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Variation in Spring Nearshore Resident Fish Species Composition and Life Histories in the Lower Sacramento-San Joaquin Watershed and Delta

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ABSTRACT

Providing freshwater to human populations while protecting or rehabilitating ecosystem health is a significant challenge to water resource managers and requires accurate knowledge of aquatic resources. Previous studies of fish assemblages in the San Francisco Estuary and watershed have focused on specific habitat types, water bodies, or geographic subregions. In this study, we use seining data from two monitoring programs to provide an integrated view of spring nearshore resident fish species composition and life history characteristics in five regions: the San Joaquin River, the upper Sacramento River, the lower Sacramento River, the northern Sacramento-San Joaquin Delta (North Delta), and the Interior Delta. Data for the period March-May from 1994 to 2002, showed that spring species composition of the San Joaquin River was very different from the other four regions. Total catch in the San Joaquin River was dominated by small, short-lived batch spawning alien species (93%), particularly red shiner *Cyprinella lutrensis* (>75% of total catch). The upper and lower Sacramento River were very similar in species composition and life history characteristics and less dominated by alien fish (<45% of total catch). Ordination of species percentage abundances by non–metric multidimensional scaling confirmed that the major gradient was from assemblages dominated by native species to assemblages dominated by alien species. Two-way analysis of variance of ordination scores indicated that spatial variability was more important than annual variability in explaining patterns in species composition. The potential benefits of San Joaquin River native fish restoration appear high because there is so much potential for improvement; however, it is unclear how to best manipulate the system to achieve such restoration. Addressing such uncertainties is necessary if society desires the preservation and restoration of native biodiversity as human demands on water resources increase.

KEYWORDS

Sacramento-San Joaquin Delta, Sacramento River, San Joaquin River, native fishes, alien fishes, fish assemblages, species composition, life history characteristics, nonmetric multidimensional scaling

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INTRODUCTION

One of the major challenges facing water resource managers is providing freshwater to human populations while protecting or rehabilitating ecosystem health (Postel 1996; Vitousek et al. 1997; Postel 2000; Sala et al. 2000). Water supply infrastructure and operations often disrupt natural flow regimes in rivers, leading to changes in fish assemblages and other aspects of ecosystem function (Ligon et al. 1995; Poff et al. 1997; Pringle et al. 2000; Brown and Ford 2002). Similarly, estuaries are affected by water management and other activities, which affect important aspects of ecosystem function, such as fish recruitment (Bennett and Moyle 1996; Rose 2000). Alterations in freshwater inflow to estuaries may affect the longitudinal distribution of salinity, which can have a major influence on fish populations (Bulger et al. 1993; Jassby et al. 1995; Wagner 1999). Fish assemblages have been recognized as useful indicators of such ecosystem change in both freshwater systems and estuaries (Karr 1991; Whitfield and Elliot 2002; Matern et al. 2002; Hurst et al. 2004; O'Connell et al. 2004).

The San Francisco Estuary and its watershed have changed substantially since major development began in the mid-1800s (Conomos 1979; Nichols et al. 1986; Hollibaugh 1996; Brown and Moyle 2005). Changes in physical habitat, productivity, water quality, and flow regime have been accompanied by declines in native fishes and invasions of alien species, including many alien fishes (Cohen and Carlton 1998; Jassby et al. 2002; Moyle 2002; Brown and Moyle 2005). Several native fishes have declined to levels resulting in designation as threatened or endangered (Moyle 2002). Most of the alien fishes were intentionally introduced for sport or food purposes (Dill and Cordone 1997). Although the declines in native species occurred concurrently with a variety of ecosystem changes (Bennett and Moyle 1996; Brown and Moyle 2005), water diversions from the Sacramento-San Joaquin Delta (hereinafter, Delta) are consistently identified as contributing factors in the declines because of entrainment of young fish, changes in hydrodynamics, and export of primary and secondary production (Arthur et al. 1996; Brown et al. 1996).

Conflicts over water management eventually led to the implementation of the CALFED Bay-Delta Program (hereinafter, CALFED) in 2000 (CALFED 2000). The CALFED program includes an ambitious ecosystem restoration program (hereinafter, ERP) intended to restore and improve the health of the Bay-Delta system for all native species, while reducing water management constraints (CALFED 2000). However, recent assessments have indicated that the opportunities for native fish restoration are not clearly understood (Brown 2003). Effective management requires clear conceptual models at multiple spatial scales to minimize uncertainty regarding the outcome of management actions (Kimmerer et al. 2005). For example, local restoration efforts on a river system might have unexpected downstream effects if the larger scale watershed viewpoint is not considered. This example is particularly appropriate given that recent legal decisions make it likely that San Joaquin River flows will be increased for fish restoration purposes.

Previous studies in the Delta and the watershed have generally focused on specific habitat types such as floodplains (Sommer et al. 2001a,b; Crain et al. 2004; Ribiero et al. 2004) or specific water bodies or geographic areas such as the Delta (Feyrer and Healey 2003; Dege and Brown 2004; Nobriga et al. 2005), the Sacramento River watershed (Seesholtz et al. 2004; May and Brown 2002), or the San Joaquin River watershed (Brown 2000; Brown and Ford 2002). Connections between water bodies and associated species assemblages have generally not been explicitly studied. In this paper we use data from two monitoring programs to provide an understanding of the spring nearshore resident fish assemblages of the lower Sacramento and San Joaquin Rivers and the Delta, formed by the confluence of the two rivers (Figure 1). In particular, we evaluate fish assemblage composition and fish life history characteristics to

