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Fish assemblages of interior tidal marsh channels in relation to environmental variables in the upper San Francisco Estuary

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Abstract Tidal marsh wetlands represent critical habitat for many estuarine fishes and are particularly important to conserving and restoring native and at-risk species. We describe the seasonal and regional variation in the composition and abundance of fishes in interior tidal marsh channels in the upper San Francisco Estuary (SFE), and relate these to variation in environmental conditions. Fish were sampled quarterly using modified fyke nets from October 2003 to June 2005 in 18 interior tidal marsh channels spanning 3 distinct river systems: Petaluma River, Napa River and West Delta. We collected 116 samples and 9452 individuals of 30 fish species. Four non-native species dominated—Mississippi silverside, western mosquitofish, yellowfin goby, and rainwater killifish—with an additional 13 species occurring commonly (represented equally by natives and non-natives, residents and transients). Large seasonal differences in composition and abundance of fishes occurred, with the lowest abundances in winter and spring and highest abundances in summer and fall. Correlation of ordination scores and environmental variables further supported the importance of season, as well as fish species' status (native vs. non-native), feeding preference (pelagic vs. demersal), and marsh utilization (resident vs. transient), as factors influencing fish assemblage composition. The proximity of the marsh systems to freshwater and marine influences, which largely control salinity and temperature variation, explained 26% of the variation in fish composition, while channel geomorphology explained 22%. We recommend that both edge habitat (which may be beneficial to fish foraging success) and the extent of tidal connectivity (which allows access for fishes), in addition to location along the estuarine gradient, be considered in designing and managing tidal marsh restoration.

Keywords Tidal marsh · Fish ecology · Community composition · Estuarine ecology · Wetland restoration

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Introduction

The importance of tidal marsh systems to fish population dynamics and community ecology has become a leading research topic amongst fisheries biologists and wetland ecologists (Beck et al. 2001; Gray et al. 2002; Brown 2003; Minello et al. 2003; Sommer et al. 2007). There are no longer large commercial fisheries in The San Francisco Estuary (SFE), but there are currently several very large recreational fisheries that focus primarily on white sturgeon and striped bass which are worthy of conservation and restoration. There is additional concern about the unintended establishment of invasive fish species which compete with native fish species in the SFE, especially as tidal marsh habitat continues to be degraded or lost (Moyle 2008).

In recent years, a decline in the abundance of native and common non-native nekton species in the SFE has elevated concerns of a systematic problem now

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commonly referred to as the Pelagic Organism Decline (POD). Several possible mechanisms for this decline have been identified, including pollution, biological invasions and hydrological changes to freshwater inflow (Sommer et al. 2007). An additional threat to estuarine-dependent fish is the loss of wetland habitat, which is well documented to serve as essential nursery and feeding grounds for both resident and transient fishes (Kneib 1991, 1997; Goals Project 1999; Beck et al. 2001; McLain and Castillo 2010). Understanding how tidal marsh ecology generally and restoration in particular support fish taxa in the SFE is of great interest given the destruction, fragmentation and loss of wetland habitat throughout the region. Additional stress on the system is probable with the renewed interest of a peripheral canal which is designed to divert freshwater away from the main Western Delta (Nichols et al. 1986; Fleenor et al. 2008).

The SFE contains three types of marsh systems along a salinity gradient—salt water, brackish and freshwater—each contributing unique wetland habitat for assemblages of fishes and invertebrates. Salt marshes can be found throughout the lower SFE, bounded upstream by the furthest reaches of saltwater encroachment, a limit dependent on freshwater outflow (Walters et al. 1985). Brackish marsh, of which Suisun Marsh in the northern periphery of Suisun Bay represents the largest extent, is strongly influenced by freshwater from the Sacramento and San Joaquin River systems (Meng et al. 1994; Matern et al. 2002). Freshwater tidal habitats occur further upstream in the Sacramento – San Joaquin Delta (Brown and May 2006; Simenstad et al. 2000)

The tidal marsh systems of the SFE are dominated by a sinuous network of dendridic channels distributed throughout the marsh plain. Interior marsh channels are often highly variable in their vegetation, reflective of a distinct hydrographic signature and elevation, which in turn affects the distribution and abundance of terrestrial insects and aquatic invertebrate prey for resident and transient nekton (Minello et al. 1994; Zeff 1999). Tidal marsh creeks increase the amount of marsh-edge habitat, which is highly utilized in salt marshes (Minello and Rozas 2002). Interior marsh plain surfaces, which flood during higher spring tides, are only accessible by nekton through channels that extend into the reaches with higher elevation; here food quantity and quality have been suggested to be higher and fish can benefit from a refuge from predation (West and Zedler 2000). Thus the marsh plain surface often provides higher productivity and more abundant food resources for foraging fish albeit only during higher tides when access is available (Rozas and Zimmerman 2000; Madon et al. 2001; Able et al. 2006). Additionally, high densities of larval insect prey occur in shallow, emergent marsh habitat, which also suggests a benefit for fish growth (Kneib 2003; Grimaldo et al. 2004; Cohen and Bollens 2008).

Furthermore, edge habitat in marsh systems has been shown to be an important physical predictor of fish abundance and composition (Minello and Rozas 2002). Visintainer et al. (2006) demonstrated the importance of channel complexity in both low and high order systems in saltwater marshes in the SFE and found intertidal channels could enhance adult native fish populations. Important geomorphological characteristics included sinuous length, bifurcation ratio and channel order, all of which were found to affect the composition and abundance of resident or transient nekton. However, far less is known about fishes that use intertidal channels that extend deep into marsh interiors.

Our objectives in this study were to document the occurrence, abundance and composition of fishes within interior marsh channels across a range of tidal marsh systems in the upper SFE, and to relate these to various biological and physical environmental variables.

Materials and methods

Study system

We sampled each of six tidal marsh sites—Carl's Marsh, Bull Island, Coon Island, Pond 2a, Sherman Lake and Brown's Island—during 7 approximately quarterly sampling events: October 25–28/November 10–11, 2003; February 13–18, June 14–19 and September 26–30, 2004; and January 8–13, March 26–31 and June 19–24, 2005 (Fig. 1, Table 1). Three separate channels were sampled in each of the six marsh sites, except for Sherman Lake where two additional channels were added. Each marsh site was located in one of three large tidal river systems (regional sites) of the upper San Francisco Estuary (SFE): Petaluma River (Carl's Marsh), Napa River (Bull Island, Coon Island, Pond 2a), and the West Delta (Sherman Lake, Brown's Island) (Fig. 1). The six tidal marshes varied

markedly in size and geographic position, as did the length of the channels sampled (Table 1).

Marsh channel edge

We define channel edge as twice the sinuous channel length. Channel length measurements were performed using aerial photographs taken in 2003 and 2004 which were ortho-rectified using USGS digital elevation models spaced at 10 m and re-sampled to 1 m spot elevations. Final post-processing standards conserved sub-meter accuracy to 0.3–0.75 m. Final images were imported into ArcView GIS software (version 9.0) to measure the total sinuous channel lengths from the fyke net mouth to the visible upstream end of the channel. Channel edge was then calculated as twice the sinuous channel length.

Hydrography

Salinity and temperature were measured using a YSI© (model 85) probe at each channel immediately following deployment of the fyke net. A water column mean was calculated from surface and near bottom measurements. Water flow data were obtained from the Department of Water Resources DAYFLOW program (http://www.water.ca.gov/dayflow/) which provides daily averages of Delta outflow.

