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Fish Assemblages in Reference and Restored Tidal Freshwater Marshes of the San Francisco Estuary

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ABSTRACT

We examined the spatial and temporal distributions of fishes at a reference and three restored marshes between April 1998 and July 1999 in the Sacramento–San Joaquin Delta, California, to determine the factors that influence fish assemblages in space and time. Shallow-water fishes were sampled using beach seines with and without block-net enclosures in open-water shoals and submerged aquatic vegetation (SAV). Purse seining was used to sample fishes in deep water, including offshore, tidal slough, and marsh-edge habitats. Overall, fish assemblages in reference and restored marshes were dominated by introduced species. One-way analysis of similarity (ANOSIM) did not reveal study site differences in fish assemblages in either data set. However, non-metric multi-dimensional scaling (NMS) and ANOSIM tests of the shallow-water collections revealed differences in fish assemblages using habitats with and without SAV. Introduced fishes, including predatory centrarchid fishes, were abundant in SAV. NMS and ANOSIM tests of the deep-water collections revealed differences in fish assemblages between offshore and nearshore (marsh-edge and tidal slough) habitats. Notably, native fishes were abundant in tidal sloughs. Temporal analyses revealed a suite of species more common in winter and spring, versus another group of introduced species that were more common in summer and fall. Our study findings indicate that newly restored habitats in the Sacramento–San Joaquin Delta will be invaded by introduced fishes. To promote native fish habitat, restoration planning should focus on areas and regions of the Delta where tidal marshes can be restored with little intervention, and where invasive SAV is less likely to colonize.

KEY WORDS

fish assemblages, San Francisco Estuary, restoration

INTRODUCTION

Estuarine habitats continue to be altered by human encroachment, water diversions, contaminants, and invasive species (Nichols and others 1986; Kennish 1992; Schlacher and Woolridge 1996; Cohen and Carlton 1998; Stewart and others 2004; Moyle and Bennett 2008). In many estuaries, ongoing restoration efforts are underway to bolster the abundances of aquatic organisms, but the benefits of restoration remain largely untested and unknown (Simenstad and Cordell 2000; Kimmerer and others 2005; Zedler 2005). Within urbanized landscapes, uncertainty

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about beneficial outcomes is magnified because anthropogenic stressors can mask the benefits of restoration (Kimmerer and others 2005). Although it is widely acknowledged that estuarine restoration should be based on a thorough understanding of the factors that affect aquatic assemblages, rarely are such mechanistic processes understood before such restoration efforts are implemented (Zedler and others 1997; Zedler and Callaway 1999; Kimmerer and others 2005; Zedler 2005).

In the San Francisco Estuary, restoration projects are underway to restore estuarine habitats to promote recovery of native fish populations that have hit record low abundances (Kimmerer and others 2005; Sommer and others 2007a). Along with the loss of habitat, water diversions, increased contaminant loads, and a precipitous drop in lower trophic food web production have all been identified as possible factors responsible for fish declines in the estuary (Sommer and others 2007a). Thus, measuring the expected benefits of habitat restoration to native fishes remains a difficult challenge; especially in the most degraded regions of the estuary where native fishes have been displaced by introduced fishes. Nonetheless, research should accompany restoration projects to understand how habitats and fish abundances interact at smaller spatial and temporal scales so that they can be linked with patterns of change over larger spatial and temporal scales (Kimmerer and others 2005; Zedler 2005).

In this study, we examined the fish assemblages at a reference marsh and three marshes restored unintentionally by levee breaches in the Sacramento–San Joaquin Delta (hereafter Delta), the tidal freshwater area of the San Francisco Estuary. The restored marshes are known as flooded islands because they were inundated by tidal waters after years of agricultural activity that left them below sea level (Mount and Twiss 2005). Flooded island restoration is being proposed at several more locations in the Delta to recover native fish populations and their habitat (Brown 2003). Many flooded islands in the Delta and adjacent subtidal habitats are colonized by dense stands of invasive submerged aquatic vegetation (SAV). SAV is considered an ecosystem engineer (Jones and others 1994) in the Delta because it has

altered the structure of existing shallow-water habitats (Brown 2003), provides habitat for predatory introduced fishes (Nobriga and others 2005; Brown and Michniuk 2007), and has altered historical food web pathways (Grimaldo and others 2009).

Despite these recent findings, still outstanding is a quantitative comparison of fish utilization within the dense canopies of SAV with other habitats within the San Francisco Estuary. Moreover, there have been little attempts to determine if reference marshes in the Delta support improved habitat for native fishes as a means to understanding their potential in providing desirable target endpoints (Simenstad and Thom 1996; Zedler and others 1997; Zedler and Callaway 1999; Toft and others 2003). Our study was designed to answer these two questions: (1) Do fish assemblages differ between the reference and restored marshes? (2) Do fish assemblages and densities vary by habitats within the reference and restored marshes? Hence, this study was intended to help managers and scientists prioritize and design restoration activities in the Delta.

MATERIALS AND METHODS

Study Area

The Delta is a highly complex and modified tidal freshwater ecosystem that receives the majority of its flow from the Sacramento and San Joaquin rivers (Figure 1; Atwater and others 1979; Nichols and others 1986). Natural sloughs have been dredged and deepened to accommodate shipping traffic, or movement of water towards the massive export facilities in the south Delta. As much as 8 billon m^3 y^{-1} of the total freshwater inflow into the estuary is exported for urban and agricultural needs, accounting for approximately 16% of the unimpaired flow (Kimmerer 2004). Water exports increase mortality, reduce habitat, and alter distributions of fishes along the axis of the estuary (Kimmerer 2002; Kimmerer 2004; Feyrer and others 2007; Sommer and others 2007a; Kimmerer 2008). Since the late 1800s, the tidal marsh landscape of the Delta has been transformed into a network of agricultural and urban tracts armored with rip-rap (Atwater and others 1979). Biologically, the estuary is considered one of the most highly invaded ecosystems in North
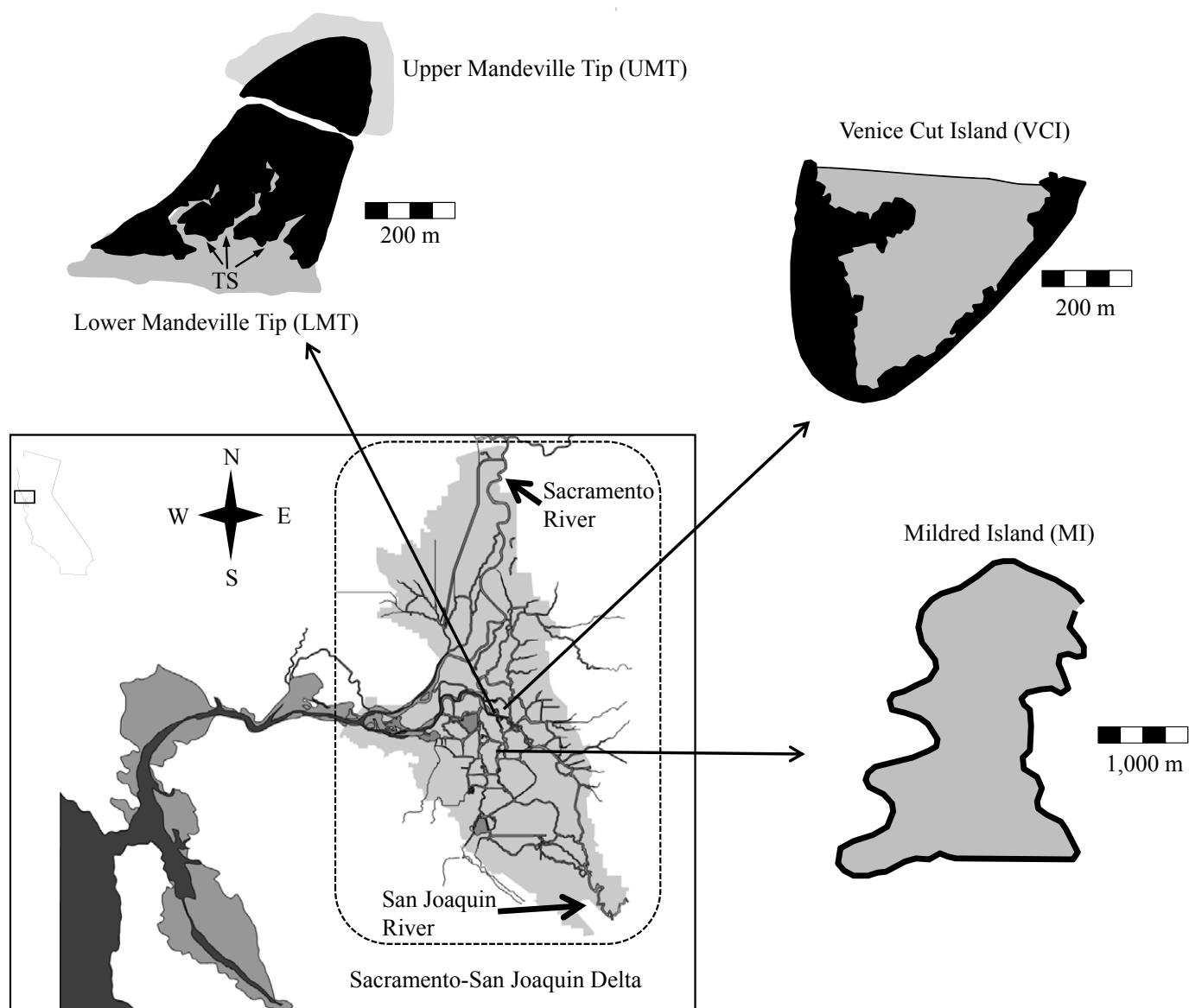
Figure 1 Diagram of the San Francisco Estuary and study sites. Study sites where located in the tidal freshwater Sacramento–San Joaquin Delta. Fishes were sampled in subtidal waters (areas shaded in grey; TS = tidal slough) and inter-tidal areas adjacent to subtidal habitats.

