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Fish Community Ecology in an Altered River Delta: Spatial Patterns in Species Composition, Life History Strategies, and Biomass

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ABSTRACT: We sampled nearshore fishes in the Sacramento-San Joaquin Delta, California, United States, during 2001 and 2003 with beach seines and gill nets. We addressed three questions. How and why did fish assemblages vary, and what local habitat features best explained the variation? Did spatial variation in assemblages reflect greater success of particular life history strategies? Did fish biomass vary among years or across habitats? Nonmetric multidimensional scaling showed that habitat variables had more influence on fish assemblages than temporal variables. Results from both gear types indicated fish assemblages varied between Sacramento and San Joaquin River sampling sites. Results from gill net sampling were less pronounced than those from beach seine sampling. The Sacramento and San Joaquin river sites differed most notably in terms of water clarity and abundance of submerged aquatic vegetation (SAV), suggesting a link between these habitat characteristics and fish relative abundance. Among-site differences in the relative abundance of periodic and equilibrium strategist species suggested a gradient in the importance of abiotic versus biotic community structuring mechanisms. Fish biomass varied among years, but was generally higher in SAV-dominated habitats than the turbid, open habitats in which we found highest abundances of striped bass *Morone saxatilis* and special-status native fishes such as delta smelt *Hypomesus transpacificus*, Chinook salmon *Oncorhyncus tschawytscha*, and splittail *Pogonichthys macrolepidotus*. The low abundance of special-status fishes in the comparatively productive SAV-dominated habitats suggests these species would benefit more from large-scale restoration actions that result in abiotic variability that mirrors natural river-estuary habitat than from actions that emphasize local (site-specific) productivity.

Introduction

The successful management, conservation, and restoration of estuarine biota depend on understanding the ecological processes that generate appropriate habitat characteristics (Day et al. 1995; Jassby et al. 1995). Many estuarine ecosystems are strongly influenced by human activities, and anthropogenic disturbances interact with natural environmental variability to control ecological processes (Livingston et al. 1997; Rose 2000). Fishes are conspicuous and economically important components of most estuaries (Houde and Rutherford 1993), and they respond to numerous environmental factors, making them useful indicators of estuarine habitat quality (Whitfield and Elliott 2002) and the subject of several recent investigations of long-term changes in North American estuaries (Matern et al. 2002; Hurst et al. 2004; O'Connell et al. 2004).

Salinity is often the major factor influencing fish assemblages in tidal river estuaries (Bulger et al. 1993; Wagner 1999). Tidal river estuaries grade from freshwater dominance at their landward edges to marine dominance at their seaward edges. Estuaries vary regarding the spatial and temporal mixing of riverine (freshwater flow) and marine (salinity) inputs. When this variability is temporally predictable, local faunas can use these forcing variables as cues to time reproduction, migrations, or other important life history traits (Jassby et al. 1995). Habitat alterations that change the interaction of water quality (river flow, salinity, or turbidity) with needed habitat structure (marshes, mangroves, shoals) can reduce estuarine habitat quality (Jassby et al. 1995; Rose 2000; Peterson 2003).

In the northern San Francisco Estuary, California, United States, nearshore fish communities, water quality, and habitat structure have all changed considerably over the last three decades (Matern et al. 2002). Estuarine productivity has declined at all trophic levels from phytoplankton (Jassby et al. 2002) to fish (Bennett and Moyle 1996). Native

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fishes have declined to a greater extent than nonnative fishes (Matern et al. 2002). This has generated considerable concern among fisheries agencies and motivated the implementation of large-scale restoration programs. The fish communities of the upper San Francisco Estuary are spatially heterogenous mixes of primarily nonnative species (Matern et al. 2002; Feyrer and Healey 2003; Grimaldo et al. 2004). The opportunities and limitations for native fish restoration remain poorly understood (Brown 2003). The present study was initiated to improve understanding of the structure and function of nearshore fish assemblages in the upper San Francisco Estuary by evaluating species relative abundance, relative abundance of life history strategies, and relative biomass. We addressed three questions. How and why did fish assemblages vary, and what local habitat features best explained the variation? Did spatial variation in assemblages reflect greater success of particular life history strategies? Did fish biomass vary among years or across habitats?