Fish sampling

Fish samples were collected using a fyke net with a mouth size of 1.0 m^2 and constructed of 3.2 mm nylon mesh. Fyke nets were set at slack high water during moderate spring tides several meters upstream of the mouth of each channel and recovered when the channel was dry. Channels in Sherman Lake did not dewater completely at low tide which resulted in standing water present when the fyke nets were removed. Samples were collected at night except in October 2003, February 2004 and January 2005 when high tide occurred during the daytime. Sectional wings (6.4 mm nylon mesh) extending onto the marsh plain were added as necessary to ensure capture of all fish species in the local channel watershed. During the ebbing tide, the live cod-end was checked every 30–60 min for captured fish. The first 50 individuals of each species captured from a given net set were identified, counted, measured for total length, weighed and promptly returned to the channel downstream of the fyke net. Individuals remaining in the net at low tide when the fyke net was removed were preserved in dilute formalin (10%) for later identification and measurement in the laboratory. Fish and hydrographic sampling of the 3 channels at any given marsh site took one full day, which resulted in a total of 6 consecutive days to sample the 6 marsh sites.

Data reduction and statistical analyses

Each fyke net set was considered one sample unit. To prepare the final data set for multivariate analysis, several steps of data transformation and total matrix review were performed. To allow for comparisons of fish abundance and composition between channels from different sites, each fish count was normalized to the edge length (fish per meter) of that particular channel. To reduce the effects of large catches, species abundances were then $\log_{10}$-transformed and species that did not appear in >5% of the total number of samples (i.e., rare species) were removed entirely. Outlier analyses were then performed; no samples or species scores were greater than 2 SD above the mean average distance and thus all were retained for subsequent analyses. The final data matrix included 116 samples (fyke net sets) and 30 species.

For each sample, we also calculated three biological indices based on the percentage of fish species that were 1) native vs. alien, 2) resident vs. transient, and 3) demersal vs. pelagic (Moyle 2002). We define a resident fish as a species that is capable of residing in a marsh system during all life stages and is able to feed primarily on marsh prey. Transient fish are generally more motile and can migrate through a marsh quickly with reduced site fidelity. Multivariate analyses were performed using the software package PC-ORD (McCune and Mefford 2006) v5.0.

Cluster analysis of samples used a hierarchical agglomerative clustering, Sørensen (Bray-Curtis) distances, with a Flexible-Beta (β=−0.25) linkage method. Determining where to cut the dendrogram was based on interpretability and meaningful clusters, i.e., conserving the most amount of information without diluting the samples. Indicator Species Analysis (ISA) identified taxa that were both frequently occurring and abundant and assigned each taxon an indicator value based on cluster fidelity.

To examine variation in the community composition of fish, we used non-metric multidimensional

scaling (NMS) of log-transformed abundance values normalized to channel edge using the Sørensen (Bray-Curtis) distances measure. To further explain variation therein, we correlated NMS axis scores with seven environmental variables: salinity, temperature, daily average water flow, channel length, month, region, time, and distance to the mouth of the estuary (i.e., the Golden Gate), and to the three biological (fish) indices: 1) native vs. alien, 2) resident vs. transient, and 3) demersal vs. pelagic

Results

Hydrography

Salinity and temperature fluctuations followed typical seasonal patterns, with the highest recorded values for both variables occurring in September and October across all sites (Table 4). Temperature minima occurred in January and salinity minima in March, reflective of winter storm activity and cooler air temperatures. Regional differences in hydrographic properties were representative of the sites' proximity to the freshwater source of the San Joaquin-Sacramento rivers (West Delta sites) and/or the marine influence of the Pacific Ocean (Petaluma River site). In June 2005, salinity was markedly lower than in June 2004 across all sites. An expected salinity gradient occurred across the Napa sites: Bull Island was often the freshest (particularly during spring), while Coon Island and Pond 2A (closest to the Bay) were the most saline. Carl's Marsh showed the largest variation in salinity from a low of 5.4 ppt in January to a high of 27.8 ppt in September. Salinity variation in the West Delta sites, Brown's Island and Sherman Lake, ranged from 0 to 3.5 ppt, and was often less than 1. Temperature variability followed a similar pattern seen at the other sites.

Regional and seasonal variation in abundance of fishes

From 116 fyke net sets, we collected 9452 individual fish represented by 30 species. Four non-native species dominated the catches (Mississippi silverside, mosquitofish, yellowfin goby and rainwater killifish) and accounted for 90% of all fish captured (Table 2). Another 17 species were frequent and abundant and were represented equally by natives and non-natives, residents and transients.

Fig. 1 The study area included three main regions along the axis of the upper San Francisco Estuary: 1a. Petaluma River, 1b. Napa River, and 1c. Western Delta. Each region contained 1–3 distinguishable tidal marshes, and we sampled at least 3 tidal channels (marked with an *open circle*) for fish and hydrography in each marsh

The seasonal variation in fish abundance was high, with the largest catches often occurring in fall (September/October), and the lowest during February or March (Fig. 2). The seasonal patterns were consistent across each of the six marsh sites. Regional variation in abundance was much lower, with similar fish densities occurring at all Petaluma and Napa sites, but with notable differences occurring between the two West Delta sites. The lowest abundances consistently occurred at Sherman Lake and the highest occurred at Brown's Island (Fig. 2). Carl's Marsh had the lowest abundances during spring, with increased abundance during June and again in October (Fig. 2a). The Napa sites were dominated by Mississippi silversides year-round, but particularly during the fall (Fig. 2b). The West Delta sites also exhibited seasonal differences in abundance between spring and fall and were numerically dominated by western mosquitofish (Fig. 2c).

Ordination analysis: community composition and environmental correlates

A 3-axis configuration was determined to be the most appropriate multivariate solution based on a significant Monte Carlo randomization test, low stress (stress= 0.18), and low instability of the final ordination (Table 3). Axes 2 and 3 were the most informative, explaining 48% of the total matrix variation (axis 2: 26%, axis 3: 22%), with axis 1 explaining 19%.

Environmental variables most highly correlated with axis scores included month and water flow, temperature, and to a lesser degree, salinity (Table 3). Axis 2 was also strongly correlated with samples dominated by native species (low axis score) vs. samples dominated by non-native species (high axis score). Axis 3 had the strongest correlation with channel edge, while all other environmental variables correlated extremely poorly. Axis 3 also reflected differences in scores among samples dominated by residents (which scored higher) vs. samples dominated

