

Fish communities and their associations with environmental variables, lower San Joaquin River drainage, California

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Synopsis

Twenty sites in the lower San Joaquin River drainage, California, were sampled from 1993 to 1995 to characterize fish communities and their associations with measures of water quality and habitat quality. The feasibility of developing an Index of Biotic Integrity was assessed by evaluating four fish community metrics, including percentages of native fish, omnivorous fish, fish intolerant of environmental degradation, and fish with external anomalies. Of the thirty-one taxa of fish captured during the study, only 10 taxa were native to the drainage. Multivariate analyses of percentage data identified four site groups characterized by different groups of species. The distributions of fish species were related to specific conductance, gradient, and mean depth; however, specific conductance acted as a surrogate variable for a large group of correlated variables. Two of the fish community metrics – percentage of introduced fish and percentage of intolerant fish – appeared to be responsive to environmental quality but the responses of the other two metrics – percentage of omnivorous fish and percentage of fish with anomalies – were less direct. The conclusion of the study is that fish communities are responsive to environmental conditions, including conditions associated with human-caused disturbances, particularly agriculture and water development. The results suggest that changes in water management and water quality could result in changes in species distributions. Balancing the costs and benefits of such changes poses a considerable challenge to resource managers.

Introduction

Aquatic habitats around the world are rapidly being altered by human activities (Dudgeon 1992, Moyle & Leidy 1992, Allan & Flecker 1993). Habitat alterations are often accompanied by declines in the native species that are dependent on those habitats. Alterations to stream environments can take many forms, including changes in water quality, instream habitat, riparian habitat, and the introduction of new species. If native species and the communities they form are to be preserved, their responses to such human-induced

changes must be understood. Only with such understanding can human activities be modified to reverse, or at least moderate, the detrimental effects on native biodiversity.

The lower San Joaquin River drainage of California exemplifies many of the problems that can occur as a result of human activities. The San Joaquin Valley, part of the San Joaquin Basin and the associated Tulare Basin (Figure 1), once had a wide variety of terrestrial and aquatic habitats that provided rich resources for Native Americans and early settlers. However, as the San Joaquin Valley was converted to agricultural