Materials and Methods

Study Area

The San Francisco Estuary and its large watershed have been modified substantially for a variety of human uses (Nichols et al. 1986). Damming of most major tributaries has dampened flow variability (Kimmerer 2002). Diversion of freshwater has greatly changed flow patterns in the tidal reaches of the Sacramento and San Joaquin Rivers. Conversion of marshes to agricultural and urban land uses has eliminated most historical fish and wildlife habitats. Changes in species composition at all trophic levels have significantly altered food web productivity via altered trophic linkages (Jassby et al. 2002; Feyrer et al. 2003). The Sacramento-San Joaquin Delta (Fig. 1) is the landward limit of the San Francisco Estuary and a water supply nexus for much of California's population (Arthur et al. 1996). The delta receives freshwater runoff from approximately 100,000 km^2 (40%) of California's surface area. Most natural runoff occurs during winter and spring (December-May), but significant proportions of natural runoff are captured in numerous reservoirs located throughout the Sacramento-San Joaquin watershed. Reservoir releases from the Sacramento River maintain year-around freshwater conditions in the delta. This supports regional agriculture and freshwater exports for agriculture and urban users to the south (Arthur et al. 1996; Kimmerer 2002). A highly variable average of 4.5 billion m^3 yr^{-1} of freshwater is exported (approximately 17% of annual outflow to the estuary; Kimmerer 2002), which substantially affects estuarine hydrodynamics, water quality, and fisheries (Jassby et al. 1995; Arthur et al. 1996; Bennett and Moyle 1996; Kimmerer 2002).

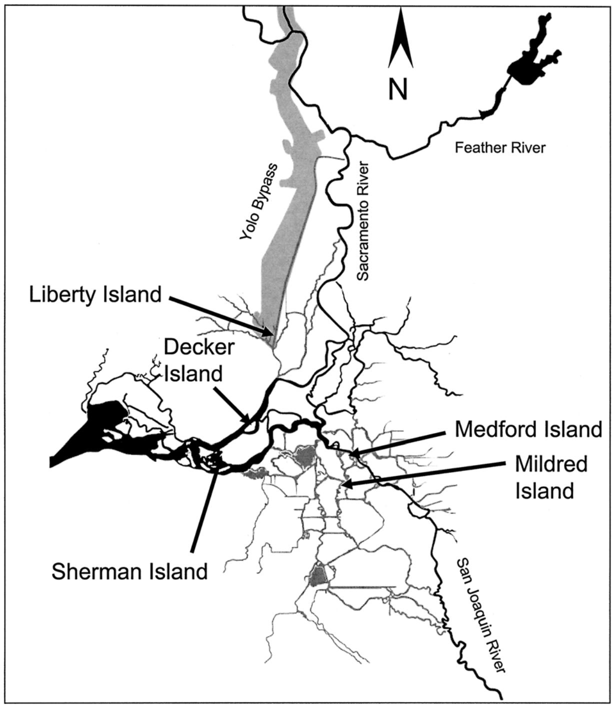

Fig. 1. Map of the Sacramento-San Joaquin Delta (Delta) showing locations of sampling sites. Primary river channels and embayments are depicted in black. The Yolo Bypass floodplain and Delta sloughs and flooded islands are depicted in gray.

Structural changes to delta habitats also have been substantial. Primarily during the latter half of the 19th century and the first half of the 20th century, the delta was converted from a seasonally brackish marsh into a network of leveed channels conveying freshwater year-around. The delta channels surround tracts of land drained to support agriculture (Fig. 1). Since the 1970s, the delta levees have been increasingly armored (usually with large rocks), and the limited shallow habitat area remaining along the channel edges has been encroached by nuisance aquatic plants such as Brazilian waterweed *Egeria densa* (Brown 2003).

Field Collections

We sampled fishes monthly (March–October 2001 and March–October 2003) using beach seines and gill nets at five sites (Fig. 1). Two sites (Decker Island and Medford Island) were low velocity areas at the edges of channels. The other sites (Sherman Island, Liberty Island, and Mildred Island) were shallow habitats along the internal remnant levees of flooded islands, a local term for former agricultural tracts that were flooded and not reclaimed. We deployed a 30 × 1.8 m, 3.2 mm mesh beach seine via small, shallow draft boats similar to Hurst et al. (2004). We conducted 2–8 beach seine hauls per site per month (mean = 4). One site was sampled per day, so 5 d were needed to complete each month's sampling. Samples were collected afternoon to dusk, usually during a flood tide. Measurements of width, depth, and length (± 0.1 m) permitted accurate estimates of the volume swept (m^3) by the beach seine (Nobriga et al. 2005). Water depth at initiation of seine hauls averaged about 1 m at all sites, but varied from 0.4 to 1.5 m in individual hauls. Fish were identified to species, enumerated, and measured to the nearest 1 mm total length (TL) or fork length (FL) if the tail was forked. When very large numbers of a species were collected, we measured a subsample of 150–200 individuals. Fishes approximately 30–300 mm in length were most vulnerable to our beach seine sampling. For most species, we also preserved a subsample of individuals spread through the length range captured. We transported these individuals to the laboratory, remeasured them, and wet weighed them on an electronic balance (± 0.01 g).