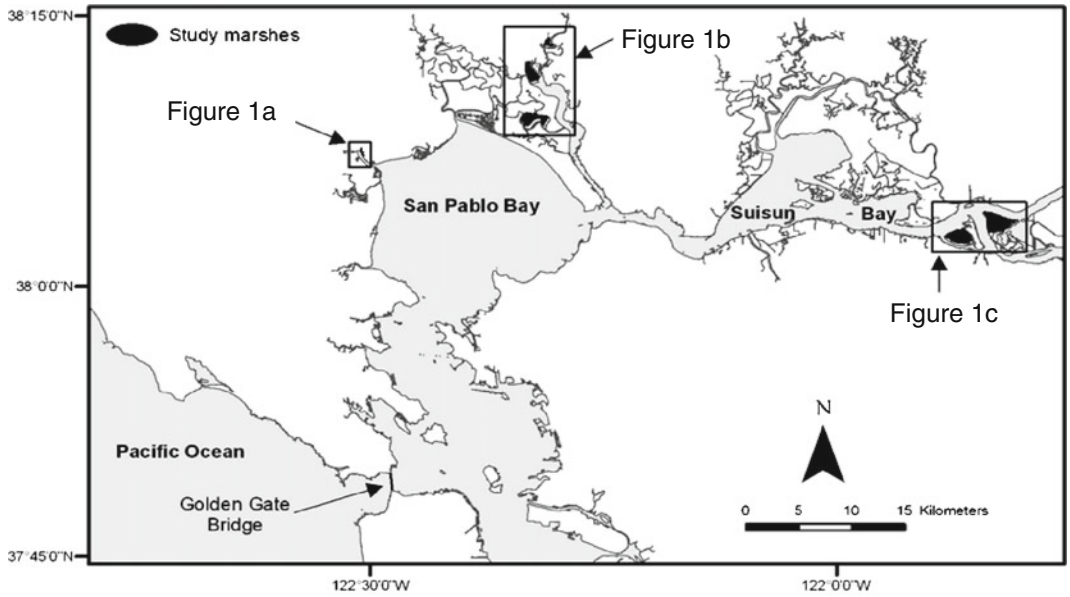

Figure 1

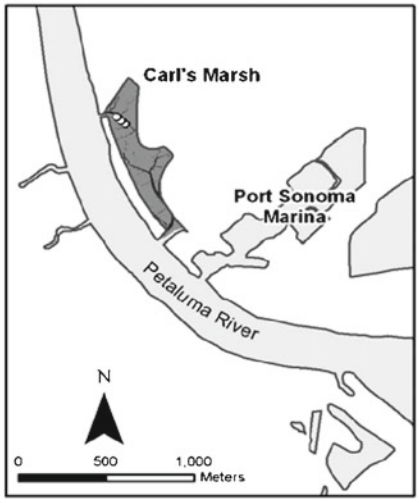

Figure 1a

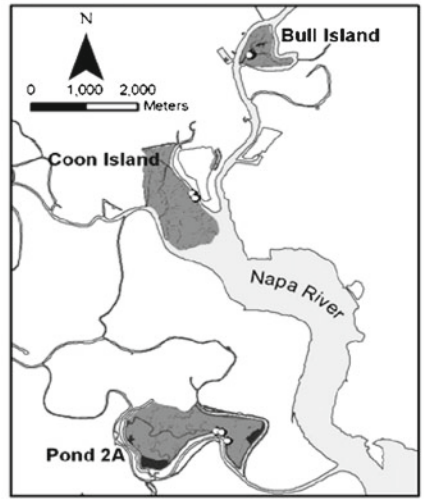

Figure 1b

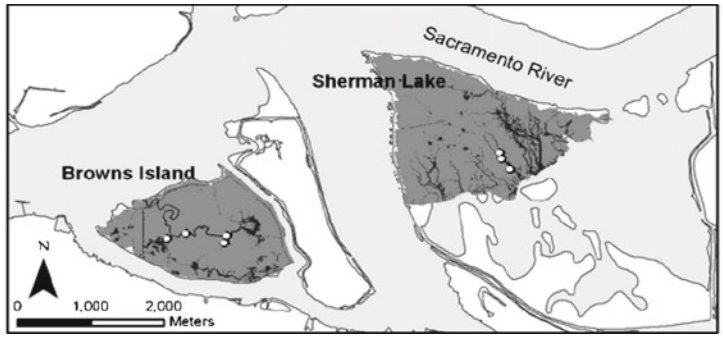

Figure 1c

Table 1 Summary table of the six marshes sampled across the three river systems. Distance to the Golden Gate measures the sinuous length along the estuary axis from the channel mouth. Channel length is given for each of the 3 channels sampled with the two additional channels sampled in the West Delta sites noted in parenthesis

River system	Marsh sampled	Distance to golden gate (km)	Channel length (m)		
			#1	#2	#3
Petaluma River	Carl's marsh	44.2	21	54	88
Napa River	Pond 2A	59.6	94	415	662
	Coon Island	63.5	221	213	167
	Bull Island	66.2	125	86	79
West Delta	Brown's Island	83.5	143	26	21
	Sherman Lake	88.3	52 (466)	95 (350)	70

by transients (which scored lower). Axis 1 correlates included region (Petaluma, Napa, and West Delta), distance to the Golden Gate, and samples dominated by demersal vs. pelagic species.

The ordination of samples is depicted with line plots to illustrate non-linear differences in sample scores and to identify where trends were not conserved across sites. The strongest differences in axis scores occurred seasonally, expressed largely on axis 2 between January, February and March on the one hand, and June, September and October on the other, particularly in Carl's Marsh and Bull's Island (Fig. 3). The West Delta sites showed the least amount of variation along axis 2. Although month did not correlate at all with axis 3, a strong division occurred at Carl's Marsh between the Winter/Spring and Summer/Fall. Strong regional differences in scores on axis 1 were present between Carl's Marsh (neutral on axis 1) and Brown's Island and Sherman Lake (very low on axis 1). Napa River sites tended to score similar to that of Carl's Marsh. Axis 3 showed the greatest amount of within-site variation (i.e., difference in scores between channels). Carl's Marsh exhibited large differences in individual channel scores during most samplings, as did the two West Delta sites (Sherman Lake, Brown's Island). Napa River sites showed only moderate differences within channel scores (e.g., Pond 2a).

Channel length was associated with the composition of fishes at certain sites (Table 3), as seen in plots of mean axis 3 scores against channel edge length. In general, longer channels scored lower on axis three and shorter channels scored higher.

Hierarchical clustering and indicator species analysis

To simplify interpretation, hierarchical clustering was utilized to reduce the 116 fyke net sets into a small number of groups. Cluster analysis revealed 7 distinguishable groups, with major divisions primarily between quarterly sampling events (vs. among channels) (Fig. 6). The first level of separation was between groups 5, 6, 4, 7 and 1, 3, 2, which reflected two predominant seasons: Winter/Spring (January, February, March) and Summer/Fall (June, September, October). There were several groups that separated by region (e.g., groups 3 and 4). For most dates, all three channels from any given marsh site were confined to one cluster group, or closely grouped to a nearby cluster branch.

Four of the 7 major clusters are represented by significant indicator taxa, with the three remaining clusters distinguishable by specific taxa (Table 5). Group 7 indicator species included yellowfin goby and prickly sculpin. Bay goby and Sacramento splittail were also numerically important species in this group, but only weakly. Group 5 indicator species included staghorn sculpin, Pacific herring, and threespine stickleback. Group 3 was strongly represented by western mosquitofish and rainwater killifish and weakly associated with tule perch. Group 2 was represented by Mississippi silverside and striped bass, and to a lesser degree, American shad and longjaw mudsucker. Group 1 contained no significant indicator species, but was weakly associated to shimofuri goby, Chinook salmon and threadfin shad. Group 6 also contained no significant indicator species; however, Chinook salmon, threadfin shad, and splittail (taxa found in Group 1) all exhibited high abundance and occurred relatively frequently within the samples of that group. Group 4 was the most unorganized group, with no indicator taxa and few loyal species.