America (Cohen and Carlton 1998). In recent years, native fish populations have declined dramatically under the stress of multiple factors (Sommer and others 2007a; Moyle and Bennett 2008; Thomson and others 2010).

Upper Mandeville Tip (UMT) was selected as a reference marsh because it is one of the few remnant areas that had not experienced any direct physical alteration, and it was close (~2 km) to the restored

marshes (Figure 1, Table 1). Venice Cut Island (VCI) and Lower Mandeville Tip (LMT) were reverted back to tidal inundation when the San Joaquin River was dredged and shunted for construction of the Stockton Deep Water Ship Channel. The re-shaping of the San Joaquin River in this area may have affected sedimentation and other geomorphic influences on UMT. Tidal inundation was restored to Mildred Island (MI) after a breach failure that was left unrepaired. Brazilian waterweed (*Egeria densa*) and Eurasian

Table 1 Study site information where fish assemblages were examined between April 1998 and July 1999 in the Sacramento–San Joaquin Delta

Site	Code	Type	Area (ha)	Date diked	Date breached	Years restored	Depth below sea level (m)	Distance from reference site (km)
Upper Mandeville Tip	UMT	Reference	38					
Mildred Island	MI	Flooded Island	406	1921	1983	15	4.5	7
Lower Mandeville Tip	LMT	Flooded Island	30	1918	1933	65	1.5	2
Venice Cut	VC	Flooded Island	83	1906	1933	67	2.5	3

water milfoil (*Myriophyllum spicatum*)—both are introduced species—were the dominant SAV found at all study sites.

Field Collections

We sampled fishes at each study site during two neap tides per month from April through September 1998 and in January and July 1999, and during one neap tide per month from October through December 1998. Fishes in shallow water (<1.5 m) were sampled using beach seine hauls inside block-net enclosures up to 110 m^2. Prior to setting the block-nets, habitats were delineated with stakes 24 h in advance to minimize disturbance. Upon sampling, block-nets were quickly wrapped around the perimeter stakes and lead lines were secured along the bottom. The surface coverage of SAV within the enclosure was visually estimated as open water (0%), low-density SAV (~1% to 25%) or high-density SAV (>25%) and then removed by hand to prevent the lead line of the beach seine from lifting off the bottom during seine hauls. A minimum of four seine hauls was made within each enclosure. Beach seines hauls without enclosures were made in a few open-water habitats where the net could be fully deployed (up to 510 m^2) without interference from SAV.

We also sampled fish in deep water (>2.0 m) using purse seines (30.4 m by 3.7 m; deployed by boat) to characterize fish assemblages in areas of the study sites not accessible by beach seine (e.g., offshore habitat). Purse seine hauls were done in offshore and marsh-edge habitats at all sites. At LMT, additional purse seine hauls were done in tidal sloughs. Tidal sloughs were not present at the other study sites. At

UMT, offshore hauls were made in the remnant San Joaquin River channel adjacent to the marsh. At the restored marshes, offshore hauls were made within the pelagic areas of the enclosed levees. Marsh-edge samples were mostly taken on the outer SAV edge adjacent to the marsh. Fishes collected with all gear types were identified to species, enumerated, and measured to the nearest millimeter fork length (FL).

Water Quality Measurements

Environmental variables were measured before, or just after each sampling event. Water temperature (°C) and specific conductance (µS × cm^{-1}) were measured 1 m below the surface using an YSI® 85-model meter. Water clarity was determined using a Secchi disk (cm).

Data Analysis

Using two-way analysis of covariance (ANCOVA) we analyzed water-quality variables taken concurrently with shallow-water collections for differences among sites and habitat; month of collection was included as a covariate to account for potential temporal effects.

Beach seine samples with and without enclosures were considered "shallow-water" collections (n = 318). We recognize that beach seine hauls *without* enclosures likely have higher capture efficiencies than beach seine hauls *with* enclosures because the method allowed for quicker deployment and covered a wider area (Rozas and Minello 1997). However, since the beach seine method without enclosure was used only in open-water shoals, we were not concerned if our methods in open-water shoals had dif-

ferent capture efficiencies. We were more concerned with determining differences in fish use among open-water shoal, low-density, and high-density SAV habitat. Therefore, we combined the open-water data for the analysis. For both methods, fish densities were calculated by dividing the catch by the volume of water sampled (fish per m^3).

Purse seine samples were considered "deep-water" collections. Because we were unsure how deep the purse seine net deployed on each haul, fish densities from these samples ($n = 290$) were calculated by dividing the catch by the estimated surface area enclosed (79.5 m^2 at maximum opening; fish per m^2). Although tidal sloughs were only accessible at LMT, we included this habitat in the data analysis with offshore and marsh-edge collections to get a better understanding of the value of tidal slough as habitat for fishes in deep-water areas of the Delta.

For both shallow-water and deep-water collections, we analyzed only fishes between 25 and 400 mm FL because this was the size range the nets captured most effectively. To determine if ontogeny influenced habitat use, we segregated species that typically grow larger than 200 mm FL into juvenile sizes (<100 mm FL) and subadult or adult sizes (>100 mm FL). To remove bias due to rare species, analyses included only species or life stages contributing more than 1% of the total relative abundance that also occurred in >5% of the samples. Finally, fish densities were transformed [ln ($x + 1$)] to reduce the heteroscedasticity in the data.

Non-metric multi-dimensional scaling (NMS; Clarke 1993) using Primer software (version 6.0; Clarke and Gorley 2006) was used to characterize differences in fish assemblages by study site and habitat. NMS is an ordination method that summarizes the rank order distances among elements of a matrix of similarity coefficients. Bray–Curtis similarity coefficients were used to construct the similarity matrices for both shallow-water and deep-water collections. Stress values, which measure the fit of the ordination, were evaluated for two-dimensional and three-dimensional solutions (Clarke and Gorley 2006).