We avoided sampling beaches with dense beds of submerged aquatic vegetation (SAV; principally Brazilian water weed) because high SAV density hindered net deployment. Mildred Island was the only site where beach access was consistently limited by SAV. At all sites, we sampled beaches with low to moderate SAV density striving to maintain net deployment speed and contact with the substrate. We indexed vegetation abundance among sites by recording the volume of SAV retained in each seine haul using a 19-l container. We recorded surface water temperature (°C) and water clarity (Secchi depth; cm) once per day offshore of our sampling sites so that measurements would not be affected by our sampling. We also summarized water temperature, water clarity, and specific conductance data ($\mu s\ cm^{-1}$) recorded during biweekly monitoring surveys conducted by the California Department of Fish and Game (unpublished data) taken near in space and time to our samples.

Deeper water (2–4 m) adjacent to the beach seine sites was sampled using a gill net (60 × 2.4 m; randomized panels of 51–102 mm stretch mesh). The gill net was set parallel to shore for 20–40 min, 2–6 times per visit (mean = 0.9 h per visit). Gill net effort was concentrated around sunset to target actively foraging fishes moving to or from the shallows. All fishes collected in the gill net were identified to species and measured for TL or FL in mm. Fishes approximately 200–400 mm in length were most vulnerable to our gill net sampling.

DATA ANALYSIS

Beach seine data were summarized as mean daily densities (fish 10,000 m^{-3}). Individual fishes > 300 mm were excluded because occasionally collected large individuals would have unduly biased biomass estimates (see below). We also excluded species that occurred in less than 10% of samples to avoid biasing multivariate results with rarely collected species. Gill net catches were summarized as mean daily catch per unit effort (CPUE; fish h^{-1}). The beach seine and gill net data provided separate measures of monthly relative abundance for fishes inhabiting wadable and shallow-deep transition habitats. Physical habitat data also were summarized as monthly means. All fish and habitat data were $\log_{10}$-transformed or $[\log_{10}(x + 1)]$-transformed prior to statistical analyses.

We summarized among-sample (mean daily beach seine density and mean daily gill net CPUE) similarity using nonmetric multidimensional scaling (NMDS; Clarke and Gorley 2001). We performed NMDS separately on the beach seine and gill net data sets. NMDS summarizes (reduces the dimensionality of) a matrix of among-sample similarity coefficients. We used the Bray-Curtis coefficient to construct the similarity matrices because joint absences do not influence among-sample similarity. The fit (or stress) of an NMDS ordination is determined by how well the ordination preserved the actual sample dissimilarities. Stress values can range from zero to one. The evaluation of stress is based on the number of dimensions chosen and sample size (Borg and Groenen 1997). We evaluated both three-dimensional and two-dimensional solutions and determined that two-dimensions were adequate for describing spatial and temporal trends in our data. For two-dimensional solutions, stress values based on random (patternless) data with sample sizes as high as ours (n = 67 gill net samples, n = 75 beach seine samples) would likely exceed 0.40 (Borg and Groenen 1997). Stress values in our ordinations did not change from the original run when we repeated each analysis several times, increasing the number of random restarts each time. This indicated the ordinations represented sample dissimilarities accurately (Clarke and Gorley 2001). For each sampling site each year, we calculated 95% confidence intervals for the NMDS axis I and II scores. This provided an objective means of determining whether sampling sites occupied different parts of the ordination space. We also used a variance partitioning technique (Lewis 1978) to evaluate the relative influence of spatial (site) and temporal (month and year)

TABLE 1. Summary of life history data for fishes collected in ≥ 10% of samples during the present study. Life history data were taken from Moyle (2002) except where noted.

Common Name (Species Code)	Maximum Adult Size	Avg. Age at Maturation	Maximum Age	Maximum Fecundity	Batch Spawner	Parental Care Index
Inland silverside (InLsil)	120	1	2	15,000	1	0
Bluegill sunfish (Bluegi)	260	2	6	50,000	0	3
Largemouth bass (LarBas)	760	2	16	94,000	0	4
Redear sunfish (RedSun)	254	2	7	80,000	0	3
American shad (AmSha)	600[a]	4	7	225,600	0	0
Threadfin shad (ThrSha)	220	1	3	21,000	0	0
Prickly sculpin (PriScu)	200	2	7	11,000	0	2
Staghorn sculpin (StaScu)	220	1	10	11,000	0	2
Golden shiner GolShi)	260	2	9	4,700	1	1
Hitch (Hitch)	350	2	5	63,000	0	0
Sacramento pikeminnow (SacPik)	1,150	3	16	40,000	0	0
Splittail (Splitt)	450	2	8	100,000	0	0
Tule perch (TulPer)	238	1	7	60	0	8
Rainwater killifish (RaiKil)	62	0	1	104	1	0
Shimofuri goby (ShiGob)	105	1	2	1000[b]	1	2
Yellowfin goby (YelGob)	270	2	3	32,000	0	2
White catfish (WhiCat)	407	3	8	3,000	0	4
Striped bass (StrBas)	1,250	4	30	5,000,000	0	0
Delta smelt (DelSme)	120	1	2	12,000[c]	0	0
Bigscale logperch (BigLog)	125	1	3	400	1	1
Starry flounder (StaFlo)	600	2	7	11,000,000	0	0
Western mosquitofish (WesMos)	65	0	1	315	1	1
Chinook salmon (ChiSal)	1,000	3	5	17,000	0	2

[a] Unpublished data from the 2004 American River shad derby.