Ordination of the 116 samples allowed the data to be viewed in 3 dimensions, vs. the 2 dimensions limited by the dendrogram. Samples were distinguished

Table 2 Fish taxa captured during the study are listed in descending order of abundance. Additional columns include common name abbreviaitons (Code), feeding preference (D) emersal or (P)elagic, marsh fidelity (R)esidents or (T)ransient, and mean size and size range

Scientific name	Common name	Code	Total Count (n)	Feeding preference	Marsh fidelity	Mean size (cm)	Size range (cm)
Menidia beryllina	Inland silverside [i]	IS	5765	P	T	5.0	1.4–10.2
Gambusia affinis	Mosquitofish [i]	GAM	1792	P	R	3.1	1.5–6.5
Acanthogobius flavimanus	Yellowfin goby [i]	YG	641	D	R	6.4	2.1–21.4
Lucania parva	Rainwater killifish [i]	RK	258	P	R	2.9	1.4–5.3
Gasterosteus aculeatus	Threespine stickleback [n]	TH	220	P	R	3.6	1.6–5.6
Hysterocarpus traskii	Tule perch [n]	TP	174	P	R	8.5	1.8–16.7
Clupea pallasi	Pacific herring [n]	PH	121	P	T	3.2	2.3–8.0
Pogonichthys macrolepidotus	Sacramento splittail [n]	SPT	96	D	T	13.6	4.4–36.6
Cottus asper	Prickly sculpin [n]	PS	77	D	R	5.7	1.6–11.0
Morone saxatilis	Striped bass [i]	SB	74	P	T	16.5	1.9–38.5
Leptocottus armatus	Staghorn sculpin [n]	SS	62	D	T	4.9	2.0–11.4
Lepidogobius lepidus	Bay goby [n]	BG	46	D	T	4.0	2.8–6.2
Dorosoma petenense	Threadfin shad [i]	TS	28	P	T	9.0	4.4–15.7
Tridentiger bifasciatus	Shimofuri goby [i]	SG	26	D	R	6.9	2.2–9.6
Lavinia exilicauda	Hitch [n]	HT	11	P	R	7.9	6.1–10.6
Oncorhynchus tshawytscha	Chinook salmon [n]	CS	9	P	T	3.7	3.1–4.4
Alosa sapidissima	American shad [i]	AS	8	D	T	11.2	8.3–19.2
Gillichthys mirabilis	Longjaw mudsucker [n]	LM	7	D	T	10.3	7.8–12.8
Archoplites interruptus	Sacramento perch [n]	SAP	7	P	R	14.1	11.8–20.4
Hypomesus transpacificus	Delta smelt [n]	DS	6	P	T	5.6	3.4–7.5
Spirinchus thaleichthys	Longfin smelt [n]	LS	5	P	T	6.0	3.8–7.0
Cymatogaster aggregata	Shiner perch [n]	SHP	4	D	R	8.1	6.0–9.3
Tridentiger trigonocephalus	Chameleon goby [n]	CG	4	P	T	5.6	2.7–10.3
Engraulis mordax	Northern anchovy [n]	NA	3	P	T	8.9	8.4–9.5
Micropterus dolomieui	Smallmouth bass [i]	SMB	2	P	T	14.3	14.3–14.3
Cyprinus carpio	Common carp [n]	CC	2	D	T	6.5	4.3–8.6
Platichthys stellatus	Starry flounder [n]	SF	1	D	T		8.8
Atherinops affinis	Topsmelt [n]	TOP	1	P	T		35.0
Ameiurus nebulosus	Brown bullhead [n]	BB	1	D	T		28.5
Ptychocheilus grandis	Sacramento pikeminnow [n]	SP	1	P	T		8.1

by 7 possible icons relating to the data reduction of the hierarchical cluster analysis (Fig. 4). Group 5 scored the lowest on axis 2. Other groups to score low on axis 2 included 4 and 6. Group 2 scored the highest on axis 2, and group 1 also scored relatively high. Along axis 3, groups 5 and 3 scored high, and groups 6, 1 and 2 scored low. On axis 1, groups 4 and 3 scored very low, with the rest of the groups scoring higher.

Ordination overlay of dominant taxa

A species overlay of the 17 dominant taxa captured in this study assisted in visualizing the environmental variables most highly correlated with individual taxa (Fig. 5). Each arrow in Fig. 5 represents a vector expressing the direction and magnitude (r^2) of a particular environmental correlate. Along axis 2, native species scored the lowest and non-natives scored the highest.

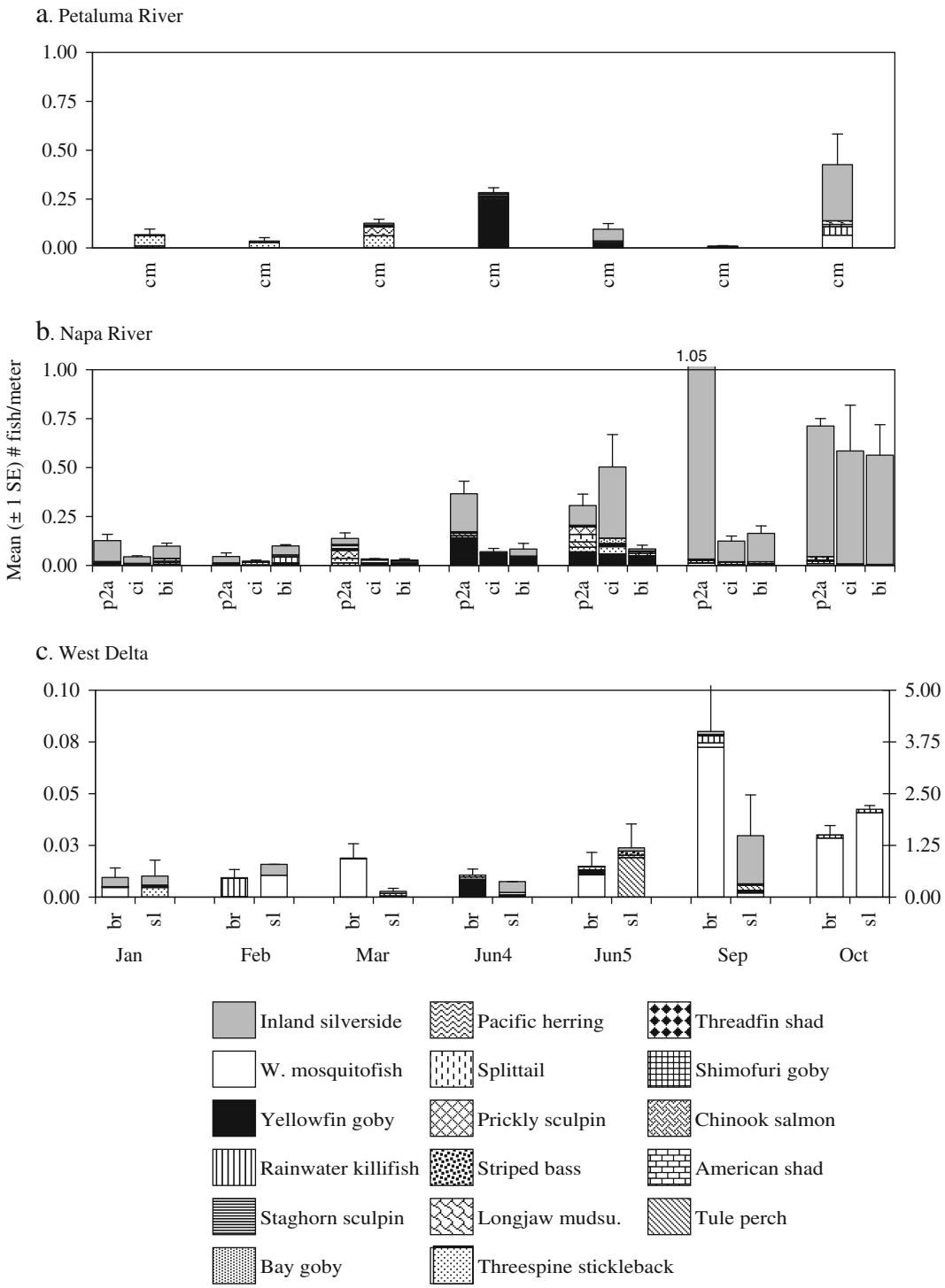

Fig. 2 Mean abundance of fishes by region **a** Petaluma River **b** Napa River **c** West Delta and season. Categories on the x-axis are listed in calendar order to emphasize seasonal variation, but do not always reflect the chronological order in which samples were collected: Jan = January, 2005, Feb = February, 2004, Mar = March, 2005, Jun4 = June, 2004, Jun5 = June, 2005, Sep = September, 2004, Oct = October, 2003. Brown's Island values are depicted on the secondary axis. Marsh abbreviations: *cm* Carl's Marsh; *p2a* Pond 2A; *ci* Coon Island, *bi* Bull Island; *br* Brown's Island; *sl* Sherman Lake