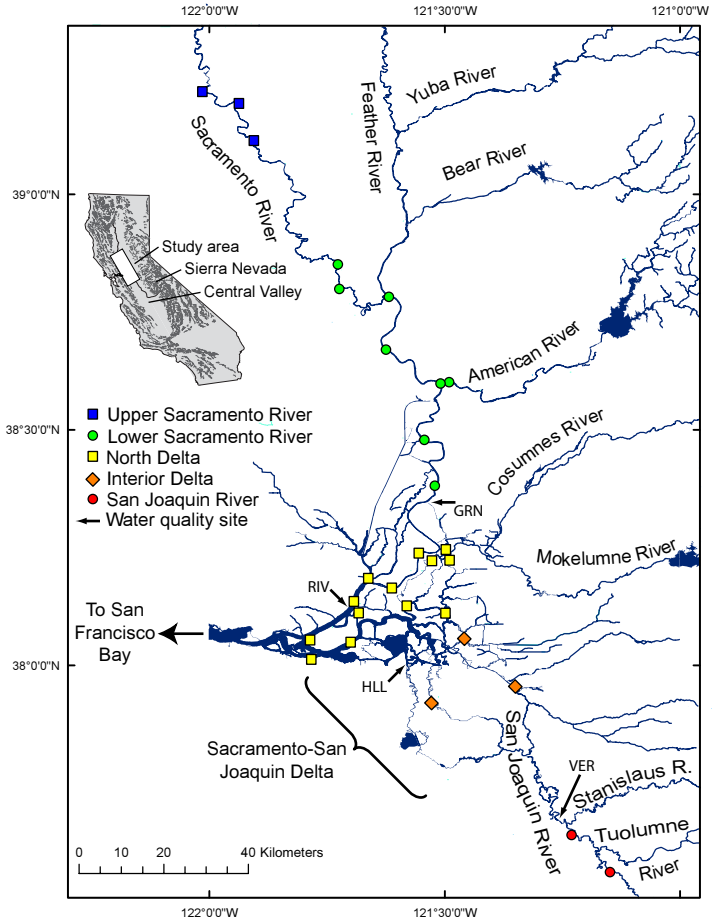

Figure 1. Study area map including site locations, regional groups of sites, and locations of water quality monitoring sites.

address the following questions: 1) How do patterns in fish species composition from the upstream reaches into the Delta vary between the two rivers?; and, 2) If there are differences in fish species composition between the two river systems, are the differences associated with different ranges in life history characteristics? We then discuss the results in the context of existing data on physical differences between the two river systems. Finally, we discuss the implications of the results in the context of native fish restoration in the Delta and its watershed.

METHODS

Study area

The Sacramento-San Joaquin watershed drains approximately 100,000 km^2 or about 40% of the surface area of California. The mean annual runoff in the Sacramento River portion is about 27.6 billion m^3 yr^{-1} and in the San Joaquin River portion is about 11 billion m^3 yr^{-1} (California Department of Water Resources 1993). Water management infrastructure is extensive with large storage reservoirs near the transition from the mountains to the Central Valley. In the Sacramento River portion, water management focuses on water delivery through river channels to the Sacramento-San Joaquin Delta where water is then diverted out of the Delta by federal and state pumping plants located in the southern Delta. Most of this water is exported to areas of California south of the Delta for agricultural and urban uses. In the San Joaquin River portion, water management focuses on diversion of water out of streams and rivers into canals for agricultural use. Some of the applied water is returned as agricultural drainage. The Delta is the most upstream portion of the San Francisco Estuary, one of the largest on the West Coast of North America. Water management activities focus on maintaining water quality, primarily minimizing salt content, for within Delta agricultural use and for export by the previously mentioned state and federal pumping plants and several smaller diversions operated by local urban water agencies.

Data sources

We used fish data from two ongoing annual monitoring programs. Both programs use daytime beach seining for fish sampling. The programs differ in longevity and the seasonal extent of sampling. Our analysis is based on sampling from March through May from 1994 to 2002. These time periods are common to both programs.

The larger monitoring program is conducted by the U.S. Fish and Wildlife Service as part of the Interagency Ecological Program. Weekly beach seining surveys are used to estimate the relative inter- and intra-annual abundance and distribution of all races of salmonid fry using the Delta as a rearing and nursery area. We used data collected from 27 sites on the Sacramento River and in the Delta (Figure 1). Although a variety of other sites have been sampled at various times during the program, these 27 sites were consistently sampled during the time periods of interest. Sampling consists of one seine haul per sampling visit using a 15 m by 1.3 m net with 3-mm mesh. All fish collected are identified to species and counted.

The second program is conducted by Turlock and Modesto Irrigation Districts (TID/MID). The purpose of the program is to monitor the abundance and downstream movements of juvenile anadromous salmonids, primarily Chinook salmon, *Oncorhynchus tshawytscha*. We used data collected from 2 sites on the San Joaquin River (Figure 1). Sampling is conducted every two weeks. Sampling usually consists of three seine hauls at each site using a 3-mm nylon mesh net, either 1.2 or 1.8 m high, in lengths of 6.1, 9.1, or 15.2 m. The specific choice of net depends on conditions at the time of sampling. All fish collected were identified to species and counted.

Although the primary focus of both programs is anadromous salmonids, they also collect high quality data on the other species present. These data have been used in a number of publications (e.g., Brown and Ford 2002; Feyrer et al. 2005). Nobriga et al. (2005) have also established that seining is a useful technique for understanding nearshore fish assemblage composition in the study area. Seining is most effective at capturing small species and the juveniles of larger species that occupy nearshore habitats. Therefore, the results of this study should not be interpreted as representative of patterns in pelagic species or adults of large species.

We compiled data on water temperature and specific conductance from continuous monitoring stations to provide a general comparison of physical conditions among regions of the Delta (CDEC 2006). These data were not available for upstream reaches of the Sacramento or San Joaquin Rivers. General descriptions of sampling sites were obtained from the U.S. Fish and Wildlife Service.

Data analysis

We excluded several anadromous species from analysis, specifically Chinook salmon, steelhead rainbow trout, *Oncorhynchus mykiss,* and American shad, *Alosa sapidissima*. Only juvenile Chinook salmon were abundant in the samples. These species primarily use the study area as a migratory corridor between upstream areas and the ocean. Because we were interested in the species composition and life histories of resident assemblages of fishes, these exclusions were appropriate.

We analyzed percentage abundances of species rather than numerical abundances for several reasons. There were differences in the frequency of sampling, and number of seine hauls between the two programs. Also, flows fluctuated seasonally and annually and may have affected sampling efficiency. Although analysis of percentage abundances precludes comparisons of numerical abundance (or catch per unit effort) between sites or years, such data are sufficient for analyses of assemblage composition. For each site, catches were summed over the period from March through May of each year. Catches were then converted to percentage abundances.