[b] Estimated per spawn fecundity based on the following statement from Moyle (2002) ‘‘Females spawn repeatedly and males spawn with multiple females, so thousands of embryos...can be found in a single nest.’’

[c] Unpublished data from Bradd Baskerville-Bridges, United States Bureau of Reclamation.

variables on fish assemblages. Factor variance components were derived from expected effects (group) mean squares based on a fixed-effects factorial design analysis of variance (ANOVA) using the NMDS sample scores as response variables.

For question two, we summarized life history data for fishes occurring in more than 10% of our beach seine samples (Table 1). The life history attributes were $\log_{10}$-transformed, standardized using z-scores, then ordinated using principal components analysis (PCA) to develop a local version of the trilateral model of fish life history strategies proposed by Winemiller and Rose (1992) and recently confirmed on a larger sample of the world fish fauna (Vila-Gispert et al. 2002). This model has three end point strategies. Periodic strategists are large, long-lived fishes with high fecundity. Opportunistic strategists are short-lived fishes with low fecundity per spawning event, but often have protracted spawning seasons. Equilibrium strategists are typically of intermediate size compared to periodic and opportunistic strategists. Equilibrium strategists have well-developed parental care of eggs or larvae. Though Winemiller and Rose (1992) used 16 life history traits in their model, we selected a subset of 6 traits for which we could find data (maximum adult size, average age at maturation, maximum age, maximum fecundity, whether or not the fish is a batch spawner, and parental care index; Table 1). The 6 variables were major contributors to Winemiller and Rose’s model and adequately reproduced its structure. We used scatterplots of each species’ principal component (PC1 and PC2) scores weighted by their mean $[\log_{10}(x + 1)]$-transformed beach seine density at each site to portray and contrast species assemblages and life history strategies found at our five sites.

For question three, we converted beach seine densities into biomass densities (kg 10,000 m^{-3}) using length-weight conversions developed during this study or by Kimmerer et al. (2005). We assumed that fish biomass was a suitable proxy for local productivity. We tested for year and sampling site effects on log-transformed biomass density using two-way ANOVA.

Results

We observed considerable environmental heterogeneity during our sampling (Table 2). Each year, water temperature changed 11–13°C between lows

TABLE 2. Means and ranges (in parentheses) of habitat data recorded during this study. Shoal widths are the mean distances from shore at initiation of beach seine hauls and are provided as an index of relative shallow water habitat availability.

Site	Shoal Width (m)	Specific Conductance (μs cm^{-1})	Water Temp (°C)	Secchi Depth (cm)	SAV (l)
Sacramento River					
Sherman Island[a]					
2001	26 (13–39)	1455 (273–2392)	19 (15–21)	37 (27–49)	0.2 (0–1.3)
2003	21 (16–28)	1151 (154–4499)	18 (15–22)	41 (33–47)	0.1 (0–0.3)
Decker Island[b]					
2001	11 (9–15)	402 (205–834)	19 (16–21)	37 (30–47)	0.2 (0–0.6)
2003	11 (9–13)	243 (146–477)	19 (15–22)	47 (35–58)	0.2 (0–1.1)
Liberty Island[a]					
2001[c]	16 (14–18)	235 (199–260)	22 (16–25)	17 (9–26)	0.0
2003	22 (17–28)	207 (142–304)	20 (13–25)	21 (12–42)	0.0
San Joaquin River					
Medford Island[b]					
2001	17 (14–19)	425 (358–505)	21 (16–24)	65 (55–81)	1.3 (0–2.7)
2003	17 (15–19)	369 (204–598)	20 (15–25)	76 (64–93)	0.9 (0–1.8)
Mildred Island[a]					
2001[c]	13 (11–15)	400 (362–465)	23 (16–26)	63 (52–73)	1.3 (0.3–2.1)
2003	13 (11–15)	314 (219–430)	21 (14–26)	94 (59–160)	2.1 (0.5–2.8)

[a] Flooded island site (internal levees of flooded agricultural tracts).

[b] Channel edge site.

[c] Not sampled in March.

in March and highs in June–July, and mean temperature among sites varied by up to 5°C. Specific conductance was higher at all sites in 2001 than 2003. Specific conductance was more variable and averaged an order of magnitude higher at Sherman Island than other sites. Sherman Island also had the most shallow water habitat as indexed by shoal width. Mean shoal widths at Liberty and Medford Islands were intermediate, whereas Decker and Mildred Islands had comparatively narrow shoal widths. Water clarity and SAV abundance covaried; both were lowest at Liberty Island, intermediate at Sherman and Decker Islands, and highest at Medford and Mildred Islands.