To address our first question about whether study sites (i.e., reference vs. restored) supported different

species assemblages, we performed a one-way analysis of similarity (ANOSIM) on Bray–Curtis similarity coefficients generated from the species abundance data by habitat and season (winter = December–February; spring = March–May; summer = June–August; fall = September–November). ANOSIM test generates a value of R that is scaled to lie between –1 and 1, with zero representing the null hypothesis that there are no differences among groups. Our initial analysis using this approach revealed significant differences in fish assemblages among sites for each data set ($P < 0.01$), but the global R values were only 0.05 and 0.013 for shallow-water and deep-water collections, respectively. Such low R values indicate that significant differences were likely influenced by the number of replicates used in the analysis (Clarke and Warrick 2001). Shallow-water and deep-water data sets were then pooled by season and habitat, respectively, and re-tested for site differences using one-way ANOSIM as described above.

To investigate the spatial and temporal aspects of the fish assemblages, we performed a two-way ANOSIM (crossed with replicates) on the species abundance data pooled across sites. Habitat and season were tested as the main factors. In addition, using the program SIMPER (Clarke and Gorley 2006), we identified the species most responsible for similarities within habitats and seasons, and the species most responsible for dissimilarities between habitats and seasons. Where appropriate, we calculated mean and 95% confidence intervals for NMS scores on each NMS axis by habitat and season. We used two-way analysis of variance (ANOVA), using habitat and season as factors, to explore the relative importance of spatial and temporal variability for each NMS axis. We calculated Spearman rank correlations of individual fish species abundance data with NMS axis scores to further interpret the ecological meaning of the axes. We arbitrarily chose correlations with absolute values of greater than 0.40 as important for interpretation and presentation.

Finally, to aid interpretation of ordination results, we analyzed the average densities of clustered species for differences using two-way ANOVA with habitat and season as factors. Species clusters were identified using unweighted cluster analysis performed on

the Bray–Curtis similarity coefficients generated from the matrix computed among species, not samples. We selected species groups arbitrarily at 10% similarity, because initial runs indicated that both data sets could be reduced to four groups, which seemed appropriate for the intended purpose of displaying key differences in the abundance data. We also recognize the species groups are not independent, which affects interpretation of *P* values. However, we believe this analysis is informative in deciphering aspects of less dominant species (i.e., natives) whose spatial and temporal variability can be masked by interactions of dominant species in the ordinations.

RESULTS

A total of 47,138 fishes representing 32 fish species was collected during the 16–month study period (Table 2). The five most abundant fishes collected were introduced species: threadfin shad (*Dorosoma petenense*), Mississippi silversides (*Menidia audens*), redear sunfish (*Lepomis microlophus*), bluegill (*Lepomis macrochirus*), and largemouth bass (*Micropterus salmoides*). These five introduced species made up over 90% of the total catch. The most abundant native species collected were tule perch (*Hysterocarpus traski*), splittail (*Pogonichthys macrolepidotus*), Chinook salmon (*Oncorhynchus tshawytscha*), and prickly sculpin (*Cottus asper*). Overall, native species represented only 2% of the total catch.

Water Quality

Two-way ANCOVA revealed specific conductance differed by site (F = 24.39; df = 3, 322; $P < 0.001$) and habitat (F = 3.25; df = 2, 322. $P = 0.040$). Tukey pairwise tests revealed that specific conductance was higher in open-water shoals compared to dense SAV, and was higher at MI compared to VCI, LMT, and UMT. All three water quality variables differed by months: water temperature (F = 10.86; df = 1, 322; $P < 0.001$), Secchi disk depth (F = 19.25; df = 1, 322; $P < 0.001$), and specific conductance (F = 28.15; df = 1, 322; $P < 0.001$). The winter months were characterized by cooler water temperatures, higher specific conductance, and clearer water compared to the summer months (Figure 2).

Did Fish Assemblages Vary with Study Site?

One-way ANOSIM of shallow-water data pooled by habitat and season detected a significant difference in fish assemblages by site ($P < 0.01$), but the global *R* was low (0.10), indicating site differences were not truly distinguishable. Site differences were not detected in deep-water collections (one-way ANOSIM; $P = 0.39$).

Did Fish Assemblages and Densities Vary by Habitats within Study Sites?

Shallow-water Collections. The two-way ANOSIM identified habitat ($P < 0.01$, $R = 0.62$) and season ($P < 0.01$, $R = 0.39$) as factors that contributed to differences in fish assemblages from the shallow-water collections. Subsequent pairwise comparisons indicated that fish assemblage differences were greatest between open-water shoals and high-density SAV, and different between all seasons except for summer and fall (Table 3). Subsequent SIMPER analyses revealed that high-density SAV samples were characterized by high percentages of juvenile centrarchids and rainwater killifish (*Lucania parva*), whereas open-water shoals were characterized by Mississippi silversides, adult redear sunfish, and Chinook salmon (only a small percentage) (Table 4). Average dissimilarity percentages were highest between open-water shoal and high-density SAV (80%), and lowest between low-density SAV and high-density SAV (63%). Mississippi silversides, bluegill, and redear sunfish accounted for the largest dissimilarity percentages in most habitat comparisons. Native species—tule perch and Chinook salmon—accounted for only small percentages of dissimilarity between open-water and high-density SAV samples (4% cumulative). Centrarchids and Mississippi silversides accounted for the highest percentages of similarity within seasons, and the largest dissimilarity among seasons. Splittail only accounted for 2% of the similarity in the spring samples.

A two-dimensional NMS ordination plot was selected to represent the shallow-water data (Figure 3). Thirteen species had Spearman rank correlations with absolute values greater than 0.40, with one or more of the NMS axes of the shallow-water data (presented

Table 2 Numbers of the most abundant fish species collected in shallow water and deep water (by study site and overall) between April 1998 and July 1999 in the Sacramento–San Joaquin Delta. Codes are provided for species used in statistical analyses. Origin labels: I = introduced, N = native.