As an aid to understanding spatial variability, we assigned sites to five regions (Figure 1) based on large-scale habitat characteristics. We acknowledge that results for these regions likely represent specific points on a gradient of changing species composition rather than actual separable groups, and we interpret the results accordingly. The upper Sacramento River included three sites. Upstream of these sites the river is characterized by setback levees enclosing remnant floodplains and a narrow meandering river channel (Feyrer et al. 2005). Downstream of these sites, the levees are closer together, and there is little floodplain between them. The lower Sacramento River included 8 sites located in the section with little floodplain between the levees. The two downstream sites in this group were in a section that is almost completely riprapped. The San Joaquin River included 2 sites. The San Joaquin River areas studied are characterized by setback levees, a meandering channel, and access to remnant floodplains. The North Delta included 13 sites. This region is characterized by complex hydrodynamics associated with tidal exchanges of water between the Sacramento, San Joaquin, and Mokelumne Rivers (Cathy Ruhl, U.S. Geological Survey, personal communication). The Interior Delta included 3 sites. This region is also tidal but is influenced primarily by the San Joaquin River (Cathy Ruhl, U.S. Geological Survey, personal communication). Sites in both regions of the Delta are characterized by leveed banks. Sampling sites were generally on the edge of the main channel but a few were located in more protected coves along main channels. Substrate was either sand or concrete boat ramps. Each region had a

mixture of site types. We calculated monthly means of daily values for water temperature and specific conductance from water quality monitoring stations in the lower Sacramento River, lower San Joaquin River, North Delta and Interior Delta (Figure 1) as a general indication of physical conditions during the sampling period.

We used non-metric multidimensional scaling (NMS) (Kruskal 1964a,b; Mather 1976) to explore patterns of species composition. NMS is an ordination technique that summarizes (reduces the dimensionality of) a matrix of among sample similarity coefficients. NMS is similar in concept to other ordination techniques, such as principal components analysis or correspondence analysis. Species percentage abundances were arcsine square-root transformed for analysis, and Bray-Curtis similarities were used as the similarity coefficient. The "fit" of the ordination is assessed by the stress value. Conceptually, stress compares the original similarities between samples calculated from the full data matrix with the similarities calculated between samples in the lower dimension ordination space. Stress of less than 0.20 indicates that the lower dimension ordination successfully reproduces the patterns present in the higher dimension ordination space (Clarke and Warwick 2001). For each site group, we calculated mean and 95% confidence intervals for NMS scores on each NMS axis.

We calculated Spearman rank correlations of individual fish species arcsine square-root transformed percentage abundances with NMS axis scores to help interpret the ecological meaning of the axes. Because of the large number of samples (n = 261), even very small correlations were statistically significant. We arbitrarily chose correlations with absolute values of greater than 0.4 as important enough for presentation. In addition, we identified the species most responsible for similarities within regions and the species most responsible for dissimilarities between regions using the program SIMPER (Primer-E 2005). The program determines the percentage contribution of each species to the similarity or dissimilarity value of interest. Finally, we used two-way analysis of variance (ANOVA), using region and year as factors, to explore the relative importance of spatial and temporal variability for each NMS axis.

We explored patterns of life history characteristics by developing a local version of the trilateral model of fish life history strategies proposed by Winemiller and Rose (1992), as applied by Nobriga et al. (2005) in the Delta. The Winemiller and Rose (1992) model includes three endpoint life history strategies. Periodic strategists are large, long-lived fishes with high fecundity. Opportunistic strategists are short-lived species with low fecundity per spawning event but often with protracted spawning seasons. Equilibrium strategists are typically of intermediate size and have well developed parental care of eggs or larvae. We used data from the literature compiled by Nobriga et al. (2005) and Moyle (2002) for 6 of the 16 life history characteristics included in the original analysis by Winemiller and Rose (1992). Maximum fecundity of wakasagi, *Hypomesus nipponensis,* was obtained from Katayama (2001). The 6 variables—maximum adult size, average age of maturity, maximum age, maximum fecundity, batch spawning, and parental care—were among the most important variables noted by Winemiller and Rose (1992). Values for the life history characteristics were analyzed by principal components analysis, following Nobriga et al. (2005), to identify patterns in life history strategies among the species. We used values for largemouth bass to represent *Micropterus* spp. because this was the species most often identified in the field data. Scores for each species with total percentage abundance greater than 1% were then weighted by the percentage of the total catch, and plotted for each of the five regions.

RESULTS

Water temperatures were very similar among regions for years that data were available (Figure 2). Substantial warming occurred between March and May, but May temperatures were generally less than 20°C, except in 2001. Specific conductance was more variable among regions (Figure 3). Values were generally less than 500 μScm^{-1}, except in the San Joaquin River. The San Joaquin River and Interior Delta regions usually had higher values than the other regions. There was no consistent pattern of monthly change at particular sites from year to year.

A total of 49,396 fish belonging to 37 taxa were collected (Table 1) excluding anadromous Chinook

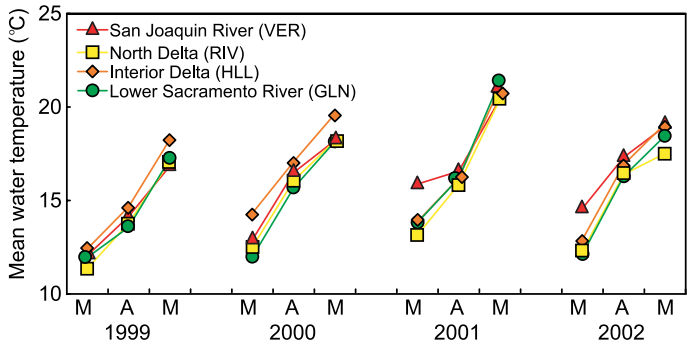

Figure 2. Mean monthly water temperatures for study regions for March, April, and May from 1999 to 2002.