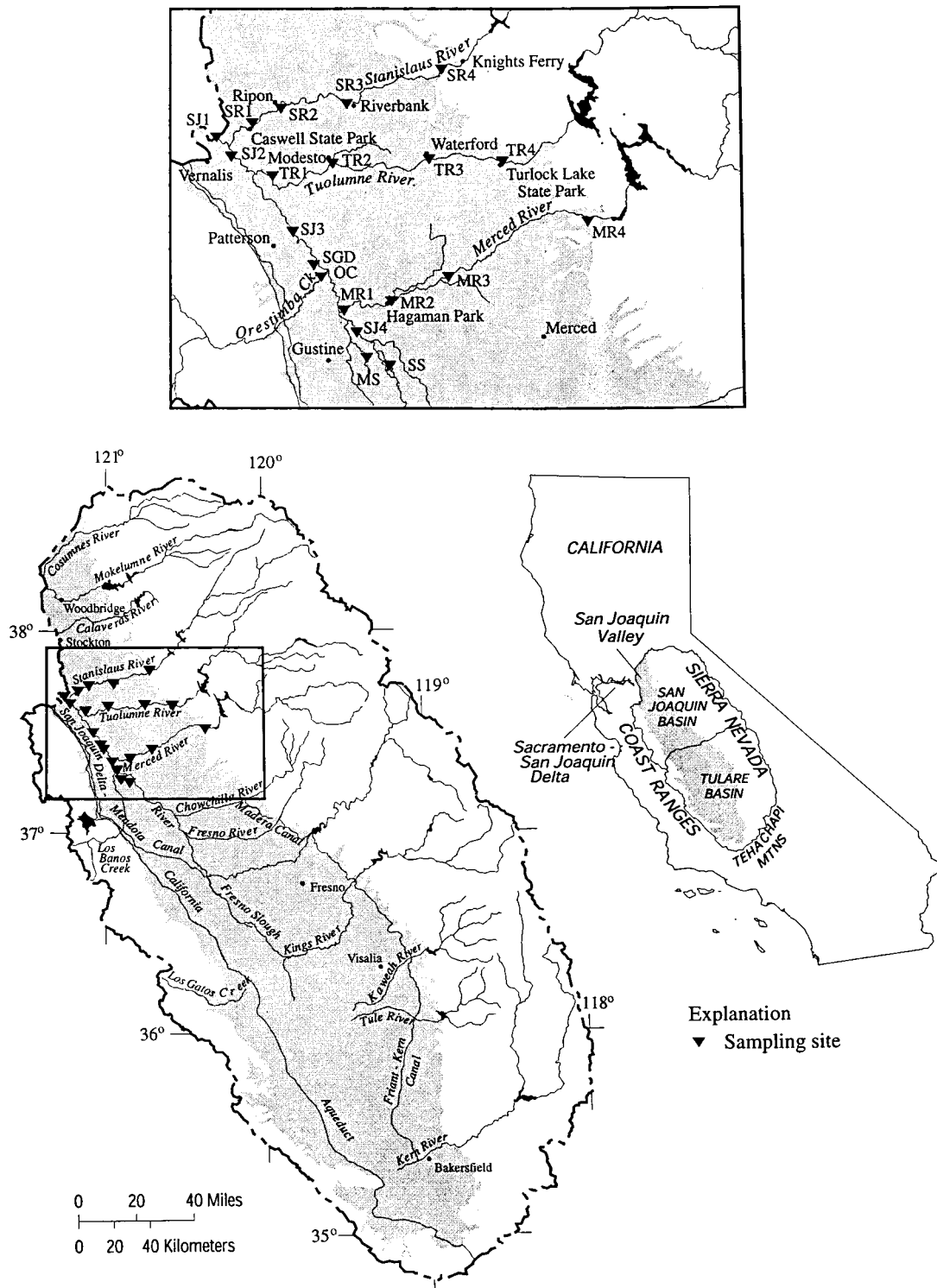


Figure 1. Locations of study sites in the lower San Joaquin River drainage, California. Refer to Table 1 for full site names.

land use, native ecological communities declined (San Joaquin Valley Drainage Program¹, Brown²). On the valley floor, intensive agricultural activity, accompanied by increasing urbanization, has resulted in changes in water quality and aquatic habitats through several mechanisms. Intensive use of pesticides and fertilizers, which enter surface waters in various ways, has altered water quality (Kuivila & Foe 1995, Domagalski et al. 1997, Kratzer & Shelton³, Brown et al. 1999). Pesticide concentrations sometimes reach concentrations acutely toxic to sensitive invertebrates (Kuivila & Foe 1995). Agricultural return flows also may contain high concentrations of dissolved solids (salinity) and trace elements (Saiki 1984, Hill & Gilliom⁴, Brown²) that can degrade water quality. Clearing of land for agriculture and flood control activities have resulted in the loss of wetland and riparian habitat, leaving less than 10% of the historical area (San Joaquin Valley Drainage Program¹, Brown²). Finally, the natural hydrologic regime and geomorphic processes of the rivers have been substantially changed because of dams and diversions that provide water supply and flood control for agricultural and municipal purposes (Kahrl et al. 1978, Mount 1995).

The San Joaquin and Tulare basins also include forest lands in the Sierra Nevada foothills and mountains. Changes in water and habitat quality at elevations above the valley floor have been less dramatic with streams affected by logging, grazing, urbanization, and smaller-scale dams and diversions operated for municipal water supply and production of hydroelectricity (Moyle & Randall 1998).

These changes in water quality and habitat have been accompanied by changes in the fish fauna, including declines or extinctions of native species and the

introduction of new species (Moyle & Nichols 1974, Moyle 1976, Jennings & Saiki 1990, Brown & Moyle 1993). These authors have suggested that the introduced species appear to be better adapted for the altered water quality, habitat, and hydrologic conditions. The importance of natural flow regimes to maintaining native fish communities in California has been noted in several recent studies (Brown & Moyle 1997, Moyle & Light 1996a,b). Competition and predation between native and introduced species have also been suggested as important; however, evidence in support of these suggestions is limited.

Fish have been suggested as valuable indicators of environmental quality (Karr 1991, Moyle 1994). The purpose of this paper is to characterize the fish communities of the lower San Joaquin River drainage of California and to assess their associations with measures of water quality and habitat quality. In addition, four fish community metrics commonly included in metric-based approaches to the use of fish as indicators of environmental degradation, such as the Index of Biotic Integrity (e.g. Fausch et al. 1984, Hughes & Gammon 1987), are calculated to assess the potential for developing such a system for the study area. The metrics calculated are percentages of native fish, omnivorous fish, fish intolerant of environmental degradation, and fish with external anomalies, including lesions, tumors, parasites, and infections.

Methods

Study design

Twenty sites on eight streams were sampled at varying levels of intensity from 1993 to 1995 (Table 1). Four sites each were located on the lower San Joaquin River and its major tributaries, the Stanislaus, Tuolumne, and Merced rivers, to assess longitudinal gradients in environmental conditions and fish community structure. The remaining four sites were located on smaller tributary creeks, drains, and sloughs affected by agricultural activities typical of the drainage.

In 1993, a total of nine sites were sampled. In 1994, 16 sites were sampled – 11 sites sampled for the first time and 5 sites previously sampled in 1993. In 1995, three of the sites sampled during the previous 2 years were sampled for a third year; two additional stream reaches were also sampled at each of the three sites during the 1995 sampling. The multiple year sampling

¹ San Joaquin Valley Drainage Program. 1990. Fish and wildlife resources and agricultural drainage in the San Joaquin Valley. Final Report of the San Joaquin Valley Drainage Program, U.S. Department of the Interior and California Resources Agency, Sacramento. 440 pp.