Common name	Species name	Code	Origin	UMT	MI	LMT	VCI	Total
Threadfin shad	*Dorosoma petenense*	ts	I	516	16,940	409	2,856	20,721
Mississippi silversides	*Menidia audens*	ms	I	221	5,259	487	7,588	13,555
Bluegill	*Lepomis macrochirus*	bg	I	632	2,803	230	1,025	4,690
Redear sunfish	*Lepomis microlophus*	rs	I	470	413	293	859	2,035
Largemouth bass	*Micropterus salmoides*	lb	I	644	601	101	269	1,615
Golden shiner	*Notemigonus crysoleucas*	gs	I	222	64	729	238	1,253
Yellowfin goby	*Acanthogobius flavimanus*	yg	I	103	126	136	201	566
Rainwater killifish	*Lucania parva*	rk	I	136	4	33	366	539
American shad	*Alosa sapidissima*	as	I	127	30	114	98	369
Tule perch	*Hysterocarpus traskii*	tp	N	193	11	78	25	307
Splittail	*Pogonichthys macrolepidotus*	sp	N	59	101	91	34	285
Chinook salmon	*Oncorhynchus tshawytscha*	cs	N	3	110	26	63	202
Black crappie	*Pomoxis nigromaculatus*	bc	I	18	48	48	113	227
Prickly sculpin	*Cottus asper*	ps	N	54	33	23	64	174
Black bullhead	*Ameiurus nebulosus*	bb	I	34	16	11	59	120
Bigscale logperch	*Percina macrolepida*	bl	I	1	48	24	13	86
White catfish	*Ameiurus catus*		I	10	18	6	32	66
Striped bass	*Morone saxatilis*	sb	I		15	21	23	59
Sacramento pikeminnow	*Ptychocheilus grandis*		N	3	4	37	14	58
Warmouth	*Lepomis gulosus*		I	25	5		18	48
Western mosquitofish	*Gambusia affinis*		I	21	5	8	12	46
Pacific staghorn	*Leptocottus armatus*		N	5	1	3	30	39
Brown bullhead	*Ameiurus melas*		I	10			11	21
Channel catfish	*Ictalurus punctatus*		I	4	8	5	1	18
Common carp	*Cyprinus carpio*		I	4	5	1	6	16
Delta smelt	*Hypomesus transpacificus*		N	2	2	5	1	10
		Total		3,518	26,676	2,919	14,025	47,138
		% Native		9	1	9	2	2
		% Introduced		91	99	91	98	98
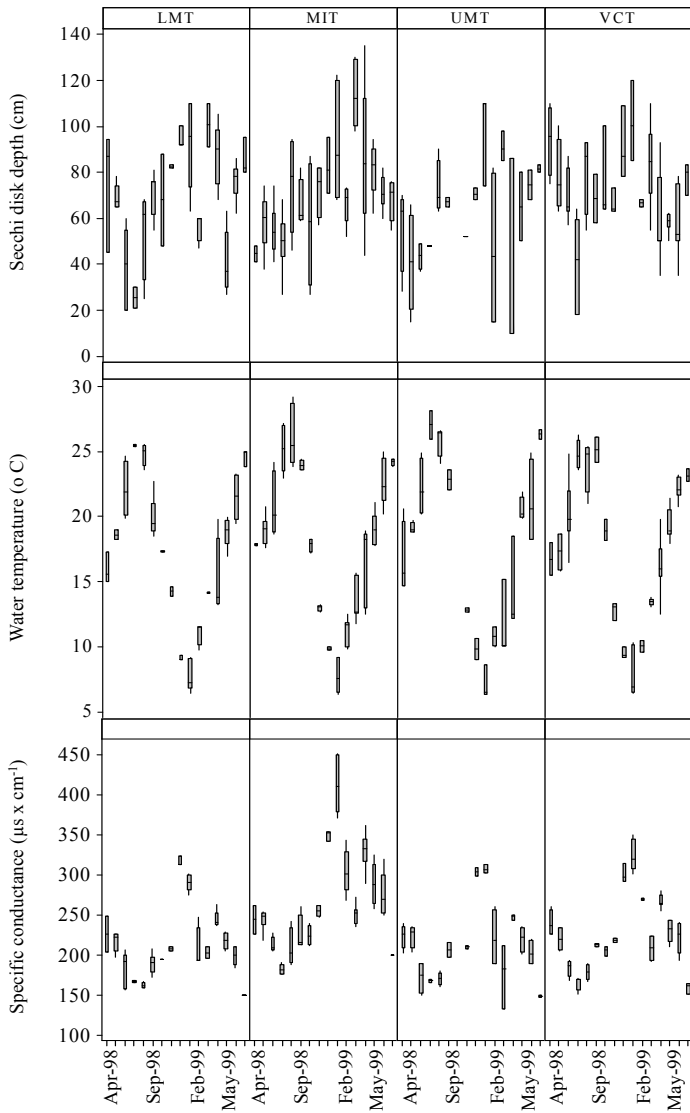
Figure 2 Water temperature (°C), specific conductance (μm × cm⁻¹), and Secchi disk depth (cm) data by study site and month of collection. Data represent those taken concurrently with shallow-water collections only. The bottom and top of the box represent the 25th and 75th percentiles, respectively, and the band (-) in the box is the median.

Table 3 Two-way ANOSIM results examining habitat and season effects on fish abundance data from shallow-water collections derived from Bray–Curtis coefficients. Habitats sampled were open-water shoals (OWS), low-density SAV (ld SAV), and high-density SAV (hd SAV). Significant effects were determined at alpha values less than 0.05.

Factor	Comparison	*R*	*P*-value
Habitat	All	0.54	0.00
	OWS vs ld SAV	0.25	0.02
	OWS vs hd SAV	0.83	0.00
	ld SAV vs hd SAV	0.48	0.00
Season	All	0.39	0.00
	Spring vs. Summer	0.31	0.01
	Spring vs. Fall	0.33	0.03
	Spring vs. Winter	0.48	0.00
	Summer vs. Fall	0.13	14.20
	Summer vs. Winter	0.69	0.00
	Fall vs. Winter	0.39	0.09

Table 4 Two-way ANOSIM results examining habitat (marsh-edge, tidal slough, and offshore) and season effects on fish abundance data from deep water collections. Significant affects were determined at alpha values less than 0.05.

Factor	Comparison	*R*	*P*-value
Habitat	All	0.69	0.01
	Marsh-edge vs. offshore	0.63	0.01
	Marsh-edge vs tidal slough	0.80	0.01
	Offshore vs. tidal slough	0.78	0.01
Season	All	0.06	0.23
	Spring vs. Summer	0.01	0.40
	Spring vs. Fall	0.23	0.90
	Spring vs. Winter	-0.26	0.93
	Summer vs. Fall	0.28	0.30
	Summer vs. Winter	0.00	0.44
	Fall vs. Winter	0.23	0.13

on Figure 3). Consistent with results identified from ANOSIM and SIMPER analyses, NMS axis 1 represents a gradient in species associated with high density SAV, such as centrarchids and rainwater killifish, versus those found in open-water shoals (Chinook salmon and Mississippi silversides). This interpretation is supported by the two-way ANOVA on NMS 1, which showed significant habitat (F = 21.09; df = 2, 46; $P < 0.001$), but not seasonal effects (F = 0.08; df = 3, 46; $P = 0.97$). Based on the two-way ANOVA of NMS axis 2, it appears axis 2 represents seasonal (F = 11.65; df = 3, 46; $P < 0.001$) and habitat (F = 10.54; df = 2, 46; $P < 0.001$) variability, mainly separating introduced fishes and tule perch from Chinook salmon.

Deep-water Collections. The two-way ANOSIM identified habitat ($P < 0.01$, $R = 0.68$), but not season ($P = 0.23$, $R = 0.06$), as a factor that influenced fish assemblages differences in the purse seine data. Subsequent pairwise habitat comparisons revealed the greatest differences between marsh-edge and tidal slough samples, though all habitats were different from each other (Table 5). The SIMPER analysis characterized marsh-edge samples by centrarchids and threadfin shad, offshore samples by threadfin shad and American shad (*Alosa sapidissima*), and tidal sloughs by adult and juvenile golden shiner (*Notemigonus crysoleucas*), centrarchids, and tule perch (Table 6). Average dissimilarity percentages were highest between offshore and tidal slough samples. Threadfin shad and bluegill accounted for the highest dissimilarity percentages between offshore and marsh-edge samples (75% cumulative). Golden shiner, threadfin shad, and bluegill accounted for the highest dissimilarity percentages between tidal slough and marsh-edge samples (80% cumulative). Threadfin shad, splittail, golden shiner, and Mississippi silversides accounted for the largest dissimilarity percentages between tidal slough and offshore samples (40% cumulative). A two-dimensional NMS ordination plot was also appropriate to represent the deep-water data based on stress (0.19; Figure 4). Four species had Spearman rank values with absolute values greater than 0.40, with one or more of the NMS axes with the deep-water data (presented on Figure 4). NMS axis 1 is represented as a
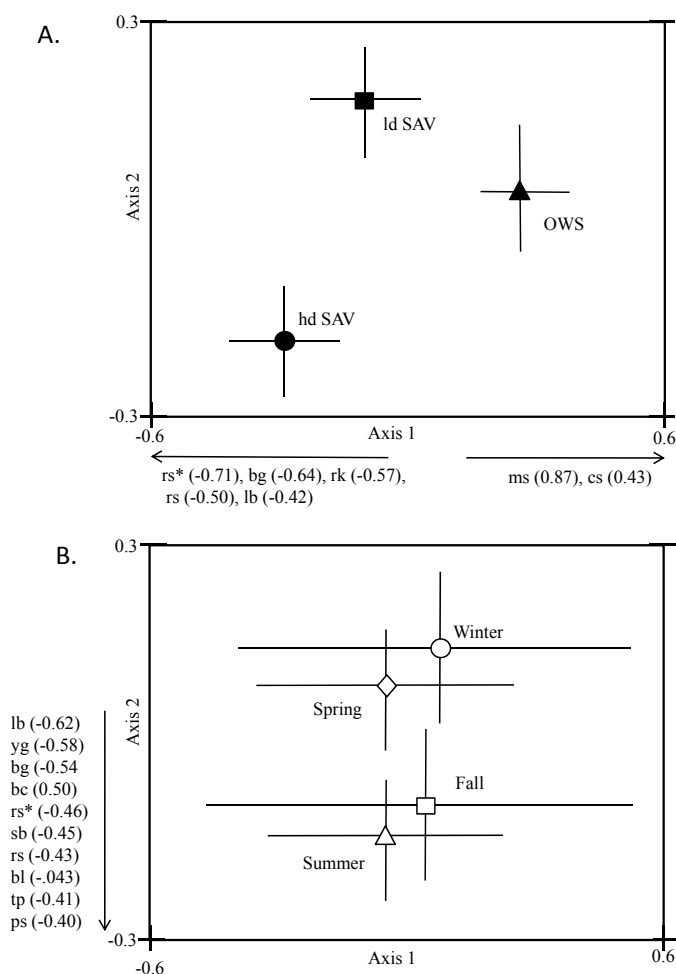