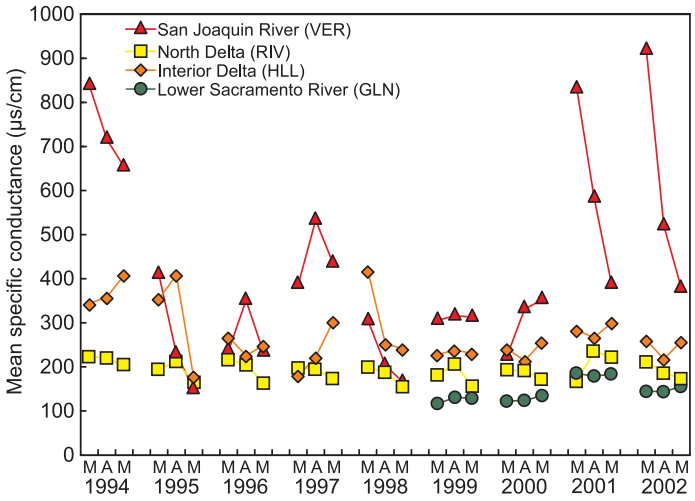

Figure 3. Mean monthly specific conductance for study regions for March, April, and May from 1994 to 2002.

salmon, steelhead rainbow trout, and American shad. Of the taxa captured, 23 were alien and 14 were native. Overall, the catch was dominated by alien species (59%); however, this varied greatly among the regions (Table 1). The San Joaquin River and Interior Delta were dominated by alien species (93% and 89%, respectively). Alien red shiner, *Cyprinella lutrensis,* was over 75% of the total catch in the San Joaquin River. Alien inland silverside, *Menidia beryllina,* was 52% of the catch in the Interior Delta. The catch in the North Delta was evenly split between alien and native fishes (50% each). Alien inland silverside and yellowfin goby, *Acanthogobius flavimanus,* each made up over 10% of the catch as did native Sacramento pikeminnow, *Ptychocheilus grandis,* and Sacramento splittail, *Pogonichthys macrolepidotus.* Both the upper and lower Sacramento River were dominated by native fishes (77% and 55%, respectively). In the lower Sacramento River, native Sacramento pikeminnow, Sacramento sucker, *Catostomus occidentalis,* and Sacramento splittail were each over 10% of the catch. In the upper Sacramento River, Sacramento pikeminnow and Sacramento sucker composed 64% of the catch.

We selected the three-dimensional NMS ordination with a stress value of 0.15 as the best representation of the data (Figure 4) because the two-dimensional NMS ordination had a marginal stress value of 0.21. Eleven species had Spearman rank correlations of greater than 0.40 or less than -0.40 with one or more of the NMS axes (Figure 4). NMS axis 1 appears to represent an alien-native gradient with the highest percentages of native species occurring in the upper Sacramento River with alien species becoming more important in the North Delta and Interior Delta. NMS axis 2 mainly separates the San Joaquin River from the other regions on the basis of large percentages of alien red shiner. NMS axis 3 mainly separates the North Delta from the other groups on the basis of a variety of alien and native species.

The NMS and correlation results were supported by the SIMPER results (Table 2). Within group similarities were greater than 50% in the rivers but lower than 50% in the North Delta (49%) and Interior Delta (42%). This indicates more variability in species composition in the Delta. The San Joaquin River sites were characterized by high percentages of alien red shiner and lower percentages of alien inland silverside and native Sacramento sucker. The Interior Delta was characterized by high percentages of inland silverside. The upper and lower Sacramento River and North Delta regions were all characterized by the presence of Sacramento sucker, Sacramento pikeminnow, and Sacramento splittail. Inland silverside was also important in the lower Sacramento River and North Delta.

Dissimilarities among groups were all 50% or greater (Table 2). The San Joaquin River was most dissimilar from the other regions (>70%), primarily because of the high percentages of red shiner. The Interior Delta also had high dissimilarity with the other groups.

Table 1. Scientific name, common name, code, total number of fish collected (in parentheses), and percentage of each species (in parentheses) for total catch and for each of five regions from 1994 to 2002. Native species are indicated with an asterisk.