² Brown, L.R. 1997. Aquatic biology of the San Joaquin-Tulare basins: analysis of available data through 1992. Water-Supply Paper 2471, U.S. Geological Survey, Reston. 89 pp.

³ Kratzer, C.R. & J.L. Shelton. 1998. Water-quality assessment of the San Joaquin-Tulare Basins, California: analysis of available data on nutrients and suspended sediment in surface water, 1972-1990. USGS Professional Paper 1587, U.S. Geological Survey, Reston. 92 pp.

⁴ Hill, B.R. & R.J. Gilliom. 1993. Streamflow, dissolved solids, suspended sediment, and trace elements, San Joaquin River, California, June 1985–September 1988. U.S. Geological Survey, Water Resources Investigation Report 93-4085, Reston. 21 pp.

Table 1. Site name, site code, type of site and sampling period for all sites sampled during the study in the lower San Joaquin River, California. Site types: MR = sites where three reaches were sampled in one year, MY = sites where one reach was sampled in more than one year, and SY = sites where one reach was sampled in only one year.

Site name	Site code	Site type	Sampling period
Merced River at River Road	MR1	MY, MR	1993–1995
Merced River at Hagamann County Park	MR2	SY	1994
Merced River at McConnell State Park	MR3	SY	1994
Merced River near Snelling Diversion Dam	MR4	SY	1994
Mud Slough near Gustine	MS	SY	1993
Orestimba Creek at River Road	OC	SY	1993
Salt Slough at Lander Avenue	SS	SY	1993
San Joaquin River near Vernalis	SJ1	MY	1993–1994
San Joaquin River at Maze Road	SJ2	SY	1994
San Joaquin River near Patterson	SJ3	MY	1993–1994
San Joaquin River at Fremont Ford	SJ4	SY	1994
Spanish Grant Drain	SGD	SY	1993
Stanislaus River at Caswell State Park	SR1	SY	1994
Stanislaus River near Ripon	SR2	MY, MR	1993–1995
Stanislaus River near Riverbank	SR3	SY	1994
Stanislaus River near Knights Ferry	SR4	SY	1994
Tuolumne River at Shiloh Road	TR1	SY	1994
Tuolumne River at Modesto	TR2	MY, MR	1993–1995
Tuolumne River near Waterford	TR3	SY	1994
Tuolumne River at Turlock State Recreation Area	TR4	SY	1994

conducted from 1993 to 1995 was designed to indicate the annual variability of fish communities. The multiple reach sampling was designed to indicate the spatial variability in a particular year. Multiple reach and multiple year sampling could not be conducted at all sites because of logistic and economic constraints. Multiple year sites were located at sites included in a more detailed study of water quality in the drainage (Brown et al. 1999). Multiple reach sites were selected from the multiple year sites on the basis of long-term accessibility, availability of three homogenous stream reaches, and the presence of diverse aquatic communities, including macroinvertebrates and algae that were sampled as part of companion studies.

The fishes were sampled in August or September of each year. The period from July through September is typically sampled in studies of California stream fishes (e.g. Brown & Moyle 1993, Moyle & Nichols 1973, 1974) and provides comparable data on summer fish community structure. Habitat data and nutrient samples were collected within a month of fish sampling (nutrient samples were not collected in 1995). The interval between fish sampling and environmental

sampling was not anticipated to substantially affect the results because the water system is closely managed and is at base flow during the summer. This results in fairly consistent environmental conditions throughout the summer.

Data collection

Length of the sampling reach was determined in one of two ways. If there were repeating habitat units (pools, riffles, runs), then the reach was defined as the length of stream containing two repetitions of the habitat units present. When repeating habitat units were not present, reach length was defined as 20 times the channel width to an upper limit of approximately 1000 m. Actual reach lengths varied from 120 to 1200 m. Mean stream widths varied from 3.8 to 93.2 m.

At each site, fishes were sampled by an appropriate combination of electrofishing (boat or backpack), seining (3, 9 or 15 m length with 6-mm mesh), or snorkeling. Electrofishing consisted of one pass along each bank of the stream. Midstream structure was also sampled if present and accessible. Snorkeling consisted of

one pass through the stream by one or two snorkelers. Seining effort was variable because of the scarcity of seining beaches. Effort consisted of one or more seine hauls at all available seining beaches. The Mud Slough site was an exception because high conductivity limited the effectiveness of electrofishing and turbidity precluded snorkeling. Fortunately, the stream was shallow and free of obstructions so the entire reach was effectively sampled by seine. Captured fish were identified and counted, and at least the first 30 individuals of each species examined for external anomalies on site. Anomalies were classified as deformities, eroded fins, lesions, tumors, black spot (a parasitic infection identified by the presence of black cysts), anchor worm (*Lernaea* spp.), leeches, anomalies of the eye, or other. For data analysis, fish were classified as having or not having one or more anomalies. Fish observed while snorkeling were identified and counted.