Figure 3 Mean and 95% confidence intervals of NMS axis scores determined from fish abundance data from shallow-water collections by habitat and season. The NMS stress was 0.17. Species with correlation coefficient absolute values greater than 0.4 are provided next to respective axes; correlation coefficients for each species are provided in parentheses. See Table 2 for species codes. The asterisks indicate adult life stage.

habitat gradient between pelagic and tidal slough or marsh-edge samples, based on Spearman rank correlation loadings of American shad, threadfin shad, and Mississippi silversides. This result is consistent with the two-way ANOVA of NMS axis 1, where a habitat effect was found (F = 31.89; df = 2, 39; $P < 0.001$). A seasonal effect was also detected on NMS axis 1 scores (F = 3.59; df = 3, 39; $P < 0.05$). Even though the two-way ANOSIM failed to detect a season effect, NMS axis 2 appears to represent a habitat and season gradient, given that both American shad and golden shiner had negative Spearman rank coefficients with

Table 5 Percentages of species contributing to similarity of habitats and seasons, and percentages of species contributing to dissimilarity between habitats and seasons from the shallow-water collections identified from the SIMPER analysis. Species contributions are distinguished into three percentage levels. See Table 2 for species codes.

Habitat	Open-water shoals	Low-density SAV	High-density SAV
Within habitat sim:	45%	37%	60%
>20%	ms, rs[a]	rs[a]	bg
11% to 20%		bg, ms	rs, rs[a], rk
<10%	cs, lb[a], yg	rs[a], lb, lb[a], gs, yg	lb, ms, gs
Diss. with ld SAV:	68 %		
> 20%	ms, rs[a]		
11% to 20%	rs[a], rk, bg, yg, rs, lb[a], gs, c		
< 10 %	s, sp, lb		
Diss. with hd SAV	80 %	63 %	
>20 %	ms, bg	bs	
11% to 20%	rs	rs	
<10 %		rs[a], lb, rk, ms, gs	

Season	Winter	Spring	Summer	Fall
Within season sim:	52%	44%	48%	47%
>20%	ms	bs, rs[a]		ms, bg
11% to 20%	rk, bl	ms	bg, rs[a], lb, ms	rs, rs[a], lb
<10%	rs, rs[a]	rs, lb[a], sp	rs, yg, gs, lb	
Diss. with Spring	65 %			
>20%	ms			
11% to 20%	rs[a], rk			
<10%	bg, rs, cs, sp, tp, lb[a]			
Diss. with Summer	70%	60%		
>20%				
11% to 20%	ms, lb, rs[a]	ms, lb, yg, rs[a]		
<10%	bg, yg, gs, rk, rs, cs, tp, lb[a]	gs, bg, rs, tp, rk, sp, lb[a]		
Diss. with Fall	61%	63%	56%	
>20%	ms	ms	ms	
11% to 20%	bg, rk, rs[a]	bg, rk, rs[a]	rs[a], rk, yg, gs, rs, lb, lb[a]	
<10%	rs, lb, cs	rs, lb, sp, bl, lb[a]		

[a] Indicates adult life stage.

Table 6 Percentages of species contributing to similarity of habitats and seasons, and percentages of species contributing to dissimilarity between habitats and seasons from deep-water collections identified from the SIMPER analysis. Species contributions are distinguished into three percentage levels. See Table 2 for species codes.

Habitat	Offshore	Marsh edge	Tidal slough	
Within habitat sim:	32%	41%	15%	
>20%	ts	bs	gs[a], bg	
11% to 20%	ms	ts	rs[a], gs	
<10%		ms, rs, bg[a], rs[a]	ts, ms, tp	
Diss. with ME:	80%			
>20%	ts			
11% to 20%	bg			
<10%	as, ms, bg[a], rs[a], sp			
Diss. with TS	98%	84%		
>20%	ts	gs		
11% to 20%	sp, ms, gs	gs[a], ts, bg		
<10%	bg, bg[a], gs[a], rs	rs, ms, lb, bg[a]		
Season	**Winter**	**Spring**	**Summer**	**Fall**
Within season sim:	15%	44%	40%	15%
>20%	gs	ts, bg	bg, ts	ms, ts
11% to 20%	bg, rs[a], gs			
<10%	ts, ms	bc, rs, lb, ms, bg[a]	rs[a], bg[a], ms	rs[a]
Diss. with Spring	80 %			
>20%	gs, gs[a]			
11% to 20%				
<10%	bg, ts, rs, tp, bc, rs[a]			
Diss. with Summer	84%			
>20%	gs, gs[a]	ts, bg		
11% to 20%				
<10%	ms, rs, gs, bg[a], as, gs[a], lb, rs[a]			
Diss. with Fall	91%	89%	88%	
>20%	sp, gs[a]	ts	ts	
11% to 20%	bg, bg[a]	ms	ms	
<10%	gs, ts, rs, rs[a]	as, gs, sp, gs[a]	as, gs, sp, gs[a]	

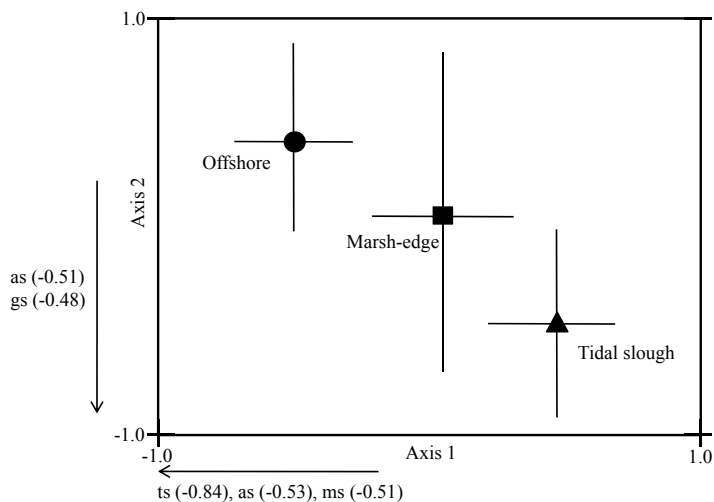[a] Indicates adult life stage.