Scientific name, common name	*Code*	*Total (49,396)*	*Upper Sacramento River (4,105)*	*Lower Sacramento River (15,815)*	*Northern Delta (14,729)*	*Interior Delta (1,986)*	*San Joaquin River (12,761)*
Cyprinella lutrensis, red shiner	RSH	21.7 (34)	0.9 (30)	5.5 (51)	1.1 (24)	3.4 (30)	75.5 (100)
Menidia beryllina, inland silverside	ISS	14.6 (85)	0.6 (52)	9.8 (82)	22.6 (95)	51.9 (85)	9.9 (94)
*Catostomus occidentalis** Sacramento sucker	SKR	14.0 (80)	39.9 (100)	21.1 (99)	9.4 (77)	2.9 (30)	3.9 (78)
*Ptychocheilus grandis**, Sacramento pikeminnow	PKM	13.4 (87)	23.7 (96)	21.4 (93)	14.6 (97)	2.0 (48)	0.4 (50)
*Pogonichthys macrolepidotus**, Sacramento splittail	ST	9.7 (85)	7.8 (89)	10.0 (89)	17.5 (96)	5.8 (63)	1.2 (33)
Dorosoma petenense, threadfin shad	TFS	4.2 (47)	3.2 (74)	9.1 (61)	1.5 (35)	12.8 (41)	0.2 (44)
Acanthogobius flavimanus, yellowfin goby	YFG	4.1 (47)	0	<0.1 (6)	13.1 (88)	4.6 (67)	0
Gambusia affinis, western mosquitofish	GAM	3.4 (52)	5.0 (67)	2.9 (58)	2.3 (48)	2.9 (44)	4.9 (44)
Pimephales promelas, fathead minnow	FHM	2.6 (34)	0.2 (19)	7.2 (71)	0.3 (17)	0.1 (7)	0.6 (61)
Notemigonus crysoleucas, golden shiner	GSH	1.9 (54)	6.2 (78)	2.2 (61)	2.1 (58)	1.6 (33)	0
Micropterus spp.[a], black bass	BASS	1.7 (68)	1.3 (59)	2.0 (60)	2.3 (75)	4.9 (85)	0.3 (56)
Percina macrolepida, bigscale logperch	LGP	1.0 (28)	0.9 (33)	2.0 (26)	0.5 (27)	0.9 (22)	0.2 (44)
*Hysterocarpus traskii**, tule perch	TP	1.0 (37)	0.7 (37)	0.4 (28)	2.7 (50)	<0.1 (4)	0.2 (44)
Lepomis macrochirus, bluegill	BG	0.9 (40)	2.1 (67)	0.5 (33)	1.1 (37)	1 (33)	0.6 (61)
*Hypomesus transpacificus**, delta smelt	DS	0.7 (24)	0	0.4 (22)	1.7 (40)	0	0
Pomoxis annularis, white crappie	WC	0.7 (12)	0.9 (48)	0.2 (11)	<0.1 (6)	0	<0.1 (11)
Morone saxatilis, striped bass	SB	0.6 (23)	0	<0.1 (6)	1.5 (37)	3.4 (33)	<0.1 (17)
*Lavinia exilicauda**, hitch	HCH	0.5 (24)	2.2 (63)	0.6 (31)	0.5 (19)	<0.1 (4)	0
Lepomis microlophus, redear sunfish	RSF	0.5 (24)	0.5 (41)	0.2 (13)	1.1 (24)	0.9 (30)	0.3 (33)
*Cottus asper**, prickly sculpin	PSCP	0.4 (19)	0.2 (26)	0.1 (10)	0.8 (25)	0.5 (4)	0.3 (33)
*Leptocottus armatus**, staghorn sculpin	STAG	0.4 (13)	0	0	1.3 (29)	0	0
Cyprinus carpio, common carp	CP	0.3 (16)	0.4 (19)	0.6 (24)	0.1 (8)	0.1 (4)	0.2 (61)
*Mylopharodon conocephalus**, hardhead	HH	0.3 (9)	1.8 (15)	0.2 (13)	0.1 (7)	<0.1 (4)	0.1 (11)
Carassius auratus, goldfish	GF	0.2 (10)	0.1 (15)	0.2 (18)	<0.1 (2)	0	0.3 (44)
*Gasterosteus aculeatus**, threespine stickleback	STBK	0.2 (12)	0.1 (7)	0	0.5 (26)	0	0
*Hesperoleucas symmetricus**, California roach	RCH	0.2 (5)	0	0.6 (17)	<0.1 (1)	0	0
*Orthodon microlepidotus**, Sacramento blackfish	SBF	0.2 (5)	0	<0.1 (4)	<0.1 (3)	<0.1 (4)	0.5 (39)
Tridentiger bifasciatus, shimofuri goby	SHGOB	0.2 (10)	0	0	0.7 (23)	<0.1 (4)	0
Hypomesus nipponensis, wakasagi	WAK	0.1 (9)	0.2 (4)	0.3 (28)	0.1 (2)	0	0
Pomoxis nigromaculatus, black crappie	BC	0.1 (10)	0.3 (30)	0.2 (11)	0.2 (9)	0	0
Ameiurus catus, white catfish	WCF	<0.1 (2)	0.1 (4)	1.9 (14)	0.1 (2)	0	0
Ameiurus melas, black bullhead	BLB	<0.1 (1)	0	<0.1 (1)	<0.1 (1)	0	<0.1 (6)
Ictalurus punctulatus, channel catfish	CCF	<0.1 (2)	0	<0.1 (4)	0	0	<0.1 (11)
Lampetra spp.[b]*, lamprey	LMP	<0.1 (6)	0.1 (11)	0.1 (11)	<0.1 (4)	0	0
Lepomis cyanellus, green sunfish	GSF	<0.1 (5)	0.1 (15)	<0.1 (3)	<0.1 (1)	0	0.1 (28)
Lepomis gulosus, warmouth	WAR	<0.1 (1)	<0.1 (4)	<0.1 (1)	0	0	0
*Spirinchus thaleichthyes**, longfin smelt	LFS	<0.1 (5)	0	0.1 (1)	0.1 (9)	0	0

[a]Because young-of-year *Micropterus* are sometimes difficult to distinguish, we combined them. The majority of fish were identified as largemouth bass, *Micropterus salmoides*.

[b]Lampreys were often not identified to species.

