechanisms are primarily responsible for low native fish use.

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REFERENCES

Abrahams, M, Kattenfeld, M. 1997. The role of turbidity as a constraint on predator-prey interactions in aquatic environments. Behavioral Ecology and Sociobiology 40:169-174.

Arthur, JF, Ball, MD, Baughman, MY. 1996. Summary of federal and state water project environmental impacts in the San Francisco Bay-Delta Estuary, California, p. 445-495 In Hollibaugh, JT (ed.) San Francisco Bay: the ecosystem. Pacific Division of the American Association for the Advancement of Science, San Francisco.

Baker R, Sheaves M. 2005. Redefining the piscivore assemblage of shallow estuarine nursery habitats. Marine Ecology Progress Series 291:197-213.

Brown, LR. 1990. Age, growth, feeding, and behavior of Sacramento squawfish (Ptychocheilus grandis) in Bear Creek, Colusa Co., California. The Southwestern Naturalist 35:249-260.

Brown LR. 2003. Will tidal wetland restoration enhance populations of native fishes? San Francisco Estuary and Watershed Science 1: http://repositories.cdlib.org/jmie/sfews/vol1/iss1/art2.

Brown, LR, Michniuk, D. 2007. Littoral fish assemblages of the alien-dominated Sacramento-San Joaquin Delta, California, 1980-1983 and 2001-2003. Estuaries and Coasts 30:186-200.

Brown, R, Greene, S, Coulston, P, Barrow, S. 1996. An evaluation of the effectiveness of fish salvage operations at the intake of the California Aqueduct, 1979-1993, p. 497-518 In Hollibaugh, JT (ed.) San Francisco Bay: the

ecosystem. Pacific Division of the American Association for the Advancement of Science, San Francisco.

Buckel JA, Conover DO, Steinberg ND, McKown KA. 1999. Impact of age-0 bluefish (Pomatomus saltatrix) predation on age-0 fishes in the Hudson River estuary: evidence for density-dependent loss of juvenile striped bass (Morone saxatilis). Canadian Journal of Fisheries and Aquatic Sciences 56:275-287.

Buckel, JA, Stoner, AW. 2000. Functional response and switching behavior of young-of-the-year piscivorous bluefish. Journal of Experimental Marine Biology and Ecology 245:25-41.

de Almeida, VLL, Hahn, NS, Vazzoler, AEA de M. 1997. Feeding patterns in five predatory fishes of the high Paraná River floodplain (PR, Brazil). Ecology of Freshwater Fish 6: 123-133.

de Merona, B, Mendes dos Santos, G, Gonçalves de Almeida, R. 2001. Short term effects of Tucuruí Dam (Amazonia, Brazil) on the trophic organization of fish communities. Environmental Biology of Fishes 60:375-392.

Dill, WA, Cordone, AJ. 1997. History and status of introduced fishes in California, 1871-1996. California Department of Fish and Game Fish Bulletin 178.

Feyrer, F, Healey, M. 2003. Fish community structure and environmental correlates in the highly altered southern Sacramento-San Joaquin Delta. Environmental Biology of Fishes 66:123-132.

Feyrer, F, Herbold, B, Matern, SA, Moyle, PB. 2003. Dietary shifts in a stressed fish assemblage: consequences of a bivalve invasion in the San Francisco Estuary. Environmental Biology of Fishes 67:277-288.

Feyrer F. 2004. Ecological segregation of native and alien larval fish assemblages in the southern Sacramento-San Joaquin Delta. American Fisheries Society Symposium 39:67-80.

Greenberg, LA, Paszkowski, CA, Tonn, WM. 1995. Effects of prey species composition and habitat structure on foraging by two functionally distinct piscivores. Oikos 74:522-532.

SAN FRANCISCO ESTUARY & WATERSHED SCIENCE

Gregory RS, Levings CD. 1998. Turbidity reduces predation on migrating juvenile Pacific salmon. Transactions of the American Fisheries Society 127:275-285.

Grimaldo LF, Miller RE, Peregrin CP, Hymanson ZP. 2004. Spatial and temporal distribution of native and alien ichthyoplankton in three habitat types of the Sacramento-San Joaquin Delta. American Fisheries Society Symposium 39:81-96.

Hagan, SM, Able, KW. 2003. Seasonal changes of the pelagic fish assemblage in a temperate estuary. Estuarine, Coastal, and Shelf Science 56:15-29.

Hartman, KJ. 2000. The influence of size on striped bass foraging. Marine Ecology Progress Series 194:263-268.

Hartman KJ, Brandt SB. 1995. Trophic resource partitioning, diets, and growth of sympatric estuarine piscivores. Transactions of the American Fisheries Society 124:520-537.

Hartman, KJ, Margraf, FJ. 1992. Effects of prey and predator abundances on prey consumption and growth of walleyes in western Lake Erie. Transactions of the American Fisheries Society 121:245-260.

Henderson, PA, Corps, M. 1997. The role of temperature and cannibalism in interannual recruitment variation of bass in British waters. Journal of Fish Biology 50:280-295.

Jassby, AD, Kimmerer, WJ, Monismith, SG, Armor, C, Cloern, JE, Powell, TM, Schubel, JR, Vendlinski, TJ. 1995. Isohaline position as a habitat indicator for estuarine populations. Ecological Applications 5:272-289.

Juanes, F, Conover, DO. 1994. Piscivory and prey size selection in young-of-the-year bluefish: predator preference or size-dependent capture success? Marine Ecology Progress Series 114:59-69.

Kimmerer, WJ. 2006. Response of anchovies dampens effects of the invasive bivalve Corbula amurensis on the San Francisco Estuary food web. Marine Ecology Progress Series 324:207-218.

Kimmerer, WJ. 2002. Physical, biological, and management responses to variable freshwater flow into the San Francisco Estuary. Estuaries 25:1275-1290.