Water samples collected for field measurements of specific conductance, pH, alkalinity, and nutrient analyses were grab samples from slightly below the surface and near midstream, except for the 1993 nutrient samples, which were composite samples collected from several points across a stream transect (transect perpendicular to stream flow) and including water from all depths. Field measurements of specific conductance, pH, water temperature, and dissolved oxygen were made with electronic meters. Alkalinity was determined by titration. Nutrient samples were analyzed using standard analytical methods (Fishman & Friedman 1989). Water temperature and dissolved oxygen measurements were taken directly in the river. Instantaneous discharge was determined at ungauged sites.

Habitat variables were measured at each of six transects within each sampling reach. At sites with distinct habitat types (pool, riffle, run), transects were placed to reflect the availability of each habitat with at least one transect in each habitat type; otherwise, the transects were placed at equally spaced intervals. Stream width (wetted channel) was measured directly from the transect tape. Open canopy was measured from midstream with a clinometer as the number of degrees of sky above the transect not obscured by objects. Instream cover for fish was visually estimated as the percentage of stream area with object cover within 2 m of both the upstream and downstream sides of the transect tape. In a few cases, when visibility was limited by water clarity, instream cover was estimated by probing with a foot or pole while moving

along the transect. Depth, velocity, and substrate were measured at three or four points at each transect, including points at about one-quarter, one-half, and three-quarters of the stream width. Additional measurements were made to account for morphological features, such as channel bars and islands. Depth was measured with a wading rod. Velocity was measured with an electronic meter (Marsh-McBirney). Substrate was estimated as the dominant substrate at each transect point, and was classified as (1) organic detritus, (2) silt, (3) mud, (4) sand (0.02–2 mm), (5) gravel (2–64 mm), (6) cobble (64–256 mm), (7) boulder (>256 mm), or (8) bedrock or hardpan (solid rock or clay forming a continuous surface). Stream gradient, stream sinuosity, and elevation were determined from U.S. Geological Survey 1 : 24 000 topographic maps. Stream sinuosity was measured as river distance divided by the straightline distance between the upstream and downstream ends of a segment of stream (minimum length of 2 km) containing the sample site. Basin areas were determined from digitized U.S. Geological Survey Hydrologic Unit Code maps (1 : 250 000). Percentage agricultural and agricultural + urban land use within each basin area were determined using a digitized land use database (U.S. Geological Survey⁵).

Data analysis

The data set used for two-way indicator species analysis (TWINSPAN) and canonical correspondence analysis (CCA) consisted of one sample from each of the 20 sites. For the 5 sites sampled in more than 1 year, the 1994 samples were used to minimize the effect of any inter-year variability in fish communities, physical conditions, or sampling team experience. Data from four sites sampled only in 1993 also were included. The possible effects of inter-year variation are considered in a separate analysis described later in this section.

For data collected during both fish sampling and habitat/nutrient sampling, maximum values of temperature, specific conductance, pH, and alkalinity were used, as were minimum values for discharge and dissolved oxygen. These values represent levels most stressful to fish and would most likely affect their survival and distribution. This strategy was chosen

⁵ U.S. Geological Survey. 1986. Land use and land cover digital data from 1 : 250 000 and 1 : 1 000 000 scale maps. National Mapping Program, Technical Instructions, Data Users Guide 4, U.S. Geological Survey, Reston. 36 pp.

because water quality variables were often measured at different times on the two days and weather conditions varied somewhat between the two days. By selecting the most stressful values, the range of conditions affecting fish distribution were characterized as well as possible given the available data. Habitat variables were analyzed as the mean of the 6 transect values or the mean of the 18 or more point values because analyses were conducted on a site basis, allowing only one value for each variable for each site.

Water quality variables with fewer than 50% detections were deleted from analyses. The remaining water quality and habitat variables were examined for normality and $\log_{10}(x + 1)$ transformed (when appropriate), standardized to a mean of zero (0) and standard deviation of 1, then analyzed with principal components analysis (PCA). Only principal components (PC) with eigenvalues greater than one were retained for interpretation. A reduced set of environmental variables was selected for association with fish communities by choosing one variable to represent groups of variables with high ($\geq|0.70|$) loadings on one of the PCs. This selection was somewhat arbitrary, but emphasis was placed on variables that were accurately measured in the field or from maps. All variables that did not load highly ($\geq|0.70|$) on one of the retained PCs were also included because a lack of correlation with other environmental variables does not necessarily imply a lack of biological importance.

For multivariate analysis, fish data were converted to percentage abundance of each species in a sample. To reduce the influence of rare species, only species present in 10% or more of the samples, and making up at least 5% of the fish captured at one site, were included. Calculation of metric values included all individuals captured. Native species were determined from Moyle (1976). Omnivory and intolerance to environmental degradation were derived from Moyle (1976), Hughes & Gammon (1987), Moyle & Nichols (1973), Brown & Moyle (1993), and P.B. Moyle (written communication 1996).