Table 3 Correlation coefficients (r-sq) of two general categories of environmental variables (physical and biological) and axis scores from the main ordination

Axis:	1	2	3
% Variation	0.190	0.256	0.216
Physical variables			
Edge	0.054	0.015	0.248
Month	0.014	0.244	0.000
Region	0.209	0.000	0.005
Temperature	0.093	0.206	0.008
Salinity	0.076	0.170	0.042
Day/night	0.105	0.024	0.000
Flow	0.009	0.188	0.010
Distance to GG	0.186	0.006	0.003
Biological variables			
Native	0.124	0.515	0.099
Pelagic	0.329	0.014	0.085
Resident	0.045	0.162	0.503

Strongly correlated native species included staghorn sculpin, Pacific herring, Chinook salmon and threespine stickleback. Non-native species that scored the highest on axis 2 included Mississippi silversides, American shad, striped bass, bay goby and western mosquitofish.

Axis 3 generally separated resident vs. transient species, where residents scored higher and transients scored lower. Strongly correlated residents included threespine stickleback, western mosquitofish, yellowfin goby, tule perch, and killifish; transients were represented by threadfin shad, shimofuri goby, Chinook salmon, Mississippi silverside and American shad.

Discussion

Seasonal variability in fish abundance and composition

The taxa collected during this study were generally consistent with earlier studies in nearby systems

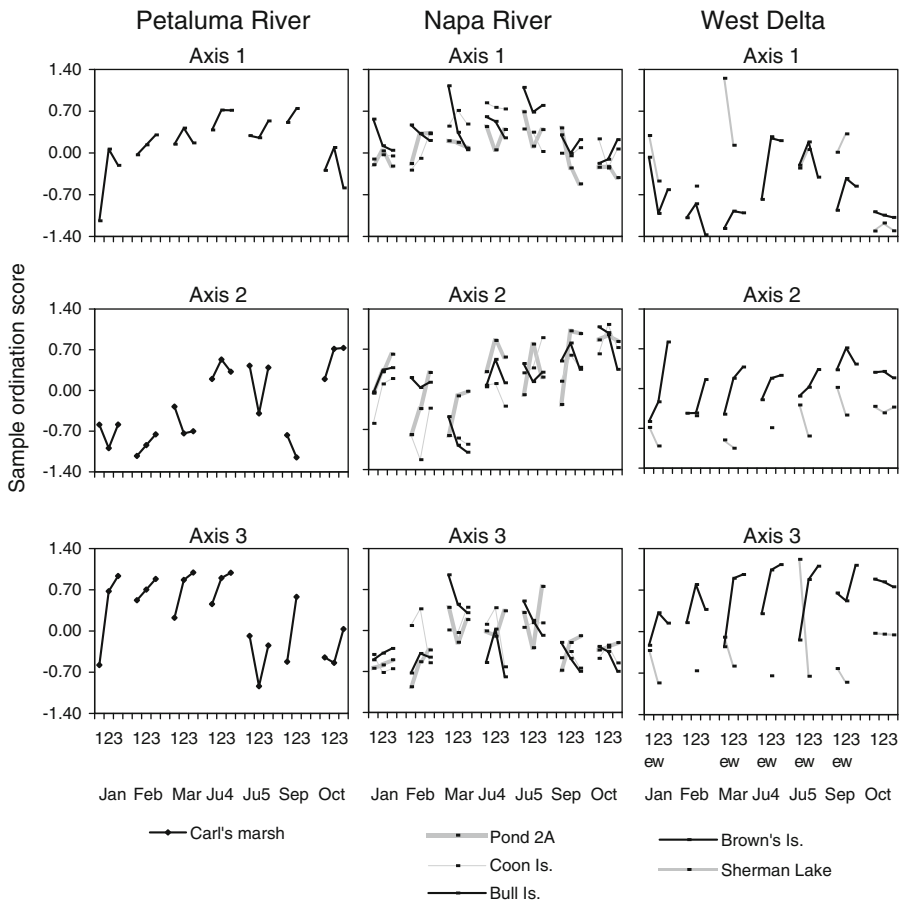

Fig. 3 Non metric multidimensional scaling 3-axis solution sample points expressed as line plots. Sample ordination scores are plotted separately for each axis to identify any trends and variation within each region. The x-axis represents the 3 channels sampled within each of the six marshes (labeled 1, 2, 3), and clustered in calendar order, not necessarily chronological order. At Sherman Lake in the West Delta, the 3 primary channels were abandoned after the second cruise, and two new channels were subsequently sampled and named (e) East and (w) West

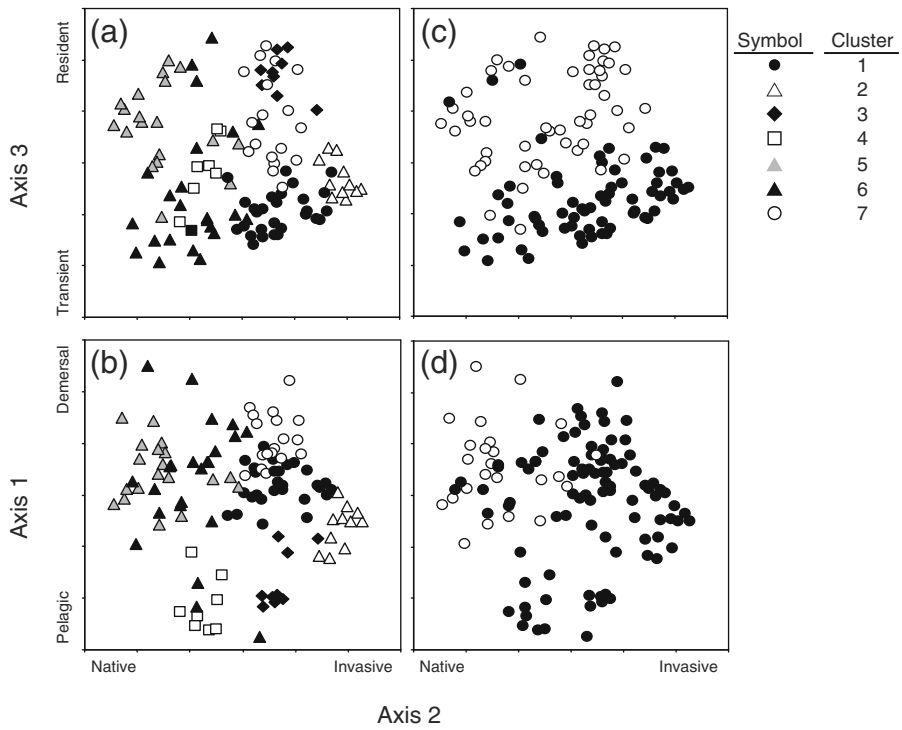

Fig. 4 Highlights of the 192 sample/3 axis main ordination. **a** Axes 2 vs. 3 for the seven main cluster groups. **b** Axes 2 vs. 1. **c** Samples dominated by natives (*open circles*). **d** Samples dominated by pelagics (*open circles*)

(Meng et al. 1994; Matern et al. 2002; Visintainer et al. 2006; Cohen and Bollens 2008). Many of the dominant species (e.g., Mississippi silverside, western mosquitofish and yellowfin goby) are common inhabitants of shallow water environments in the SFE and can tolerate large fluctuations in salinity and temperature as they move along the upper estuary corridor between freshwater, brackish and saltwater tidal marshes (Feyrer and Healey 2003; Brown and May 2006). The slight to modest difference in rank-order of fish abundance in our study is likely a result of different sampling methods and habitats sampled.