Kimmerer WJ, Cowan, JH, Jr, Miller, LW, Rose, KA. 2000. Analysis of an estuarine striped bass (Morone saxatilis) population: influence of density-dependent mortality between metamorphosis and recruitment. Canadian Journal of Fisheries and Aquatic Sciences 57:478-486.

Laprise, R, Dodson, JJ. 1989. Ontogenetic changes in the longitudinal distribution of two species of larval fish in a turbid, well-mixed estuary. Journal of Fish Biology 35:39-47.

Lee, DP. 2000. The Sacramento-San Joaquin Delta largemouth bass fishery. Interagency Ecological Program for the San Francisco Estuary Newsletter 13(3):37-40.

Lindley, ST, Mohr, MS. 2003. Modeling the effect of striped bass (Morone saxatilis) on the population viability of Sacramento River winter-run chinook salmon (Oncorhyncus tschawytscha). U.S. Fishery Bulletin 101:321-331.

Lucas LV, Cloern JE, Thompson JK, Monsen NE. 2002. Functional variability of habitats within the Sacramento-San Joaquin Delta: restoration implications. Ecological Applications 12:1528-1547.

Manderson, JP, Phelan, BA, Meise, C, Stehlik, LL, Bejda, AJ, Pessutti, J, Arlen, L, Draxler, A, Stoner, AW. 2002. Spatial dynamics of habitat suitability for the growth of newly settled winter flounder Pseudopleuronectes americanus in an estuarine nursery. Marine Ecology Progress Series 228:227-239.

Manderson, JP, Phelan, BA, Bejda, AJ, Stehlik, LL, Stoner, AW. 1999. Predation by striped searobin (Prionotus evolans, Triglidae) on young-of-the-year winter flounder (Pseudopleuronectes americanus, Walbaum): examining prey size selection and prey choice using field observations and laboratory experiments. Journal of Experimental Marine Biology and Ecology 242:211-231.

Matern SA, Moyle, PB, Pierce, LC. 2002. Native and alien fishes in a California estuarine marsh: twenty-one years of changing assemblages. Transactions of the American Fisheries Society 131:797-816.

May, JT, Brown, LR. 2002. Fish communities of the Sacramento River basin: implications for conservation of native fishes in the Central Valley, California. Environmental Biology of Fishes 63:373-388.

McIvor CC, Odum WE. 1988. Food, predation risk, and microhabitat selection in a marsh fish assemblage. Ecology 69:1341-1351.

Meffe, GK. 1984. Effects of abiotic disturbance on coexistence of predator-prey fish species. Ecology 65:1525-1534.

Mittelbach GG, Persson L. 1998. The ontogeny of piscivory and its ecological consequences. Canadian Journal of Fisheries and Aquatic Sciences 55:1454-1465.

Moyle, P. B. 2002. Inland fishes of California: revised and expanded. The University of California Press, Berkeley.

Nichols, F, Cloern, J, Luoma, S, Peterson, D. 1986. The modification of an estuary. Science 231:567-573.

Nobriga ML, Feyrer F, Baxter RD, Chotkowski, M. 2005. Fish community ecology in an altered river delta: spatial patterns in species composition, life history strategies, and biomass. Estuaries 28:776-785.

Nobriga ML, Feyrer F, Baxter RD. 2006. Aspects of Sacramento pikeminnow biology in nearshore habitats of the Sacramento-San Joaquin Delta. Western North American Naturalist 66:106-114.

Osmundson, DB, Ryel, RJ, Lamarra, VL, Pitlick, J. 2002. Flow-sediment-biota relations: implications for river regulation effects on native fish abundance. Ecological Applications 12:1719-1739.

Paterson AW, Whitfield AK. 2000. Do shallow-water habitats function as refugia for juvenile fishes? Estuarine, Coastal and Shelf Science 51:359-364.

Peterson, MS. 2003. A conceptual view of environment-habitat-production linkages in tidal river estuaries. Reviews in Fisheries Science 11:291-313.

Quist, MC, Hubert, WA, Rahel, FJ. 2004. Relations among habitat characteristics, exotic species, and turbid-river cyprinids in the Missouri River drainage of Wyoming. Transactions of the American Fisheries Society 133:727-742.

Reimchen, TE. 1990. Size-structured mortality in a threespine stickleback (Gasterosteus aculeatus) – cutthroat trout (Oncorhyncus clarki) community. Canadian Journal of Fisheries and Aquatic Sciences 47:1194-1205.

Rodríguez, MA, Lewis, WM, Jr. 1994. Regulation and stability in fish assemblages of neotropical floodplain lakes. Oecologia 99:166-180.

Scharf, FS, Buckel, JA, McGinn, PA, Juanes, F. 2003. Vulnerability of marine forage fishes to piscivory: effects of prey behavior on susceptibility to attack and capture. Journal of Experimental Marine Biology and Ecology 294:41-59.

Sheaves M. 2001. Are there really few piscivorous fishes in shallow estuarine habitats? Marine Ecology Progress Series 222:279-290.

Stevens DE. 1966. Food habits of striped bass, Roccus saxatilis, in the Sacramento-San Joaquin Delta. Pages 68-96 in Turner JL, Kelley DW (eds). Ecological studies of the Sacramento-San Joaquin Delta, part II, fishes of the Delta. California Department of Fish and Game Fish Bulletin 136.

Utne-Palm, AC. 2002. Visual feeding of fish in a turbid environment: physical and behavioral aspects. Marine and Freshwater Behaviour and Physiology 35:111-128.

Werner, EE, Gilliam, JF, Hall, DJ, Mittelbach, GG. 1983. An experimental test of the effects of predation risk on habitat use in fish. Ecology 64:1540-1548.