TWINSpan (Hill 1979) was used to derive site groupings and species groupings. TWINSpan is a divisive classification technique that produces an ordered data matrix of sites and species. The analysis was limited to three sequential divisions that could potentially produce eight groups. The four site groups defined by the second level of division were used for comparison of environmental variables and fish metrics using one-way analysis of variance (ANOVA). Site groups after three divisions were used for more

fine-scaled interpretation of site and species groupings. Groups defined by the third level of division were not used for ANOVA analyses because some groups consisted of only one site.

CCA (ter Braak 1986, 1987, Jongman et al. 1995) was used to explore the associations of fish communities with the final set of environmental variables resulting from the PCA procedure. The reduction of the number of environmental variables was necessary because for multivariate analysis the number of environmental variables can not exceed the number of sites. CCA was conducted with the forward selection procedure with the significance of each variable tested with a Monte Carlo simulation algorithm before being added to the final model. All variables significant at $p < 0.05$ were included in the final model.

Similarity among years and reaches at the multiple year and multiple reach sites were evaluated with correspondence analysis (CA). Data for all years and reaches were included. Only species present in 10% or more of the samples, and making up at least 5% of the fish captured at one sample, were included. Correspondence analysis is a multivariate technique derived from reciprocal averaging that maximizes the correlation between species scores and sample scores along an assumed gradient (Hill & Gauch 1980). Thus, sample scores are constrained by species scores, and species scores are constrained by sample scores in an iterative process until a solution is obtained.

Results

A total of 31 taxa of fish were captured on the basis of all samples collected, including one hybrid (bluegill-green sunfish). Ten taxa were native to California and 21 taxa were introduced (Table 2). Western mosquitofish, *Gambusia affinis*, and lampreys, *Lampetra* spp., were not included in further analyses because they were not sampled in a consistent manner at all sites. In the 20 samples used for the community analyses, 29 taxa of fish were captured, including 9 native species. Tule perch was only abundant in the lower Stanislaus River (SR1-SR4) with a few individuals captured at a San Joaquin River mainstem site (SJ2). Sacramento split-tail were only captured at two sites (MR1 and TR2) and only in 1995. The lamprey ammocoetes captured in the lower drainage could not be identified to species because species identification is based on adult characters. The lampreys were most likely Pacific lamprey,

Lampetra tridentata, but could also have been river lamprey, *Lampetra ayersi*.

TWINSPAN site groupings

The first TWINSPAN division separated the sites on the valley floor from sites in the upper reaches of the large eastern tributaries, except several lower sites on the Stanislaus River were included with the higher elevation group (Figures 1, 2). The division was based on high percentages of a wide variety of introduced species at the valley floor sites and high percentages of native species and introduced smallmouth bass at the other sites.

The second TWINSPAN division of the valley floor sites separated a group of sites that includes the mainstem San Joaquin River sites and the small southern and western tributaries to the San Joaquin River (San Joaquin mainstem sites) and a group of sites that includes the lower elevation locations on the large east-side tributaries (lower large tributary sites). The first group was strongly associated with high percentages of fathead minnow, red shiner, threadfin shad and inland silverside. The lower tributary group was associated with high percentages of largemouth bass, smallmouth bass, bluegill, redear sunfish and white catfish.

The second TWINSPAN division of the sites in the upper reaches of the large tributaries resulted in the sites in an upper large tributary group being separated from the middle two Stanislaus River sites. The upper large tributary sites were characterized by high percentages of hardhead, Sacramento squawfish, Sacramento sucker, prickly sculpin, largemouth bass, redear sunfish and white catfish. The Stanislaus River sites were characterized by large percentages of native tule perch and introduced smallmouth bass.

The third level of division separated sites on the basis of different percentages of characteristic species identified at the second level of division, with a couple of exceptions (Figure 2). Spanish Grant drain was separated from the other San Joaquin mainstem sites because of high percentages of black bullhead, goldfish, and carp. The two Stanislaus River sites were separated because of high percentages of smallmouth bass at one and Sacramento sucker at the other. Tule perch were common at both sites.

The four groups of sites defined at the second level of TWINSPAN division had distinctly different physical characteristics (Table 3). Twelve of 24 comparisons among the site groups were statistically significant

(ANOVA, $p < 0.05$). The San Joaquin mainstem sites were most often distinct from the other site groups. The Stanislaus River sites appeared to be intermediate between the upper large tributary site group and the other two site groups. These results are also consistent with the PCA analysis.

The fish community metrics also varied among groups (Table 4). The percentage of fish with external anomalies was highest at the lower large tributary sites but not significantly different from the San Joaquin mainstem group. The percentage for the San Joaquin mainstem group was higher than the other two site groups, but was not statistically different because of high variability. Percent intolerant fish was lowest and percent introduced fish highest for the San Joaquin mainstem group and lower large tributary group. Percent omnivorous fish also varied significantly among groups. The highest percentages were found at the San Joaquin mainstem and upper large tributary sites. The Stanislaus River sites were intermediate, and the lower large tributary sites had the lowest percentage of omnivorous fish.