We collected 79,391 fishes of 36 species in the beach seine (Table 3). The catch was dominated by inland silverside *Menidia beryllina*, and threadfin shad *Dorosoma petenense*, which accounted for 77% of the total. We also collected more than 1,000 individuals of six other species: striped bass *Morone saxatilis*, yellowfin goby *Acanthogobius flavimanus*, redear sunfish *Lepomis microlophus*, largemouth bass *Micropterus salmoides*, American shad *Alosa sapidissima*, and splittail *Pogonichthys macrolepidotus*. Of these, only splittail is a native species. We collected 1,139 individuals of 21 species in the gill net. Gill net catches were dominated by white catfish *Ameiurus catus* (35%), striped bass (19%), and splittail (17%).

The NMDS stress values (beach seine = 0.17, gill net = 0.20) and the extracted variance components from the sample scores (Table 4) suggested two-dimensional solutions suitably represented fish assemblage similarity for both the beach seine and gill net data sets. Sampling site accounted for most of the variation captured on axis I of both ordinations (beach seine = 88%, gill net = 77%), but confidence intervals indicated the gill net assemblages had less difference among sites than the beach seine assemblages (Fig. 2). Both ordinations tended to differentiate Sacramento from San Joaquin River fish assemblages, but again, this was more pronounced in the beach seine data.

Year of collection had little influence on fish assemblages based on beach seine sampling (Table 4). Month of collection explained the majority of variance captured on NMDS axis II (73%). This contrasted a spring (March–June) assemblage in which migratory (e.g., Chinook salmon *Oncorhyncus tschawytscha* and staghorn sculpin *Leptocottus armatus*) and resident (e.g., splittail, Sacramento pikeminnow *Ptychocheilus grandis*, and tule perch *Hysterocarpus traski*) native fishes were in nearly equal abundance to nonnative fishes, from a summer (July–October) assemblage characterized by low abundance of most native species and higher abundance of nonnatives like inland silverside, threadfin shad, American shad, and redear sunfish. Year and site accounted for comparable percentages of variance (38% and 40%, respectively) in axis II of the gill net data, indicating year of collection had more influence on assemblages of larger fish. Month of collection did not strongly influence fish assemblage composition based on gill net sampling, accounting for < 10% of the variance reflected on NMDS axes I and II.

TABLE 3. Numbers of fishes collected during gill net sampling and numbers of fishes ≤ 300 mm collected during beach seine sampling, March–October 2001 and 2003. Native species are denoted with an asterisk.

Species	Gill Net	Beach Seine
American shad *Alosa sapidissima*[a]	7[c]	1229
Threadfin shad *Dorosoma petenense*	3[c]	18,264
Chinook salmon *Oncorhyncus tschawytscha**[b]	2[c]	823
Rainbow trout *Oncorhyncus mykiss**[b]	1[c]	0
Delta smelt *Hypomesus transpacificus**	0	553
Sacramento sucker *Catostomus occidentalis**	14	41[c]
Sacramento pikeminnow *Ptychocheilus grandis**	30	551
Sacramento blackfish *Orthodon microlepidotus**	4[c]	4[c]
Splittail *Pogonichthys macrolepidotus**	189	1282
Hitch *Lavinia exilicauda**	62	112
Common carp *Cyprinus carpio*	6[c]	2[c]
Goldfish *Carassius auratus*	0	1[c]
Golden shiner *Notemigonus crysoleucas*	10	342
Red shiner *Cyprinella lutrensis*	0	4[c]
Fathead minnow *Pimephales promelas*	0	1[c]
Channel catfish *Ictalurus punctatus*	83	17[c]
White catfish *Ameiurus catus*	404	97
Black bullhead *Ameiurus melas*	1[c]	0
Brown bullhead *Ameiurus nebulosus*	6	1[c]
Inland silverside *Menidia beryllina*	0	42,994
Western mosquitofish *Gambusia affinis*	0	153
Rainwater killifish *Lucania parva*	0	72
Three-spine stickleback *Gasterosteus acculeatus**	0	9[c]
Prickly sculpin *Cottus asper**	0	104
Staghorn sculpin *Leptocottus armatus**[b]	0	64
Bigscale logperch *Percina macrolepida*	0	318
Bluegill *Lepomis macrochirus*	6	933
Redear sunfish *Lepomis microlophis*	38	1256
Warmouth *Lepomis gulosus*	0	14[c]
Black crappie *Pomoxis nigromaculatus*	8	45[c]
Largemouth bass *Micropterus salmoides*	7	1241
Spotted bass *Micropterus punctulatus*	0	2[c]
Striped bass *Morone saxatilis*	221	5665
Tule perch *Hysterocarpus traski**	37	619
Yellowfin goby *Acanthogobius flavimanus*	0	2366
Shimofuri goby *Tridentiger bifasciatus*	0	132
Shokihaze goby *Tridentiger barbosus*	0	2[c]
Starry flounder *Platyichthys stellatus**[b]	0	78

[a] Marine transient species: young predominantly in our study area during summer (July–October).