The greatest variation in abundance in our study occurred seasonally, with the majority of species exhibiting pronounced seasonal peaks followed by months of absence. This reflects a well documented pattern of abundance in the SFE in which native species (e.g. staghorn sculpin, Chinook salmon and Pacific herring) are often the most abundant in spring months, in contrast to non-native species (Mississippi silversides and yellowfin goby) which are more abundant in late summer and fall (Moyle 2002; Dege and Brown 2004). Our ordination results suggest that low salinity, low temperature and high water flow can positively affect native species. We observed this not only in spring, but also in June 2005, during a later-than-usual high flow event in which three native species (prickly sculpin, splittail and threespine stickleback) showed increased abundance across all six of our marsh sites.

This seasonal change in fish composition paralleled a well-documented shift in the hydrology from cold temperature and lower salinities in winter and spring to warmer and more saline conditions in summer and late fall. Salinity, temperature and outflow are well-known drivers that can affect the distribution of fish in estuarine environments (Meng et al. 1994; Thiel et al. 1995; Kimmerer 2002; Rountree and Able 2007). In our study, spring samples were dominated by species associated with lower salinities and cooler temperatures (e.g., juvenile Pacific herring and tule perch), while fall and summer exhibited high abundance of Mississippi silverside, which are associated with warmer temperatures and more saline waters, although populations have been reported in nearby lakes and reservoirs (Moyle 2002). Salinity and temperature were moderately correlated with axis 2 scores, as the relationship was weakened by the freshwater tidal marshes of the West Delta, which showed very little variation along axis 2.

Indeed, our results suggest that salinity and temperature do not always drive changes in composition of fish assemblages. For example, in June 2005

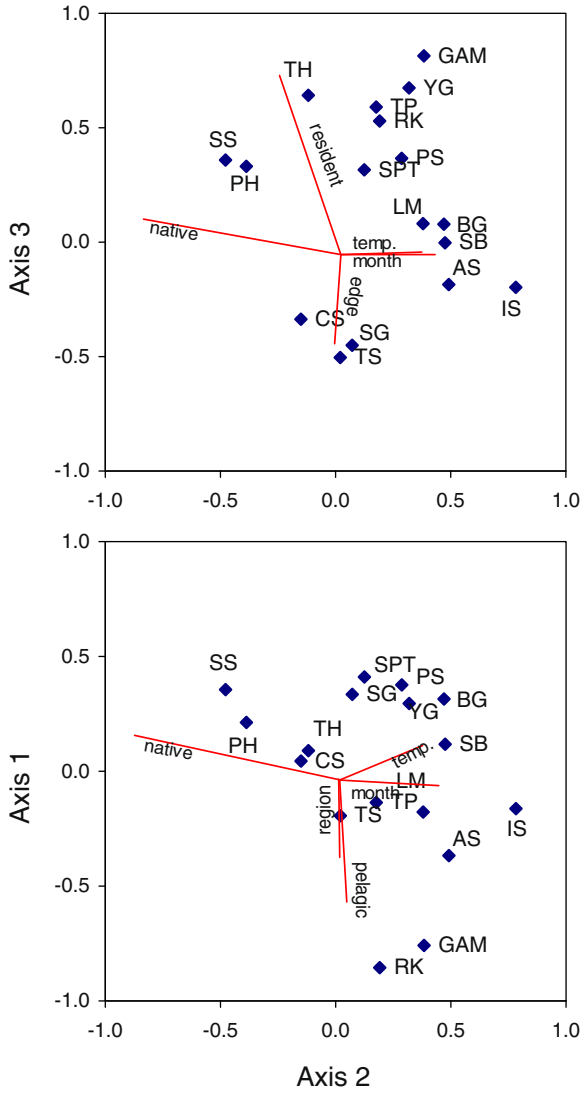

Fig. 5 Ordination overlay of the seventeen taxa used in the NMS analyses comparing axis 2 against axis 3 (*top panel*) and axis 1 (*lower panel*). Environmental variables that correlated highly with sample scores are expressed as vectors, such that arrow length is proportional to r-sq value, and direction relates axes to either a positive or negative correlation. Each vector is labeled with its corresponding environmental variable

unseasonably low salinities were recorded at all six marshes yet hierarchical classification placed a majority of the samples collected during both June sampling periods (2004 and 2005) into the same group, which underscores the ability of many estuarine fish species to endure large fluctuations in salinity. Furthermore, during January and February, a salinity gradient between the three Napa sites occurred without an apparent response in the composition of fishes. Finally, higher and more variable flows in June 2005 may have simply moved the center of mass of native fishes more into our sampling areas, in which case the higher abundances observed were a function of distribution, not increased population size.

Spatial variability in fish abundance and composition

Regional (between site) variation in abundance of fishes was generally quite low, with the notable exception of the West Delta sites (Brown's Island and Sherman Lake). This was due to two reasons: the large catches of a single species (western mosquitofish) at Brown's Island, and the likely underestimation of fish densities at Sherman Lake due to sampling difficulties caused by floating and submerged aquatic vegetation. Also, the channels at Sherman Lake never dewatered completely, resulting in standing water at low tide, which decreased sample efficiency.

Regional variation in composition of fish assemblages was also low, with the largest (but still modest) differences occurring between the West Delta marsh sites (Brown's Island and Sherman Lake) and the four downstream marsh sites in the Napa and Petaluma Rivers. The West Delta sites are markedly different hydrographically than the Petaluma and Napa River sites as they are positioned further upstream and are less affected by marine influence of the lower estuary and more influenced by the large Sacramento - San Joaquin river system upstream. For example, Pacific herring and staghorn sculpin, two species that utilize the upper SFE during their spawning, were never captured within the West Delta sites, likely because they were unable to tolerate these primarily freshwater habitats. However, for the fish assemblage as a whole, the low spatial (regional) variation in composition is not surprising given the wide environmental tolerances of many estuarine species (Baxter et al. 1999).

Environmental variables and correlates

Our results suggest that both biological and physical environmental variables influence the abundance and composition of fish in tidal marshes of the upper SFE. More specifically, with regard to biological processes, our ordination results showed that taxa with similar patterns of seasonal abundance ordinated similarly, with certain taxa overlapping. This partial overlap of important taxa in time and space suggests potential competition on the one hand, e.g., between yellowfin

goby and bay goby, and predatory pressure on the other hand, e.g., of striped bass on splittail. Nobriga and Feyrer (2007) reported similar findings from other parts of the SFE, showing that striped bass, Mississippi silverside and American shad were strongly correlated to the same ordination axes.