TWINSPAN species groups

The first TWINSPAN division separated native from introduced species, except smallmouth bass was included with the native species group. The second level of division resulted in four groups of species (Table 2). A group of species characteristic of the San Joaquin mainstem sites included black bullhead, bluegill, common carp, channel catfish, fathead minnow, goldfish, green sunfish, inland silverside, red shiner, and threadfin shad (San Joaquin mainstem species). The third TWINSPAN division of this group divided fathead minnow, inland silverside, red shiner, and threadfin shad from the other species. The former species were found almost exclusively at the San Joaquin mainstem sites, and all four species were found together at all the sites except Orestimba Creek and Spanish Grant Drain. The remaining species were more broadly distributed and were often found at the lower large tributary sites at low percentages.

The second division also identified a group of species associated with the lower large tributary sites (Table 2). This group included largemouth bass, redear sunfish, and white catfish. These species were widely distributed, but tended to have their highest percentage abundances in the lower reaches of the large east-side tributary streams. All of these species were consistently

Table 2. Common and scientific names of species captured, origin, species codes, and frequency of occurrence in the 20 sample data set and all samples collected from the lower San Joaquin River drainage, California (all samples, n = 34). Trophic group, tolerance to environmental degradation, and TWINSPAN grouping after 2 and 3 divisions are also given. Origin: I = introduced to California, N = native to California. Number of sites: Data set = the twenty samples collected in 1993 and 1994, All samples = all 34 samples collected in the study. Trophic groups: Det = detritivore, Inv = invertivore, Inv/Pis = combination invertivore and piscivore, Omn = omnivore, Pis = piscivore, and Plank = planktivore. Tolerances to environmental degradation: I = intolerant, M = moderately tolerant, and T = tolerant. TWINSPAN group: the first number indicates membership in the four groups resulting from the second TWINSPAN division and the second number indicates membership in the eight groups resulting from the third TWINSPAN division.

Family name		Origin	Species code	Number of sites		Trophic group	Tolerance	TWINSPAN group
Common name	Scientific name			Data set	All samples			
Petromyzontidae (lampreys)								
unknown lampreys	<i>Lampetra</i> spp.	N	(¹)	1	2	Det	I	(¹)
Clupeidae (shad and herring)								
Threadfin shad	<i>Dorosoma petenense</i>	I	TFS	6	8	Plank	M	1,1
Salmonidae (salmon and trout)								
Rainbow trout	<i>Oncorhynchus mykiss</i>	N	(¹)	1	1	Invert	I	(¹)
Cyprinidae (minnows)								
Common carp	<i>Cyprinus carpio</i>	I	CP	18	30	Omn	T	1,2
Fathead minnow	<i>Pimephales promelas</i>	I	FHM	8	10	Omn	T	1,1
Goldfish	<i>Carassius auratus</i>	I	GF	10	20	Omn	T	1,2
Hardhead	<i>Mylopharodon conocephalus</i>	N	HH	5	8	Omn	I	4,7
Hitch	<i>Lavinia exilicauda</i>	N	(¹)	2	8	Plank	M	(¹)
Red shiner	<i>Cyprinella lutrensis</i>	I	RSH	9	18	Omn	T	1,1
Sacramento blackfish	<i>Orthodon microlepidotus</i>	N	SBF	2	7	Plank	T	(¹)
Sacramento splittail	<i>Pogonichthys macrolepidotus</i>	N	ST	0	5	Omn	M	(¹)
Sacramento squawfish	<i>Ptychocheilus grandis</i>	N	SQ	5	10	Inv/Pis	M	4,7
Catostomidae (suckers)								
Sacramento sucker	<i>Catostomus occidentalis</i>	N	SKR	9	18	Omn	M	4,7
Ictaluridae (catfish)								
Black bullhead	<i>Ameiurus melas</i>	I	BLBH	8	10	Inv	T	1,2
Brown bullhead	<i>Ameiurus nebulosus</i>	I	(¹)	3	3	Inv	T	(¹)
Channel catfish	<i>Ictalurus punctatus</i>	I	CCF	11	18	Inv/Pis	M	1,2
White catfish	<i>Ameiurus catus</i>	I	WCF	14	22	Inv/Pis	T	2,3
Poeciliidae (livebearers)								
Western mosquitofish	<i>Gambusia affinis</i>	I	(¹)	15	20	Inv	T	(¹)