Figure 4 Mean and 95% confidence intervals of NMS axis scores determined from fish abundance data from deep-water collections by habitat. The NMS stress was 0.17. Species with correlation coefficient absolute values greater than 0.4 are provided next to respective axes; correlation coefficients for each species are provided in parentheses. See Table 2 for species codes.

axis 2, but occupied different habitats, as indicated by the SIMPER analysis and density comparison (presented below). The two-way ANOVA of axis 2 identified effects of both habitat (F = 4.98; df = 2, 39; $P < 0.001$) and season (F = 5.29; df = 3, 39; $P < 0.05$).

Density comparisons. Four species groupings were identified by cluster analysis from the shallow-water collections: (A) Chinook salmon and Mississippi silversides; (B) black crappie (*Pomoxis nigromaculatus*), golden shiner, juvenile and adult largemouth bass, juvenile and adult redear sunfish, bluegill, rainwater killifish , brown bullhead (*Ameiurus nebulosus*), tule perch and prickly sculpin; (C) splittail; and (D) bigscale logperch (*Percina macrolepida*), striped bass (*Morone saxatilis*), yellowfin goby (*Acanthogobius flavimanus*), and threadfin shad. Two-way ANOVA and plots of the clustered groups revealed that group B was mostly found in high-density SAV during the summer, whereas groups A and D were more abundant in open-water shoals (Table 7; Figure 5). Group D was also more abundant during late summer. Splittail (group C) did not vary by habitat, but

was found to be more abundant during May and June. Four clusters were also identified from the deep-water collections: (A) threadfin shad, American shad, and Mississippi silversides; (B) juvenile and adult golden shiner; (C) splittail and tule perch; and (D) juvenile and adult largemouth bass, adult redear sunfish, juvenile and adult bluegill, and juvenile and adult black crappie. Groups A through D all varied by habitat, whereas group A was more abundant in offshore hauls, group D was more abundant in marsh-edge, and groups B and C were more abundant in tidal sloughs (Table 8; Figure 6). Groups A and B were also more abundant during late summer and fall, whereas group C was more abundant during late spring and early summer.

DISCUSSION

The Delta has undergone a dramatic transformation from a dynamic ecosystem dominated by riverine inflow, turbid conditions, and vast marsh landscape to one characterized by dampened hydrodynamic variability, minimal marsh habitat, high biological invasions, and high contaminant loads (Moyle and Bennett 2008). The adverse consequences of this transformation on fish populations and their habitat in the estuary are well documented (Feyrer and others 2007; Sommer and others 2007a; Moyle and Bennett 2008; Grimaldo and others 2009). Our study provides yet another demonstration of how an altered ecosystem supports conditions favorable for an undesirable fish assemblage (Nobriga and others 2005; Brown and May 2006; Brown and Michniuk 2007). Our study also provides information on the habitat use of native fishes, which can be used to support future restoration efforts in the estuary or understand trophic linkages in greater detail (Brown 2003; Nobriga and Feyrer 2007; Grimaldo and others 2009).

Did Fish Assemblages Vary between Reference and Restored Sites?

Most fishes are highly mobile and are therefore expected to colonize newly restored habitats from nearby habitats as soon as they are available (Minello and Zimmerman 1992; Minello and Webb Jr. 1997; Zedler and others 1997; Williams and Zedler 1999).

Table 7 Summary statistics from two-way ANOVA models testing the hypothesis that the abundance of fishes from shallow-water collections did not vary by habitat (open-water shoal, low-density SAV, and high-density SAV) and month of collection from reference and restored study sites. Species groups were identified using group-average cluster analysis (10% similarity levels) from Bray–Curtis coefficients. Significant values were determined at alpha values <0.05.

Group	Source	DF	Seq. SS	Adj. SS	Adj. MS	F	*P*-value
A	Habitat	2	8.79	4.17	4.17	17.71	< 0.001
	Month	11	3.44	3.44	0.31	1.33	0.21
	Error	315	74.31	74.31	0.24		
	Total	329	86.72				
B	Habitat	2	12.63	10.73	5.36	30.33	< 0.001
	Month	11	8.28	8.28	0.75	4.25	< 0.001
	Error	315	55.76	55.76	55.77	0.18	
	Total	329	83.59	83.59			
C	Habitat	2	0.00	0.00	0.00	1.05	0.35
	Month	11	0.05	0.05	0.00	2.13	< 0.05
	Error	315	0.70	0.70	0.00		
	Total	329	0.75				
D	Habitat	2	0.09	0.18	0.09	4.47	< 0.05
	Month	11	1.31	1.31	0.12	5.91	< 0.001
	Error	315	6.36	6.36	0.02		
	Total	329	7.78				

A = Chinook salmon, Mississippi silverside

B = black crappie, golden shiner, juvenile and adult largemouth bass, juvenile and adult redear sunfish, bluegill, rainwater killifish, brown bullhead, tule perch and prickly sculpin

C = splittail

D = bigscale logperch, striped bass, yellowfin goby, and threadfin shad

Thus, we are not surprised to see such little variation in the fish assemblages among study sites, given that the youngest site was already 15 years restored, and the study sites were located relatively close to one another (~7 km or less). Other studies in the Delta have found fish assemblages to vary regionally, but these differences were found to be influenced by outflow (Dege and Brown 2004), habitat availability (Nobriga and others 2005), or water quality (Nobriga and others 2005; Brown and May 2006).

In relatively pristine estuaries, trajectories of restored marshes toward reference conditions can be quantified (e.g., food web support, native invertebrate and fish densities, etc.) to determine if restoration is providing expected benefits (Simenstad and Thom 1996; Simenstad and Cordell 2000; Howe and Simenstad