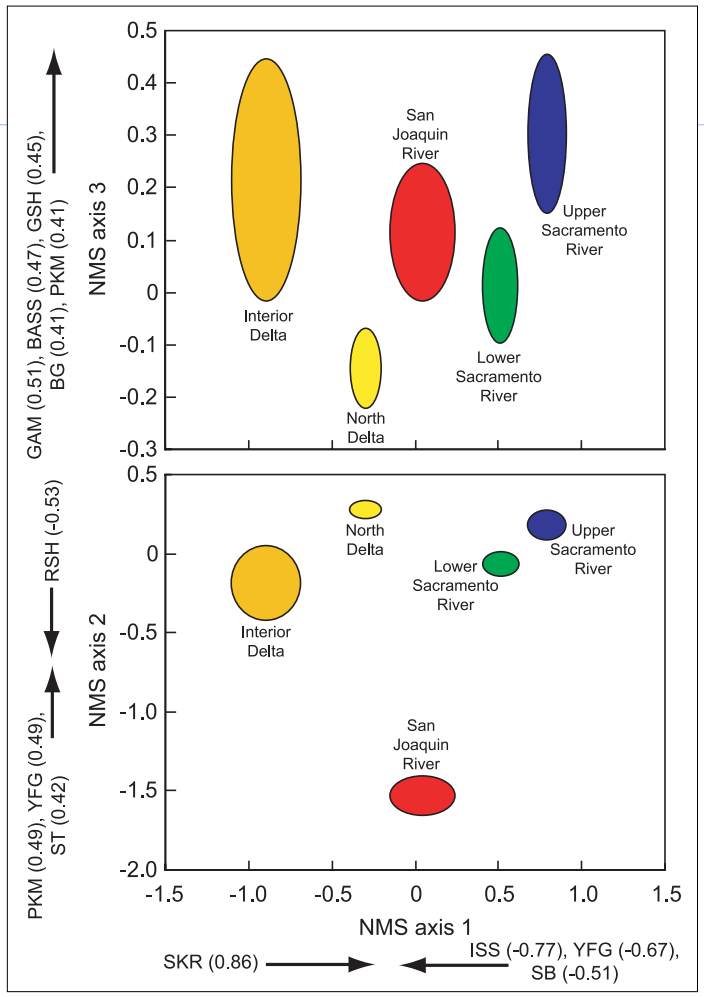

Figure 4. NMS plots from analysis of fish percentage abundances from upper Sacramento River, lower Sacramento River, North Delta, Interior Delta and San Joaquin River (stress = 0.15). Numbers in parentheses are statistically significant ($P < 0.05$) Spearman rank correlations between the NMS axis scores and percentage abundances of individual species. Only species with correlation coefficients with absolute values greater than 0.4 are shown. Arrows indicate the direction of increasing species abundance. See Table 1 for species codes.

Dissimilarities among the two Sacramento River groups and North Delta regions were lower (″ 62%). The dissimilarities among the groups other than the San Joaquin River were mainly due to somewhat different percentages of commonly shared species.

The ANOVA of the NMS axis scores showed a strong effect of region on NMS axis 1 (F_4,216 = 77, $P <$ 0.001), NMS axis 2 (F_4,216 = 116, $P < 0.001$), and NMS axis 3 (F_4,216 = 9, P < 0.001). Year was only significant for NMS axis 2 (F_8,216 = 2, $P < 0.05$). The interaction term was never significant (all $P > 0.05$). For NMS axis 1, Tukey pairwise tests indicated that all the regions were different from each other except upper

Table 2. Species contributing to similarity of sites within regions and species contributing to dissimilarity of sites between regions. Percentages represent the within region similarities and between region dissimilarities. Bolded and underlined species (see Table 1 for species codes) contributed greater than 20% to the similarity or dissimilarity value. Bolded species contributed from 11% to 20%. Other species contributed from 5% to 10%. Numbers in parentheses represent the percentage of the total catch of a species for a particular region (Table 1).

	Upper Sacramento River	*Lower Sacramento River*	*North Delta*	*Interior Delta*	*San Joaquin River*
Within region similarity:					
	60%	52%	49%	42%	64%
	SKR (40) **PKM** (24) ST (8) GSH (6) TFS (3)	**SKR** (21) **PKM** (21) **ISS** (10) **ST** (10) FHM (7)	**ISS** (23) **PKM** (15) ST (17) SKR (9) YFG (13)	**ISS** (52) **BASS** (5) **YFG** (5) ST (6)	**RSH** (75) **ISS** (10) SKR (4)
Between region dissimilarity with lower Sacramento River					
	50%				
	SKR (21) PKM (21) ISS (10) [a] ST (10) TFS (9) GSH (2) FHM (7) [a] GAM (3) [a]				
Between region dissimilarity with North Delta					
	62%	58%			
	SKR (9) **ISS** (23) [a] YFG (13) [a] PKM (15) ST (17)	**SKR** (9) YFG (13) [b] ISS (23) PKM (15) ST (17)			
Between region dissimilarity with Interior Delta					
	77%	71%	62%		
	SKR (3) **ISS** (52) [a] **PKM** (2) BASS (5) [a] YFG (5) [a] ST (6) TFS (13)	**SKR** (3) **ISS** (52) PKM (2) BASS (5) [b] YFG (5) [b] ST (6) TFS (13) [b]	**ISS** (52) ST (6) PKM (2) YFG (5) SKR (3) c BASS (5) c TFS (13) c		
Between region dissimilarity with San Joaquin River					
	79%	73%	77%	77%	
	RSH (75) [a] **SKR** (4) **PKM** (<1) ISS (10) ST (1)	**RSH** (75) [b] **SKR** (4) **PKM** (<1) ST (1) ISS (10)	**RSH** (75) c ST (1) **PKM** (<1) YFG (0) ISS (10) SKR (4)	**RSH** (75) [d] ISS (10) BASS (<1) YFG (0) ST (1)	

[a] In the upper Sacramento River: ISS < 1%, FHM < 1%, GAM = 5%, BASS = 1% YFG = 0, RSH < 1%.

[b] In the lower Sacramento River: YFG <1%, BASS = 2%, TFS = 9%, RSH = 5%.

[c] In the North Delta: SKR = 9%, BASS = 2%, TFS = 1%, RSH = 1%.

[d] In the Interior Delta: RSH = 3%.

and lower Sacramento River. For NMS axis 2, Tukey pairwise tests indicated that all the regions were different, except upper and lower Sacramento River, North Delta and upper Sacramento River, and Interior Delta and lower Sacramento River. For NMS axis 3, Tukey pairwise tests indicated that the regions were similar except North Delta and Interior Delta, North Delta and upper Sacramento River, and upper and lower Sacramento River. Tukey pairwise tests indicated no significant pairwise comparisons for year for NMS axis 2.

The first two principal components from the analysis of life history traits accounted for 57% and 22% of the variance in the life history data, respectively (Table 3). The first axis represents a gradient from large, long-lived, nonbatch spawning species with high fecundity (periodic strategy) to small, short-lived, batch spawning species with low fecundity (opportunist strategy). The opportunist strategy was dominated by alien species. The second axis represents a gradient in parental care with tule perch (TP) representing the species most representative of the equilibrium strategy. Except for threespine stickleback and tule perch, the equilibrium life history was dominated by alien centrarchids and ictalurids. The life history strategies of the native species are wholly contained within the range of life history strategies of the alien species, except for threespine stickleback and tule perch (Figure 5). Regional plots show a gradual change from the upper Sacramento River dominated by native periodic strategists, particularly Sacramento sucker and Sacramento pikeminnow, to the San Joaquin River dominated by alien opportunistic strategists, specifically red shiner, inland silverside, and Western mosquitofish (Figure 5). The equilibrium strategy represented by tule perch did not play a major role in any region.

Table 3. Loadings of original variables on the first two axes of a principal components analysis (PCA) of life history characteristics.