[b] Marine transient species: young predominantly in our study area during spring (March–May).

[c] Not included in statistical analyses because frequency of occurrence in samples was < 10%.

TABLE 4. Spatial (sampling site) and temporal (month and year) factor variance components (%) derived from expected effect (group) mean squares based on a fixed-effects ANOVA performed on NMDS ordination scores.

	Beach Seine NMDS Axis		Gill Net NMDS Axis	
Variable	1	2	1	2
Site (S)	88	4	77	38
Month (M)	1	73	9	6
Year (Y)	3	13	1	40
M × Y	1	5	3	5
M × S	2	1	5	5
Y × S	4	2	1	1
M × Y × S	1	2	3	4

The PCA of fish life history attributes produced two PC with eigenvalues > 1 (PC1 eigenvalue = 3.76, 63% of variance explained; PC2 eigenvalue = 1.23, 20% of variance explained). Differences in species richness and the relative abundance of life history strategies influenced among-site variation in fish assemblages based on the beach seine data (Fig. 3). Species richness was lower at flooded island sites, particularly Liberty and Mildred Islands, than at channel edge sites. Non-native centrarchids and rainwater killifish *Lucania parva*, were not detected at Liberty Island, whereas four native species, Chinook salmon, delta smelt *Hypomesus transpacificus*, hitch *Lavinia exilicauda*, and starry flounder *Platyichthys stellatus*, were not detected at Mildred Island. Liberty and Mildred Islands also delimited end points of life history strategy relative abundance (Fig. 3). Periodic strategist fishes (large adult size, delayed sexual maturity) decreased in relative importance in the following order: Liberty Island, Sherman Island, Decker Island, Medford Island, and Mildred Island. Equilibrium strategist fishes (medium-sized fishes with parental care) decreased in relative importance in the opposite order. Due to the ubiquitous distribution and high abundance of inland silverside and threadfin shad, opportunistic strategists (small species with rapid maturation) did not have a spatial pattern as a group. Certain opportunistic species (e.g., delta smelt) were more abundant at Sacramento River sites, while others (e.g., bigscale logperch *Percina macrolepida*) were more abundant at San Joaquin River sites.

Results for biomass density contrasted somewhat with numeric assemblage results in that interannual variation was greater than spatial variation. Mean biomass density was nearly three times higher in 2001 (144 kg 10,000 m^{-3}) than 2003 (52.6 kg 10,000 m^{-3}, $F = 8.06$, error df = 66, $p = 0.006$). There was a significant difference in biomass density among sites ($F = 9.60$, error df = 66, $p < 0.000$) that did not interact significantly with year ($F = 0.317$, error df = 66, $p = 0.87$). This suggests the among-year difference in fish productivity was reflected at all sites, but that some sites were consistently more productive (Fig. 4). Post-hoc comparisons indicated biomass density was significantly higher at Mildred Island than at each of the Sacramento River sites, and that biomass density at Medford Island was significantly higher than at Liberty Island.

Discussion

We found evidence that fish assemblages varied between Sacramento and San Joaquin River sites, particularly for young and small adult fishes collected by beach seining. We also found evidence

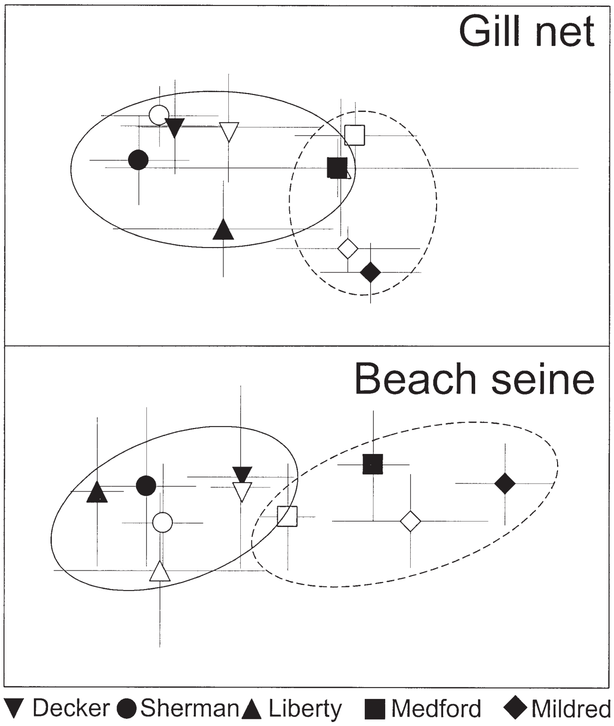

Fig. 2. Mean site scores and 95% confidence intervals for two-dimensional nonmetric multidimensional scaling ordinations performed on the beach seine and gill net data sets. Stress values were 0.17 for the beach seine ordination and 0.20 for the gill net data ordination. Open symbols are data for 2001. Solid symbols are data for 2003. Freehand ellipses encircle Sacramento River sites (solid lines) and San Joaquin River sites (dashed lines).