Few large piscivores were captured in our study, supporting the hypothesis that prey fish species may be using interior marsh habitats as a refuge from predation, although high predation rates have been shown to occur at the mouths of channels during ebb tide (Tupper and Able 2000). Low piscivore fish density is not an unexpected result given the small size of the channels sampled, and the known occurrence and abundance of piscivorous species such as striped and largemouth bass in subtidal habitats in SFE marshes (Feyrer and Healey 2003).

Prey resources can also influence nekton abundance and composition in marsh systems. Simenstad et al. (2000) determined that terrestrial insects are common in the diet of nekton from tidal freshwater marshes and are correlated with nearby marsh plant heterogeneity and abundance. Also, Grimaldo et al. (2009) identified large-scale shifts in shallow water food pathways that they attributed to declines in abundance of native pelagic fishes and other nearshore consumers. Additionally, Feyrer et al. (2007) found the diet of age-0 splittail differed between the Petaluma River and the Napa River, partially due to these rivers' position along the upper estuarine gradient. In sampling undertaken concurrently with ours, Parker et al. (unpublished) measured marsh plant composition and density at each of our marsh sites and found terrestrial plant communities varied moderately between sites, primarily reflecting the salinity gradient from the most downstream marsh (Carl's Marsh) to the most upstream marsh (Sherman Lake). These differences in plant composition along the greater estuary axis, and therefore the variability in density and type of prey resources, could explain a portion of the overall regional variation in our nekton data (e.g. Petaluma River vs. West Delta), although our results do not indicate finer-scale regional differences in fish composition, e.g., between Petaluma River and Napa River sites.

Channel geomorphology (i.e., channel length) was a particularly important environmental correlate that emerged from our results. Specifically, variation in ordination scores along axis 3 suggests a change in composition between channels of different sizes. This trend was conserved across all six marsh sites, with the strongest pattern occurring at Carl's Marsh and Brown's Island. At Sherman Lake, the two channels added to our sampling were significantly longer, wider, and deeper than the original three channels, and returned different axis scores (particularly the "west" channel). However, channels in the Napa River sites did not follow this pattern as strongly, except at Pond 2A. The individual line plots of samples scores also depict within-site compositional variability, and identify instances where the three channels scored differently (Fig. 5). The channels at Carl's Marsh and Brown's Island were the smallest of the entire study and were the strongest drivers of this correlation, thereby eliminating a regional influence. Perhaps a threshold exists whereby smaller channels (<50 m) might be more susceptible to changes in hydrology and landscape effects associated with runoff. For instance, Kirby-Smith et al. (2001) found connectivity of channels and the length of the route, which were directly related to hydrologic characteristics and tidal fluctuations, to be important to fishes. Rozas (1995) showed that nekton access to marsh systems can be directly attributed to hydroperiod and indirectly to vegetation colonization and composition. La Peyre and Birdsong (2008) showed that nekton composition and abundance varied between channels with varying degrees of slope and associated marsh elevations.

Further evidence of geomorphological influence on fish assemblage composition can be seen in the markedly different axis 3 scores between our long channels (>750 m) at Sherman Lake vs. the smaller channels at nearby Brown's Island. Similarly, Visintainer et al. (2006) found that channel system order (e.g., between single and multi-order channels) influenced fish composition, with resident species preferring single order channels. We found a similar result, with a gradient of channel utilization occurring among species from resident to transient. This gradient was most pronounced along samples dominated by threespine stickleback, mosquitofish, and raiwater killifish on one end (residents preferring short channels), and samples with Chinook salmon, threadfin shad, and American shad on the other end (transients preferring longer channels). Our results, as well as those of previous studies, point to channel geomorphology as an important driver of fish abundance and composition in tidal marsh systems.

The separation between samples dominated by resident and transient species was not related to season or region. Furthermore, many of these resident species

are native (e.g., prickly sculpin, threespine stickleback), which suggests different patterns of marsh use. Similarly, hierarchical clustering identified a division between samples dominated by demersal species and pelagic species, in this case largely driven by catches of demersal species (i.e., yellowfin goby, bay goby, shimofuri goby, and prickly sculpin) which ordinated quite differently than pelagic taxa such as mosquitofish, killifish, and the two shad species. Similarly, Moyle and Bennett (2008) found five major fish groupings in the upper SFE, separated from one another based on life history strategies and environmental tolerances. La Peyre and Birdsong (2008) also showed that resident fish species preferred gently sloping edge habitats, which permitted better access to marsh plain habitats during longer tidal inundations (also see McIvor and Odum 1988; Allen et al. 2007). Thus habitat utilization patterns driven by life history characteristics would appear to be a substantial factor driving fish assemblage structure of these estuarine species in interior tidal marsh channels in the SFE.

Finally, we note that non-native fishes dominated our catches, compromising 90% of all fish captured in our study. This is consistent with other recent studies of SFE marshes (Simenstad et al. 2000; Brown and May 2006; Brown and Michniuk 2007). Native species in the SFE have decreased dramatically in recent years (Brown and May 2006; Sommer et al. 2007), and were primarily represented in our study by seasonal inhabitants such as Pacific herring and staghorn sculpin. Delta smelt and longfin smelt, both listed currently on the State and/or Federally listed endangered and threatened animals of California, were captured in low numbers and therefore were not included in our analyses; however their presence is noteworthy given their general distribution in deeper, subtidal reaches, particularly in Suisun Bay (Hobbs et al. 2006). The SFE is a highly altered and highly invaded ecosystem, particularly in the West Delta. This dominance by invasive species could be due to a number of factors, including reduced natural variability in hydrographic properties, disrupted predator–prey interactions, and skewed food web interactions (Kimmerer 2002; Grimaldo et al. 2009; Enright and Culberson 2010).

Summary and conclusions

We found that the greatest variation in composition and abundance of fishes in interior marsh channels in the upper SFE occurred seasonally, which likely reflects taxa with different spawning patterns seeking nursery and feeding opportunities provided by these shallow water edge habitats. Regional differences in fish composition occurred primarily between sites in freshwater tidal marshes versus those in brackish marshes, which were more frequented by species with greater salinity tolerances. The strong variations in fish composition and abundance were driven largely by salinity and temperature regimes that fluctuated between the wet and dry seasons, as well as regionally along the estuary axis.

In addition, the importance of species' status (native vs. non-native), feeding preference (pelagic vs. demersal), and marsh utilization (resident vs. transient) were the most important of the seven groups, resulting in four distinct fish groups: i) native species that were abundant in spring, ii) resident species common in June, iii) Mississippi silversides dominant in September and October, and iv) a group represented by western mosquitofish and rainwater killifish that distinguished the West Delta from the Napa and Petaluma rivers. Overall, non-native species dominated our catches.

We also found an important role of geomorphology in shaping the use of marsh habitat by different fish species, i.e., by providing edge habitat and connectivity to food resources on marsh plains, and/or as predator refugia in smaller channels. For transient native species, late winter and spring are important months for age-0 and juvenile fish, while native residents are dominant in June, a period that strongly overlaps with the occurrence of non-native taxa. Our results on habitat use of different fish species, especially between native and non-native species, should assist policy makers and managers attempting ecosystem restoration and native fish conservation in the SFE and elsewhere. More specifically, we recommend that both edge habitat (which may be beneficial to fish foraging success) and the extent of tidal connectivity (which allows access for fishes), in addition to marsh location along the estuarine gradient, be considered in designing and managing tidal marsh restoration.