Atherinidae (silversides)								
Inland silverside	<i>Menidia beryllina</i>	I	ISS	6	15	Plank	M	1,1
Percichthyidae (temperate basses)								
Striped bass	<i>Morone saxatilis</i>	I	(¹)	4	7	Pis	M	(¹)
Centrarchidae (sunfish)²								
Black crappie	<i>Pomoxis nigromaculatis</i>	I	(¹)	3	6	Inv/Pis	M	(¹)
Bluegill	<i>Lepomis macrochirus</i>	I	BG	16	29	Inv	T	1,2
Green sunfish	<i>Lepomis cyanellus</i>	I	GSF	16	28	Inv	T	1,2
Largemouth bass	<i>Micropterus salmoides</i>	I	LMB	15	27	Pis	T	2,3
Redear sunfish	<i>Lepomis microlophus</i>	I	RSF	11	21	Inv	M	2,4
Smallmouth bass	<i>Micropterus dolomieu</i>	I	SMB	12	23	Pis	M	3,5
White crappie	<i>Pomoxis annularis</i>	I	(¹)	2	3	Inv/Pis	T	(¹)
Percidae (perch)								
Bigscale logperch	<i>Percina macrolepida</i>	I	(¹)	1	7	Inv	T	(¹)
Embiotocidae (surf perch)								
Tule perch	<i>Hysterocarpus traski</i>	N	TP	5	10	Inv	I	4,6
Cottidae (sculpin)								
Prickly sculpin	<i>Cottus asper</i>	N	PSCP	7	13	Inv	M	4,7

¹Species not included in statistical analyses because of rarity or because they were not sampled well with the methods used.

²A single bluegill-green sunfish hybrid was collected but is not listed in the table. The hybrid was counted as a separate taxon for the total taxa count.

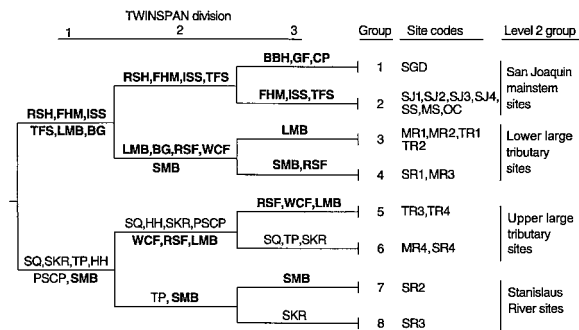


Figure 2. Site groups derived by TWINSpan analysis and the species associated with each division for the lower San Joaquin River drainage, California. The indicated species are not equivalent to the TWINSpan species groups identified in Table 2. See Table 1 for full site names and Table 2 for species names. Regular font indicates native species, and bold font indicates introduced species.

found at the San Joaquin mainstem sites. The third division of this group separated redear sunfish from large-mouth bass and white catfish.

The third species group identified after two TWINSpan divisions consisted of smallmouth bass (Table 2). This species was unique because of its broad distribution. Smallmouth bass was most abundant at Stanislaus River sites. Smallmouth bass occurred in the same geographic areas as native species; however, smallmouth bass was also widely distributed at sites dominated by introduced species. The fourth level 2 group included the native species. The third division separated tule perch because it was found almost exclusively in the Stanislaus River.

Environmental variables

The sites varied widely in water quality and habitat characteristics (Table 3). Principal components analysis resulted in 5 PCs with eigenvalues greater than one, which explained 86% of the variance in the data (Table 5). The first two PCs explained the majority of the variance (59%).

The first principal component described a gradient from sites at high elevations with coarse substrates, high gradients, low values for water quality variables, and low percentages of human land use to sites at lower elevations with low gradients, fine substrates, high values for water quality variables and higher percentages of human land use. Mean width, discharge, sinuosity, and basin area had the highest loadings on PC2. This indicates that the narrowest streams were

the straightest and also had the smallest discharges and drainage areas. There was little variability in PC2 scores for sites with high scores on PC1. Sites with low scores on PC1 had highly variable scores on PC2. Thus, sites at lower elevations with similar water quality, substrate and cover characteristics varied greatly in width, discharge, sinuosity and basin area.

Canonical correspondence analysis

The forward selection procedure resulted in the retention of three variables in the model (Table 6). The model explained approximately 40% of the variation in species composition among the sites. Specific conductance was an important variable for both CCA axes 1 and 2, though it was most important only for CCA axis 1. Gradient was an important variable on all three CCA axes and was most important on axis 3. Mean depth was the most important variable on CCA axis 2.

Separation among the TWINSpan site groups was most pronounced for the San Joaquin mainstem sites, which had positive scores on CCA axis 1 (Figure 3a). The other sites all had negative scores on CCA axis 1. The species plot (Figure 3b) indicates that the percentages of fathead minnow, inland silverside, red shiner, and threadfin shad, with high positive scores on CCA axis 1, were most important in separating the San Joaquin mainstem group from the others. The lower large tributary site group was also well separated from other groups because of large negative scores on CCA axis 2, except for SR1 (the 4 in the upper left of the group), which appeared more closely related to the upper large tributary sites. The Stanislaus River group does not appear distinctive in the ordination and is closely associated with the upper tributary sites. The presence of tule perch and high percentages of smallmouth bass were sufficient for TWINSpan to separate the groups. However, in the ordination, the species common among the two site groups (hardhead, Sacramento squawfish, Sacramento sucker, and prickly sculpin) were responsible for the sites grouping together (Figure 3b).