2007). Such trajectory comparisons are probably less meaningful in the Delta, where habitat conditions are highly altered, and introduced fishes are the dominant members of the fish community (Feyrer and Healey 2003; Nobriga and others 2005; Brown and Michnuik 2007). For example, the reference site used in this study was selected *a priori* on the basis that the marsh landscape and adjacent inter-tidal shoals had not been physically modified. However, upon study, we found that the subtidal mudflats surrounding the marsh landscape were colonized by invasive SAV, to the extent that it choked out transitional habitat between the shoals and the marsh. Thus, it was not surprising to find the fish assemblage at the reference site to be dominated by introduced fishes, especially centrarchids, which are common in SAV
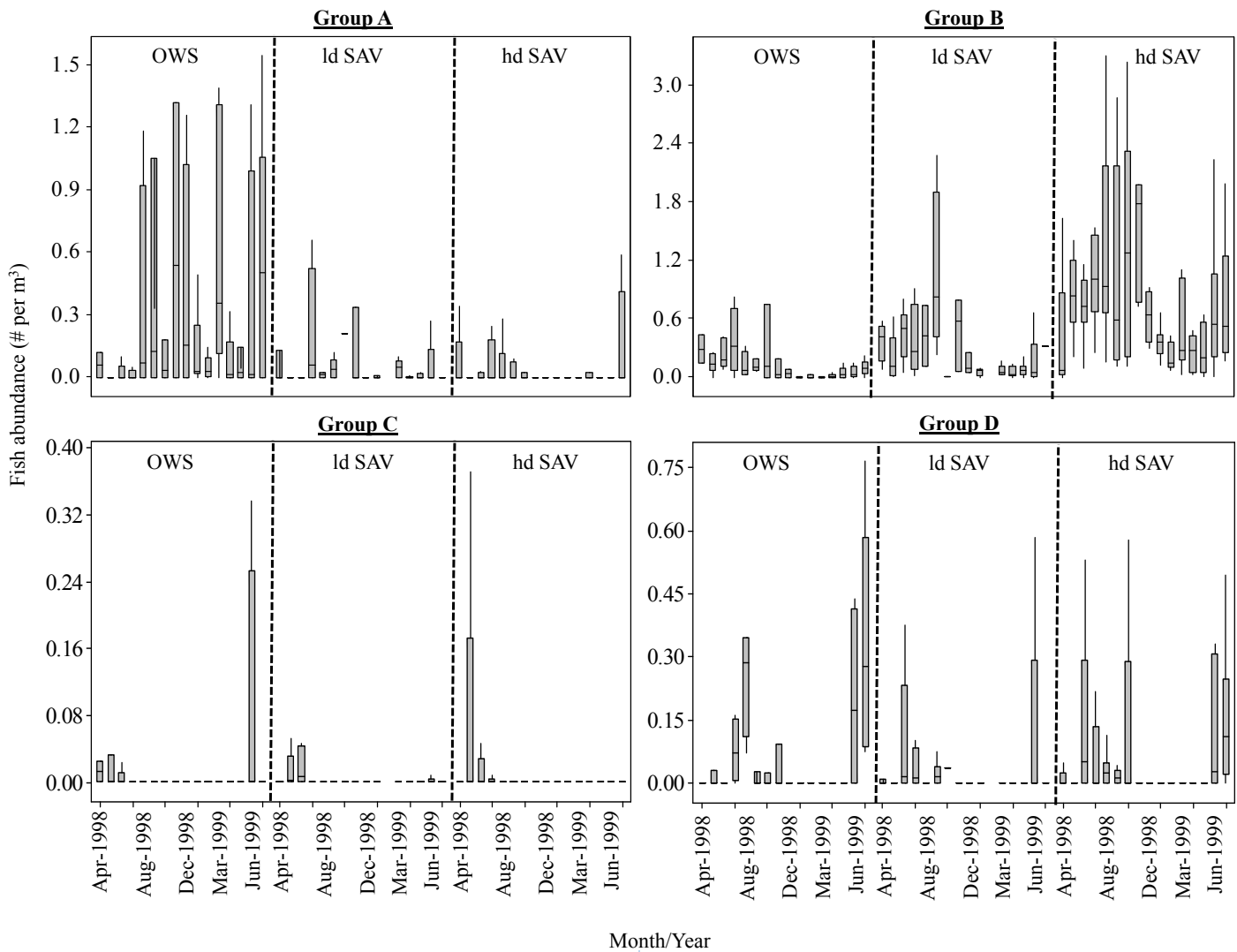
Figure 5 Box and whisker plots of fish densities from the shallow-water collections summarized by groups of species deemed similar using an unweighted cluster analysis on Bray–Curtis similarity coefficient matrices. The bottom and top of the box represent the 25th and 75th percentiles, respectively, and the band (-) in the box is the median. The four species groupings were: (A) Chinook salmon and Mississippi silversides; (B) black crappie, golden shiner, juvenile and adult largemouth bass, juvenile and adult redear sunfish, bluegill, rainwater killifish, brown bullhead, tule perch, and prickly sculpin; (C) splittail; and (D) bigscale logperch, striped bass, yellowfin goby, and threadfin shad.

(Rozas and Odum 1988; Killgore and others 1989; Duffy and Baltz 1998; Johnson and Jennings 1998).

Did Fish Assemblages and Densities Vary by Habitats within Study Sites?

Shallow-water Collections. The habitat-use patterns identified from the shallow-water data complement previous research in the estuary, showing fishes are segregated by species that associate with SAV versus open-water habitats (Nobriga and others 2005;

Brown and Michniuk 2007). Not surprisingly, centrarchids were abundant in SAV beds, but we also found native tule perch and prickly sculpin in the high-density SAV. We suspect that tule perch densities may have been underestimated in previous shallow-water studies where the interior of SAV was not sampled (e.g., Nobriga and others 2005; Brown and May 2006; McLain and Castillo 2010). Nonetheless, SAV supports high centrarchid populations, which are thought to adversely affect native fish populations through

Table 8 Summary statistics from two-way ANOVA models testing the hypothesis that the abundance of fishes from deep-water collections did not vary by habitat (offshore, marsh-edge, and tidal slough) and month of collection from reference and restored study sites. Species groups were identified using groupaverage cluster analysis (10% similarity levels) from Bray–Curtis coefficients. Significant values were determined at alpha values <0.05.

Group	Source	DF	Seq. SS	Adj. SS	Adj. MS	F	*P*-value
A	Habitat	2	1.17	1.17	0.59	7.97	< 0.001
	Month	11	6.30	4.06	0.36	5.02	< 0.001
	Error	275	20.21	20.21	0.07		
	Total	288	27.70				
B	Habitat	2	0.65	0.65	0.32	40.41	< 0.001
	Month	11	0.21	0.20	0.02	2.30	< 0.05
	Error	274	2.22	2.22	0.01		
	Total	288	3.09				
C	Habitat	2	0.01	0.01	0.00	2.95	< 0.05
	Month	11	0.04	0.04	0.00	3.17	< 0.001
	Error	274	0.30	0.30	0.00		
	Total	288	0.34				
D	Habitat	2	0.64	0.64	0.32	23.17	< 0.001
	Month	11	0.27	0.37	0.03	2.47	< 0.05
	Error	274	3.80	3.80	0.01		
	Total	288	4.71				

A = American shad, threadfin shad, and Mississippi silversides
B = juvenile and adult golden shiner
C = splittail and tule perch
D = black crappie, adult and juvenile largemouth bass, adult redear sunfish, and juvenile and adult bluegill

competition and predation (Werner and others 1983; Michniuk 2007; Nobriga and Feyrer 2007).

To date, directed research on juvenile Chinook salmon rearing in marsh habitats has been limited to the northern boundary of the Delta (McLain and Castillo 2010). Our study included a more intensive sampling array of shallow-water habtats and study sites than McLain and Castillo (2010), but our results are consistent in demonstrating that Chinook salmon are mostly associated with open-water shoal habitats. We did not address the importance of habitat connectivity in this study, but suspect it is an important attribute that influences predation mortality of Chinook salmon in the Delta, given that open-water shoals have a patchy distribution among predator-laden SAV and riprap habitat.