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Appendix

Table 4 Mean salinity and temperature±1SD, of the six marshes (across the 3 main regions) sampled over the approximate quarterly sampling from October 2003 to June 2005. Cruises are listed in calendar order not cruise order: October 2003, February 2004, June 2004 (June-04), September 2004, January 2005, and June 2005 (June-05). ND = no data

	Region					
	Petaluma River	Napa River			West Delta	
	Carl's marsh	Pond 2A	Coon Is.	Bull Is.	Brown's Is.	Sherman Lake
a. Salinity						
January	5.4±0.17	4.9±0.35	3.3±1.10	1.5±0.03	0.5±0.19	0.4±0.21
February	11.0±0.32	7.3±0.30	7.5±0.18	0.2±0.00	0.1±0.00	0.0±0.00
March	7.1±0.31	2.9±0.06	1.4±0.16	0.6±0.00	0.3±0.21	0.2±0.07
June-04	22.0±0.22	18.2±0.20	17.2±0.07	16.7±0.16	2.3±0.16	1.1±0.00
June-05	11.0±0.18	7.4±0.06	7.1±0.13	6.6±0.03	0.1±0.02	0.1±0.00
September	27.8±5.33	19.5±2.20	21.1±0.29	20.3±2.00	3.4±0.35	1.3±0.00
October	24.1±0.00	19.7±0.00	nd	19.8±0.00	nd	2.5±0.11
b. Temperature						
January	9.5±0.14	9.8±0.11	9.0±0.71	9.0±0.03	8.8±0.18	8.9±0.21
February	11.8±0.04	12.9±0.17	11.7±0.06	12.9±0.12	9.8±0.03	nd
March	13.7±0.13	13.8±0.20	12.9±0.24	13.9±0.20	14.1±0.03	13.3±0.32
June-04	22.3±0.19	18.8±0.42	19.1±0.12	18.4±0.30	20.6±0.38	21.3±0.00
June-05	20.9±0.00	19.0±0.06	19.8±0.08	19.5±0.00	19.2±0.49	19.6±0.07
September	18.3±0.06	17.8±0.18	19.1±0.30	18.4±0.30	20.4±0.18	18.9±0.64
October	17.5±0.00	19.3±0.00	nd	19.0±0.00	nd	13.4±0.07

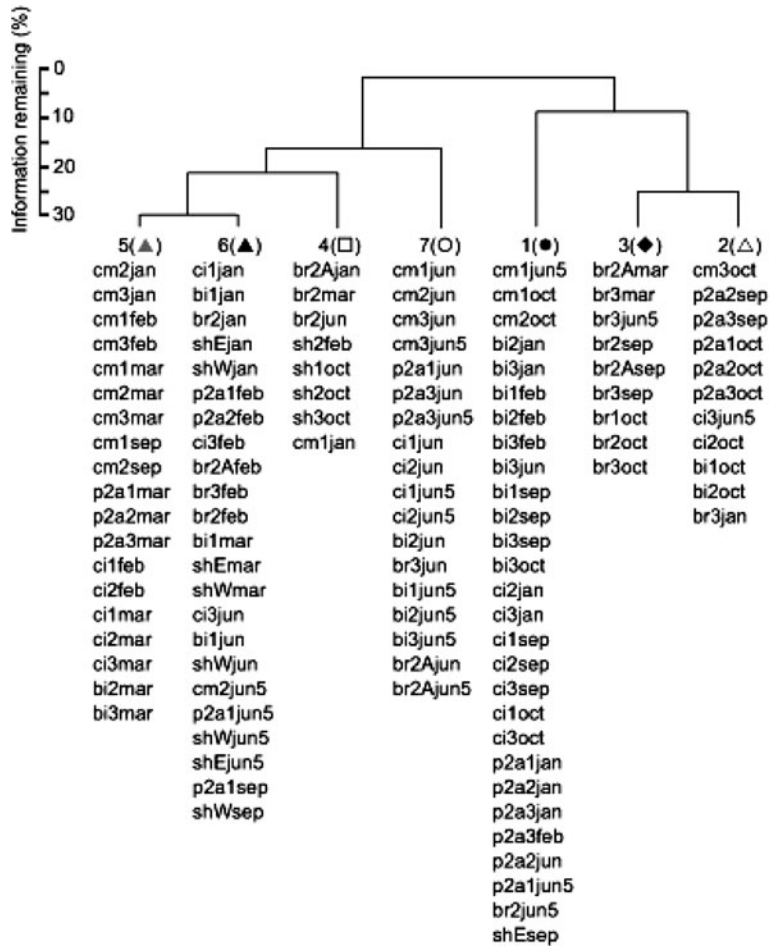

Fig. 6 A sample-cluster dendrogram showing the cut-off point which delineates the 7 major cluster groups. Wishart's Objective Function is shown as a percentage scale to convey the distance between groups, and was deemed the most interpretable (i.e., smallest number of groups, with the least amount of information lost) at approximately 30%. Listed below each cluster are the unique samples which are described by the following alpha-numeric codes (see Fig. 2 for marsh abbreviation codes): marsh abbreviation _channel#_month

Table 5 Indicator values (IV) were generated for seventeen fish species based on the 7 groups identified from the cluster analysis and tested for significance if a taxon was truly representative of that group (* $p<0.05$, ** $p<0.01$). Relative abundance is expressed as a percentage of the total abundance for any given species across the groups, and relative frequency is the percentage of the samples a taxon was present in each group

	Cluster															
	Relative abundance							Relative frequency								
Taxa	5	6	4	7	1	3	2	5	6	4	7	1	3	2	Indicator cluster	(IV)
Yellowfin goby	0	1	1	71	2	23	2	5	35	13	100	50	33	36	7	70.6**
Prickly sculpin	2	4	0	74	4	0	15	5	22	0	39	14	0	36	7	28.8**
Bay goby	1	4	0	42	3	0	50	5	9	0	28	4	0	9	7	11.7**
Splittail	7	24	0	53	10	0	7	11	9	0	17	11	0	9	7	8.9**
Staghorn sculpin	85	0	0	12	3	0	0	68	0	0	11	7	0	0	5	58.3**
Pacific herring	92	2	0	0	1	5	0	42	4	0	0	4	11	0	5	38.6**
Threespine stickleback	37	2	0	28	3	23	6	84	35	0	67	25	33	36	5	31.6**
Western mosquitofish	0	0	3	0	0	91	6	11	9	100	11	36	100	64	3	90.7**
Rainwater killifish	2	29	2	4	3	49	10	26	22	25	28	32	56	55	3	27.3**
Tule perch	1	13	11	29	8	34	3	16	43	25	33	32	33	27	3	11.3**

Table 5 (continued)

	Cluster															
	Relative abundance							Relative frequency								
Taxa	5	6	4	7	1	3	2	5	6	4	7	1	3	2	Indicator cluster	(IV)
Inland silverside	1	1	0	3	13	3	79	42	74	13	67	100	33	100	2	79.1**
Striped bass	6	3	0	31	8	0	52	21	13	0	28	18	0	45	2	23.6**
American shad	0	1	0	0	22	0	77	0	4	0	0	11	0	18	2	13.9**
Longjaw mudsucker	13	2	0	9	6	0	71	11	4	0	6	4	0	9	2	6.5**
Shimofuri goby	13	1	0	9	74	0	3	5	4	0	6	18	0	9	1	13.2**
Chinook salmon	18	21	0	0	61	0	0	5	9	0	0	11	0	0	1	6.5**
Threadfin shad	2	17	27	0	36	0	18	5	13	13	0	14	0	18	1	5.1**

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