Variable	*PCA axis 1*	*PCA axis 2*
Maximum adult size[a]	0.94	-0.03
Average age of maturity	0.91	0.07
Maximum age[a]	0.91	-0.14
Maximum fecundity[a]	0.79	0.43
Batch spawning[b]	-0.51	0.53
Parental care index[c]	-0.02	-0.92

[a] log transformed for analysis

[b] 0, nonbatch spawner; 1, batch spawner.

[c] This index from Winemiller and Rose (1992) is the sum of three metrics. The first is scored as 0 if no special placement of zygotes, 1 if zygotes are placed in a special habitat, or 2 if both zygotes and larvae are maintained in a nest. The second is scored as 0 if there is no parental care of zygotes or larvae, 1 if there is brief (<1 mo) protection by one sex, 2 if a long (>1 mo) period of protection by one sex or brief care by both sexes, and 4 if lengthy protection by both sexes. The third is scored as 0 if there is no nutritional contribution to larvae (exclusive of egg yolk), 2 if there is a brief (<1 mo) contribution to nutrition, 4 if there is a long period of nutritional contribution (1–2 mo), or 8 if there is an extremely long period of nutritional contribution (>2 mo).

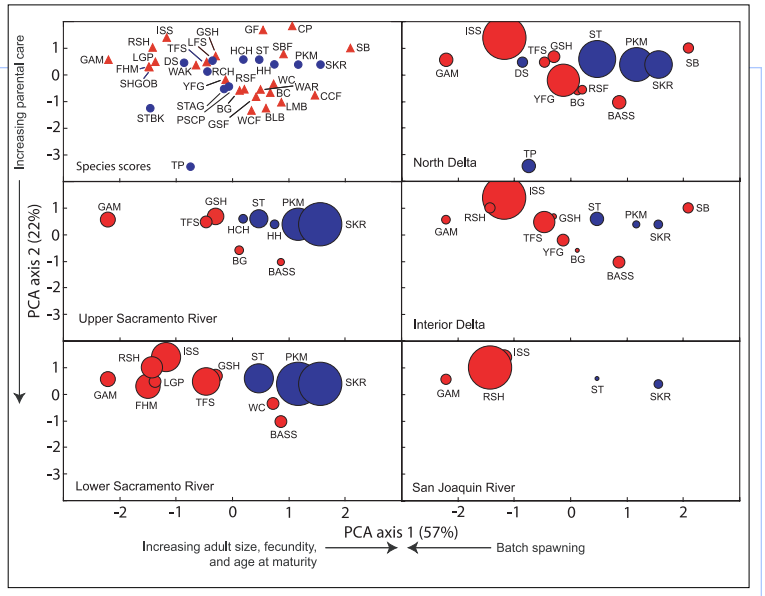

Figure 5. Species plots on the first two axes of a principal components analysis (PCA) of life history characteristics for the five sampling regions. In the plot of species scores, blue circles are native species and red triangles are alien species. In the regional plots, circles are species scores weighted by percentage abundance of that species in the total catch for the region. Arrows indicate the direction of increase for individual variables on each PCA axis. Numbers in parentheses are the percentage of variance explained by each PCA axis.

DISCUSSION

Before major human modifications in the watershed, the Sacramento and San Joaquin Rivers shared a majority of fish species organized into similar assem-

blages (Moyle 2002). Our analyses clearly demonstrate differences in species composition and dominant life history characteristics among the spring nearshore resident fish assemblages of the two rivers. The upstream region of the Sacramento River was dominated by native fishes with periodic life history strategies. Alien species became a larger part of the fish assemblage in the lower Sacramento River and North Delta, although native species remained important. The distribution of life history strategies also became more balanced in the lower parts of the watershed, and the North Delta included the tule perch, the species in the system showing the most parental care (live bearer, equilibrium strategist). The San Joaquin River showed a very different pattern with an upstream region dominated by alien opportunist species. The Interior Delta was also dominated by alien opportunist species although native species became more common and life history strategies more diverse. Moving into the North Delta, native and alien species became equally abundant and life history strategies more balanced.

These patterns are consistent with the results from other studies. Brown (2000) showed inland silverside and red shiner to be important species in defining the lower San Joaquin River summertime fish assemblage. A study of the southern Delta (our Interior Delta) (Feyrer and Healey 2003), including the uppermost tidal reaches of the San Joaquin River, confirms the very low abundance of red shiner in the Delta and the presence of a mixture of native and alien fishes similar to that observed in our analysis. May and Brown (2002) contrasted the continued presence of native species in the Sacramento River watershed with the dominance of alien species in the San Joaquin River. Within the Delta, Nobriga et al. (2005) found differences in species composition and life history strategies between fish assemblages of the Sacramento River (our North Delta) and the San Joaquin River (our Interior Delta). Brown and Michniuk (unpublished data) analyzed boat electrofishing data from the Delta and found that the North Delta had more native fishes than the Interior Delta.

We did not observe annual differences in fish species composition, but, as noted earlier, our use of percentage abundances may have reduced our ability to detect annual differences, which would likely be better reflected by measures of absolute abundances, such as catch per unit effort. Evidence from other studies is mixed. Brown and Ford (2002) detected annual differences in the percentage abundances of native and alien fishes related to flow in the Tuolumne River, a tributary to the San Joaquin River. Feyrer and Healey (2003) also noted annual differences in species composition in the southern Delta (our Interior Delta) related to flow. In their study of the Delta, Nobriga et al. (2005) did not find differences between years for their seining collections. In summary, our analyses provide strong support for spatial gradients in fish species composition and life history strategies but little evidence of annual variation.

The differences in spatial gradients in the two watersheds do not seem to be due to differences in spring water temperatures. Although the data do not cover the whole sampling period there are not large differences among regions. Specific conductance exhibited larger spatial differences but most of the species present can easily tolerate the values observed (Moyle 2002). Kimmerer (2004) also found minimal spatial variation in water temperature and salinity in the Delta during the spring, when freshwater flows are high and temperatures and salinities low. In many respects, spring studies such as ours likely represent the best case situation for native species. Most native species spawn during the spring, so there are large numbers of juvenile fish moving through the system (Moyle 2002; Dege and Brown 2004; Sommer et al. 2004). Most alien species spawn somewhat later and come to dominate the fish assemblages in summer and fall (Grimaldo et al. 2004; Nobriga et al. 2005). It seems more likely that conditions controlling the distribution and abundance of fishes occur during the more stressful summer period than during the spring.