that the functional ecology of these young and small adult fish assemblages (life-history strategies and biomass density) varied in association with community composition (Figs. 3 and 4). The implications of these findings for local fisheries management and restoration are discussed below. We think our results likely reflected spatial differences in water clarity and SAV abundance (Table 2). Grimaldo et al. (2004) also recently reported differences in larval fish assemblages within adjacent open and vegetated microhabitats. Interpretation of our community composition results based on NMDS may be influenced by spatial autocorrelation between distance among sampling sites, habitat conditions, and fish assemblages (Nash et al. 1999). SAV-dominated habitats also occur extensively in the eastern delta, which includes Sacramento River channels, and have expanded into parts of the western delta (California Department of Fish and Game unpublished data). We think our results should be interpreted mainly as a contrast of SAV-dominated and open-water-dominated shorelines rather than a contrast of the Sacramento and San Joaquin Rivers.

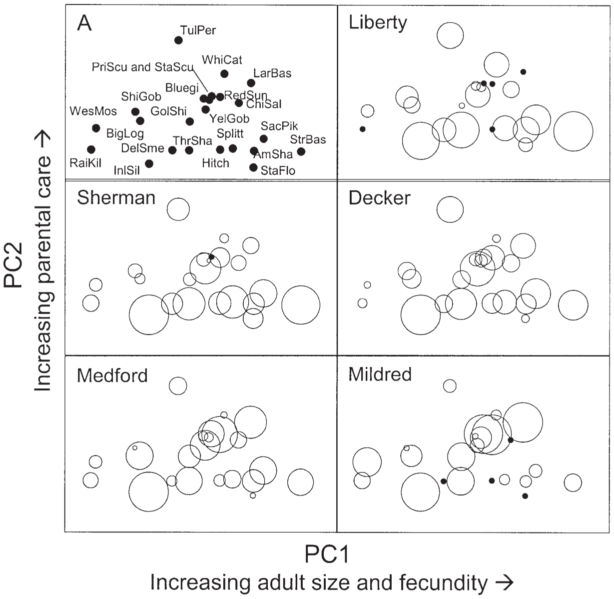

Fig. 3. Scatterplots of species scores from life-history strategy ordinations for 23 fish species collected in the Sacramento-San Joaquin Delta, March-October 2001 and 2003, weighted by mean beach seine density. Life-history strategies were based on Winemiller and Rose (1992) using six life history traits (see Table 1). Panel A shows the relative positions of each species, labeled by codes based on common names (see Table 1). In the remaining panels, fishes that were not collected at a site are depicted with solid circles.

The Sacramento and San Joaquin Rivers have numerous channel connections through which tides and water diversions mix their flows (Fig. 1). Most of the delta's freshwater comes from the Sacramento River because its basin receives more rainfall, and most San Joaquin River flow is diverted upstream of tidal influence. Local variation in physical conditions like bathymetry, flow velocities, and wind speeds, probably better explain local (site-specific) variation in SAV abundance than source-water differences. Macrohabitat changes may have influenced SAV proliferation over larger spatial scales. Sediment concentrations in the Sacramento River have declined by about 50% since 1957 (Wright and Schoellhamer 2004), which has resulted in demonstrably higher water clarity in the delta (Jassby et al. 2002). Increased water clarity, and the artificial maintenance of freshwater conditions to support water diversions, probably facilitated freshwater SAV proliferation.

The hydrologic regulation of the delta and its watershed, already shown to have numerous environmental effects (Arthur et al. 1996; Bennett and Moyle 1996; Kimmerer 2002), may have another by-product. We hypothesize that hydrologic regulation, through the mechanisms discussed above, influences the relative importance of abiotic and

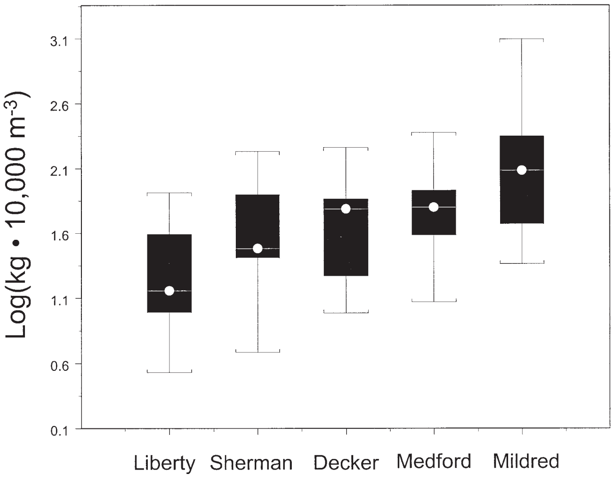

Fig. 4. Spatial distribution of combined 2001 and 2003 fish biomass densities (kg 10,000 m^{-3}) based on beach seine sampling at five sites in the Sacramento-San Joaquin Delta. Median values are depicted as white circles. The boxes delimit the 25th and 75th percentiles. The whiskers extend to 1.5 interquartile range.