In other estuaries, SAV is promoted because it provides critical nursery habitat (i.e., food and predation cover) for many small native fishes (Orth and others 1984; Rozas and Odum 1987; Rozas and others 2005; Baldizar and Rybicki 2007). Using stable isotopes and stomach-content analyses, Grimaldo and others (2009) found that SAV and its attached epiphytic algae supports food resources (e.g., amphipods, damselflies) consumed by fishes in SAV and open-water shoals. Thus, although the analyses presented here show segregation between fishes that occupy SAV and open-water shoals in shallow waters, trophic dependence and biotic forcing mechanisms (i.e., predation and competition) inextricably link the two habitats at scales unobservable in our study (Feyrer and others 2007). In contrast, Grimaldo and others (2009) found SAV-associated food subsidies to be of
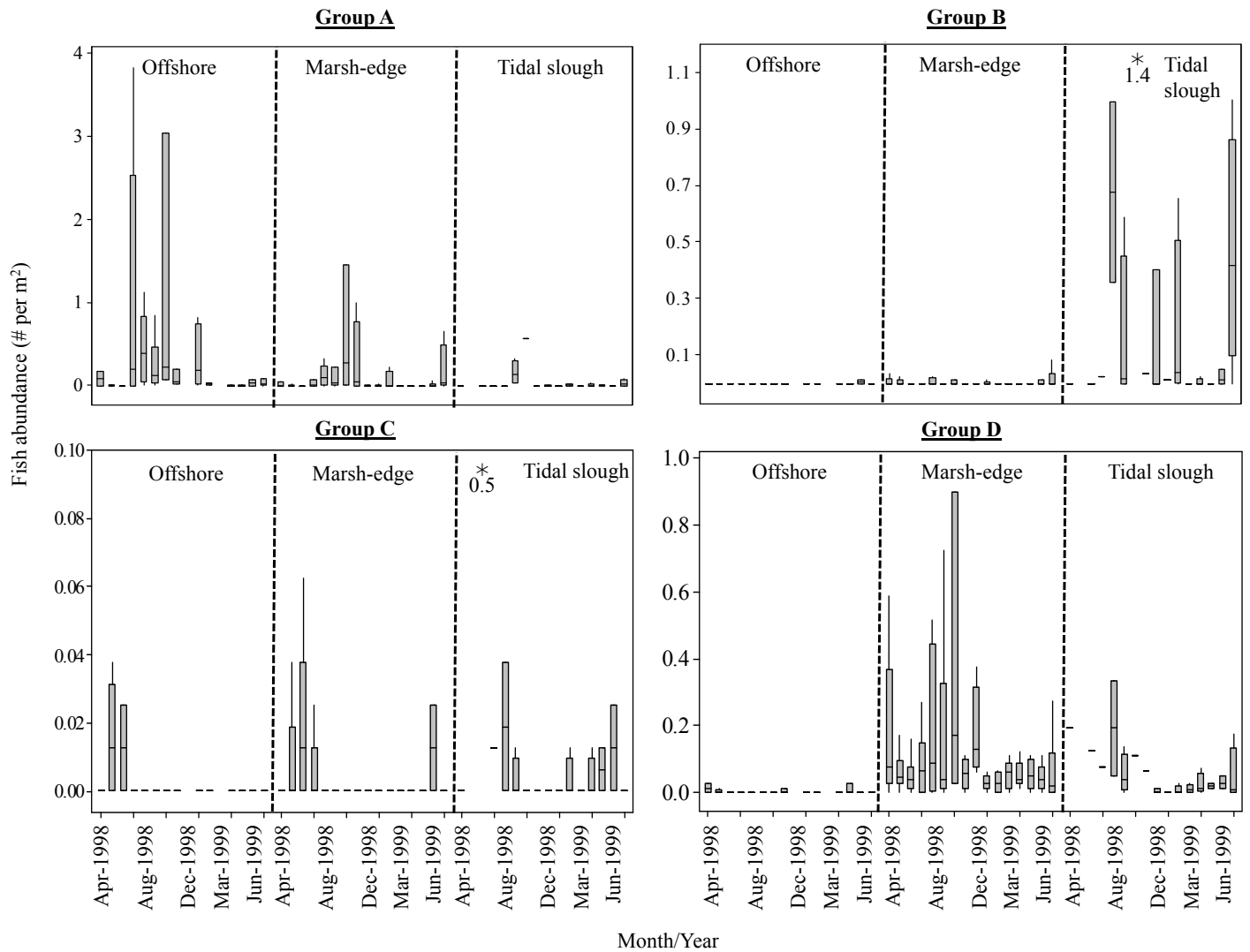
Figure 6 Box and whisker plots of fish densities from deep-water collections summarized by groups of species deemed distinct using an unweighted cluster analysis performed on Bray–Curtis similarity coefficient matrices. The bottom and top of the box represent the 25th and 75th percentiles, respectively, and the band (-) in the box is the median. The four species groupings were: (A) threadfin shad, American shad, and Mississippi silversides; (B) juvenile and adult golden shiner; (C) splittail and tule perch; and (D) juvenile and adult largemouth bass, adult redear sunfish, juvenile and adult bluegill, and juvenile and adult black crappie.

less importance to juvenile and small pelagic fishes, suggesting there is a functional decoupling between shallow-water and offshore habitats where SAV is present.

Deep-water Collections. The purse seine samples were useful in characterizing differences between near-shore and offshore habitats. Perhaps most interesting, tidal slough samples were mostly characterized by species different from those found in offshore

and marsh-edge samples. Specifically, we found high densities of golden shiner, splittail, and tule perch in tidal sloughs, indicating that tidal sloughs provide some value for native fish habitat—a result worthy of further exploration. The tidal sloughs in our study did not de-water completely on ebb tides, but they became very shallow (e.g., les than 0.5 m) and were not colonized by SAV. Perhaps, they provide some refugia habitat from large predators (e.g., striped

bass) unable to occupy them at low tides or from ambush predators (e.g., largemouth bass) which are associated with SAV.

Offshore samples were characterized by American shad and threadfin shad, which was not unexpected because they tend to school in pelagic habitats in large schools while foraging for zooplankton. However, we did not expect to find Mississippi silversides to group with the pelagic species (NMS and SIMPER analyses), given their affinity for open-water shoals (Nobriga and others 2005; Brown and May 2006). Where dense SAV prohibits access to shoreline habitats, as it did at our study sites, we suspect that it may cause Mississippi silversides to shift offshore in response to predators that aggregate along the edges of SAV (Nobriga and Feyrer 2007).

Temporal Variability in Fish Assemblages

The NMS analysis and Spearman rank correlations of shallow-water data identified a seasonal shift in the presence of native and introduced fish species. Notably, Chinook salmon grouped out in ordination space from several introduced species, reflecting the fact that they emigrate through the Delta during the late winter and early spring, when introduced fishes are at relatively low abundances. Temporal differences for other native fishes were less evident in the ordination analysis, in part, because we used broad seasonal averaging periods which masked monthly variability. However, monthly analyses revealed that tule perch and splittail were more abundant in late spring and early summer, compared to late summer and fall (Figures 5 and 6), which is consistent with their spawning periods (Grimaldo and others 2004; Nobriga and others 2005). In contrast, many introduced fishes were more abundant in the late summer and fall months, which is also consistent with their spawning periods (Feyrer and Healey 2003; Grimaldo and others 2004). Although Mississippi silversides spawn in the late summer (Grimaldo and others 2004), juveniles and adults were common in shallow-water collections throughout the year.

Restoration Implications

Our study suggests the fishes likely to occupy restored flooded islands will be highly influenced by the habitats that are available when they migrate through or recruit to the Delta. Flooded islands dominated by SAV will likely support an abundance of introduced fishes, especially centrarchids. Thus, lower priority should be given to potential restoration sites that are at elevations likely to favor SAV colonization. Even though we found native prickly sculpin and tule perch in SAV, these species are not dependent on this habitat type (Baltz and Moyle 1982; Brown and others 1995; Marchetti and Moyle 2001). Unfortunately, many of the diked tracts in the central and south Delta are up to 8 m below sea level (Mount and Twiss 2005), and it is unlikely that natural sediment accretion would be sufficient to restore such subsided areas to inter-tidal elevations, given that sediment recruitment from upstream sources has diminished in recent years (Wright and Schoellhamer 2004). Artificial sediment deliveries may be an option for restoring sites that have undergone minimal subsidence, but this method is not likely feasible at deeply subsided sites (e.g., 3 to 8 m below sea level). Priority should be given to diked tracts at inter-tidal elevations, where open-water shoals and tidal sloughs can be restored, because these habitats are more likely to support native fishes.

Although we did not conduct research in the north Delta, work from others suggests that restoration in this area holds promise for native fishes (Nobriga and others 2005; Brown and Michniuk 2007; Grimaldo and others 2009). The north Delta has relatively low densities of invasive SAV, which in turn, appears to limit use by centrarchids and other introduced fishes (Nobriga and others 2005). The area is also frequently used by the imperiled delta smelt and Chinook salmon (Sommer and others 2001; McLain and Castillo 2010), two of the target species of restoration in the estuary. Finally, potential restoration areas in the north Delta are at elevations near sea level (Mount and Twiss 2005), indicating that tidal marshes can be established at a reasonable time rate with little intervention, as compared to diked tracts in the central Delta, which are well below sea level.

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Finally, restoration activities should be considered in the context of larger landscape processes that are much more likely to explain population variability in the species of interest (Kimmerer and others 2005; Zedler 2005). This is not an impossible task, because research on floodplains draining into the Delta has shown that the survival and population abundance of Chinook salmon and other native fishes are linked to habitat and food web productivity during inundation periods (Sommer and others 2001; Moyle and others 2004; Sommer and others 2007b). In the Delta, multi-disciplinary studies that attempt to link fish abundances to their habitats and food webs at local and regional spatial scales could help reveal the underlying mechanisms responsible for annual changes in fish populations.

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