The San Joaquin River and its tributary rivers are managed for water diversions largely for agricultural use. During summer low-flow periods agricultural return flows account for most of the streamflow in the San Joaquin River (Kratzer and Shelton 1998); however, it is impossible to document exact percentages because such non-point discharges are not measured. Agricultural return flows are warm and contain high concentrations of pesticides, nutrients, salts, and suspended sediment (Kratzer and Shelton 1998; Brown

2000). The stressful, fluctuating summertime environment should favor short-lived opportunistic species (Winemiller and Rose 1992), and opportunistic red shiner and inland silverside were abundant in both spring samples (this study) and summer samples (Brown 2000). The summer fish assemblage of the lower San Joaquin River, which includes threadfin shad, *Dorosoma petenense,* and fathead minnow, *Pimephales promelas,* along with red shiner and inland silverside, appears to be very specific to the mainstem river and the smaller agricultural drains and creeks with similar water quality and physical conditions. Fish assemblages in the larger tributary rivers with better water quality and more natural habitat conditions, including the Stanislaus, Tuolumne, and Merced Rivers, are very different and include more native fishes and fewer opportunistic species (Brown 2000). The better water quality, cooler temperatures, and more natural habitat appear to favor the native periodic strategists (Brown 2000; Brown and Ford 2002) that evolved in California's fluctuating but predictable snowmelt runoff environment (Moyle 2002).

The Sacramento River is managed for a variety of purposes including water delivery to the Delta for export by state and federal pumping facilities, and maintenance of water temperatures and habitat for fishes, including endangered winter-run Chinook salmon. Large volumes of cool, high quality water are released from Shasta Dam and several tributary rivers for these purposes. Smaller tributaries are largely undiverted and maintain good populations of native fishes (Baltz and Moyle 1993; Moyle 2002; May and Brown 2002). The higher flow conditions, good water quality, cool summer water temperatures, and relatively natural habitat condition of tributaries appear to favor the maintenance of healthy populations of native stream fishes, many of which are periodic strategists that do well in seasonally dynamic, abiotically driven systems (Winemiller and Rose 1992). Sacramento pikeminnow, sucker, and splittail are all examples of native periodic strategists. However, alien fishes are often present in low numbers in both the tributaries (Baltz and Moyle 1993; Seesholtz et al. 2004; May and Brown 2002) and the mainstem Sacramento River (Table 1) and would presumably increase in abundance if environmental conditions changed.

Within the Delta, the factors governing species composition are likely more complex than in the rivers. Water temperatures may become seasonally stressful for some species (Grimaldo et al. 2004; Bennett 2005). The distribution and abundance of juvenile freshwater and estuarine fish varies with seasonal changes in flow, hydrodynamics, temperature, and salinity (Dege and Brown 2004; Feyrer 2004). Stream-oriented, riffle-spawning species, such as Sacramento sucker and Sacramento pikeminnow, and floodplain-spawning species, such as Sacramento splittail, that do not actually spawn in the Delta, migrate into the Delta from upstream areas (Feyrer et al. 2005; Nobriga et al. 2005). Habitat variables, such as presence of submerged aquatic vegetation and water clarity, and biotic interactions, particularly predation, are likely important structuring forces (Brown 2003; Nobriga et al. 2005). Given that a variety of habitat conditions may be important, it is not surprising that no single life history strategy appears to dominate.

Concepts regarding restoration of native fish populations in the Delta and watershed have evolved considerably in recent years. Restoration of tidal wetlands and other shallow water habitats, the main habitat types lost to habitat change, was originally conceived as the best way to restore native fishes in the Delta (CALFED 2000). However, a variety of studies suggest that restoring permanent tidal wetlands may not be desirable because it also produces shallow subtidal habitat that is invaded by an alien aquatic macrophyte, *Egeria densa*. *Egeria densa* habitat is very productive but supports fish assemblages dominated by alien species, including predators and competitors of native fishes (Brown 2003; Grimaldo et al. 2004; Nobriga et al. 2005). Recent work on floodplain ecology (Sommer et al. 2001a,b; Crain et al. 2004; Ribiero et al. 2004) suggests that floodplain restoration should be viewed as a key strategy to restoring native fish populations. Restoring natural flow regimes and restoring cooler temperatures have been recognized as potential tools in riverine systems (Marchetti and Moyle 2001; Brown and Ford 2002; Seesholtz et al. 2004).

Our analyses suggest that native fish restoration in the San Joaquin River and Interior Delta will be a major

challenge for ERP and other programs. Unlike the Sacramento River, the San Joaquin River no longer supports substantial populations of native fishes. Native fishes are still present in the low elevation portions of the San Joaquin River watershed but they are most abundant in tributary rivers, in the river reaches below the large storage reservoirs at the base of the Sierra Nevada (Brown 2000; Brown and Ford 2002). The potential benefits of San Joaquin River native fish restoration appear high because there is so much potential for improvement. If such restoration is initiated, the mixture of native and alien fishes extant in the Sacramento River may serve as a useful target or model of an achievable endpoint. However, it is unclear how to manipulate the San Joaquin River system to renew the connection of the tributary populations of native fishes with the mainstem San Joaquin River, through the Interior Delta, and into the North Delta. The responses of alien fishes to restoration actions will be critical to determining success. The costs of such restoration actions, once identified, might outweigh the potential benefits, especially if similar or greater benefits for native fishes could be accomplished elsewhere in the system with less difficulty. Adequate monitoring and assessment throughout the Sacramento-San Joaquin watershed will be essential to establishing the success or failure of any such restoration efforts. Ecosystem restoration, in California and elsewhere, presents many difficult challenges, but they must be addressed if our society desires the preservation and restoration of native biodiversity at the same time that human demands on water resources are increasing.

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