biotic structuring mechanisms in nearshore fish communities. This hypothesis is best supported by a comparison of Liberty and Mildred Islands. Liberty Island is the base of Yolo Bypass, a hydrologically dynamic habitat (Sommer et al. 2001) whereas Mildred Island is a tidally-influenced lake (Lucas et al. 2002), located where significant winter-spring flood flows are rare. These sites also represented extremes of water clarity and SAV abundance during our study (Table 2). Periodic strategist fishes were much more abundant at Liberty Island than Mildred Island; the converse was true for most equilibrium strategist fishes (Fig. 3). Periodic strategists are predicted to be most successful in seasonally dynamic, abiotically-driven environments, whereas equilibrium strategists are predicted to be most successful in comparatively stable environments where communities are more strongly influenced by biotic mechanisms (competition and predation; Winemiller and Rose 1992).

Tule perch, an equilibrium strategist native fish, was more abundant at Liberty Island than Mildred Island. It is one of the native fishes that have declined in abundance over the past three decades (Nobriga and Chotkowski 2000). We found tule perch of all life stages in the stomachs of largemouth bass more frequently than in the stomachs of striped bass (Nobriga unpublished data). The reduced abundance of this particular equilibrium strategist could be linked to predation. This may be further evidence for stronger influence of biotic structuring mechanisms within SAV-dominated habitats.

Though both the beach seine and gill net data suggested fish assemblages were influenced by SAV, the gill net results were less pronounced (Fig. 2). We can comment on two factors that may explain these differences. They are not mutually exclusive and we acknowledge that other, unrecorded factors also may have contributed. There were differences in species and life stages vulnerable to each gear. For instance, white catfish and adult striped bass dominated gill net catches at Liberty and Mildred Islands, but were largely invulnerable to beach seining at all sites. Differences may have been influenced by catchability, rather than actual responses to environmental conditions.

Beach seine catches were dominated by young-of-year fishes. Small fishes that are not adapted to use vegetation as cover from predators may rely on turbidity instead. Predation mediated by water clarity is hypothesized to influence fish assemblages in floodplain lakes of the Orinoco River (Rodríguez and Lewis 1994). Turbidity also appeared to moderate predation losses of juvenile Chinook salmon in a British Columbia river system (Gregory and Levings 1998). In estuaries, regions of high turbidity associated with low salinity or entrapment zones are important rearing areas for young fishes (Dauvin and Dodson 1990; Bennett et al. 2002). One of several benefits that young fishes may realize in turbid mixing zones is reduced loss to visual predators. It is possible that spatial differences in environmental conditions had more influence on beach seine fish assemblages than gill net fish assemblages because factors like water clarity mediate predator-prey interactions in open water.

The productivity of the San Francisco Estuary has declined for four decades (Kimmerer and Orsi 1996; Jassby et al. 2002; Matern et al. 2002), making increased aquatic productivity a focus of local restoration efforts (e.g., Lucas et al. 2002). Shallow vegetated habitats are typically productive rearing environments for young fishes. We found that biomass density was positively associated with SAV abundance (Table 2 and Fig. 4), suggesting that vegetated habitats in the delta also are comparatively productive. Native fishes and the recreationally important nonnative striped bass do not use vegetated habitats extensively (Fig. 3; Brown 2003). We suspect these fishes are unlikely to extensively use prey produced within beds of SAV. Our results suggest these species will respond more favorably to restoration strategies that maintain and enhance natural riverine and estuarine habitats (e.g., seasonally appropriate abiotic variation), than to strategies that maximize local productivity.

Productivity at larger spatial scales may be important to native fish and striped bass restoration. We observed a significant decrease in fish biomass density between 2001 and 2003 that occurred across habitat types and species composites. If it is possible to manipulate factors that influence productivity at the scale of the delta or estuary, such manipulations might be useful for enhancement of native fishes and striped bass. This is speculative because a substantial fraction of pelagic productivity is currently lost to invasive bivalves (Kimmerer and Orsi 1996; Lucas et al. 2002).

Many watersheds in California and elsewhere have been profoundly changed by water supply projects that simplify habitats and dampen environmental variability to increase water supply reliability (Pringle et al. 2000). These changes facilitate human uses. They invariably affect local fish assemblages because reproductive success and subsequent biotic interactions (e.g., competition and predation) are mediated by environmental variability (Jassby et al. 1995; Henderson and Corps 1997; Labbe and Fausch 2000). We hypothesize there is a mismatch between the system-scale manipulations probably needed to enhance the productivity of native fishes and striped bass, and the local-scale rehabilitation actions considered to date.

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