Annual and spatial variability

The first four CA axes explained 57.1% of the variance in the species data. The first two axes explained 19.2% and 14.8% of the variance, respectively. Axes 3 and 4 explained 12.8% and 10.3% of the variance, respectively. Visual inspection of plots of reach scores on the

Table 3. Mean and range for selected water quality and habitat variables for site groups resulting from TWINSpan analysis of fish species percentage abundances at sites in the lower San Joaquin River drainage, California. TWINSpan site groups: see Figure 3 for sites in each group. Mean = geometric mean for log-transformed variables. **Bold letters** indicate significant differences among site groups (one-way analysis of variance). Values with the same letters were not significantly different (Fischers LSD multiple comparison test). In a few cases groups were omitted from an analysis because all sites in the group had identical measurements ($\mu\text{S cm}^{-1}$ = microsiemen per centimeter at 25 degrees Celsius).

Variable	TWINSpan site groups							
	San Joaquin mainstem		Lower large tributary		Upper large tributary		Stanislaus River	
	Mean	Range	Mean	Range	Mean	Range	Mean	Range
Water quality variables								
pH ¹	8.1	7.7–8.6	8.0	7.6–8.6	7.7	7.3–8.1	7.9	7.8–7.9
Specific conductance ($\mu\text{S cm}^{-1}$) ¹	1282 A	492–4670	198 B	74–418	85 B	42–213	78 B	76–80
Dissolved oxygen (mg l^{-1})	8.1	5.8–9.7	7.7	6.9–9.3	8.8	7.6–9.3	8.3	8.1–8.5
Oxygen saturation (%)	94	68–113	90	82–115	98	90–107	91	90–92
Alkalinity ($\text{mg CaCO}_3 \text{l}^{-1}$)	171 A	72–389	72 B	30–128	40 B	18–72	35 B	34–36
Ammonia (mg l^{-1} as N) ¹	0.05 A	0.02–0.18	0.02 AB	<0.01–0.03	0.01 B	<0.01–0.03	0.02 AB	0.01–0.03
Nitrite + nitrate (mg l^{-1} as N) ¹	1.39 A	<0.05–4.00	0.71 A	0.05–3.10	0.04 B	<0.05–0.12	0.13 AB	0.12–0.15
Phosphorus, total (mg l^{-1} as P) ¹	0.22 A	0.08–0.49	0.08 B	0.03–0.28	0.02 C	<0.01–0.05	0.02 BC	0.02–0.03
Phosphorus, dissolved (mg l^{-1} as P) ¹	0.12 A	0.05–0.30	0.08 A	0.04–0.37	0.03 B	0.02–0.05	0.02 B	0.02–0.03
Ortho-phosphate (mg l^{-1} as P) ¹	0.11 A	0.05–0.29	0.06 A	0.02–0.34	0.01 B	<0.01–0.04	0.02	0.02
Habitat variables								
Discharge ($\text{m}^3 \text{s}^{-1}$) ¹	2.28	0.06–22.60	2.76	1.38–10.75	2.02	0.76–7.79	9.71	9.49–9.95
Water temperature ($^{\circ}\text{C}$)	24.1	21.0–27.0	23.8	21.5–27.5	21.7	18.5–25.5	20.7	19.5–22.0
Mean depth (m) ¹	0.74	0.52–0.95	0.57	0.37–1.17	0.76	0.61–1.69	1.21	0.97–1.51
Mean velocity (m s^{-1})	0.33	0.08–0.55	0.28	0.19–0.39	0.22	0.13–0.41	0.36	0.30–0.42
Mean dominant substrate	3.6 A	3.0–4.0	4.0 A	3.9–4.3	6.3 B	5.9–6.8	4.1 A	4.0–4.2
Mean width (m) ¹	19.4	3.8–93.2	27.6	21.2–38.9	36.4	26.9–51.7	30.3	26.8–34.2
Open canopy (degrees)	131	51–166	131	116–146	125	114–137	105	95–114
Instream cover (%) ¹	4 A	2–11	13 B	7–31	22 B	12–28	33 B	18–62
Stream gradient (%) ¹	0.03	0.01–0.17	0.04	0.02–0.06	0.11	0.09–0.21	0.03	0.01–0.06
Stream sinuosity ¹	1.41	1.04–2.12	1.62	1.06–2.77	1.18	1.11–1.31	1.66	1.42–1.95
Elevation (m) ¹	12 A	4–21	14 A	8–27	41 B	22–88	17 AB	13–22
Agricultural land (%) ¹	52.0 A	22.7–95.5	7.5 B	4.5–13.7	0.6 C	<0.1–2.2	5.5 B	5.4–9.4
Agricultural + urban land (%) ¹	53.7 A	24.1–100.0	9.1 B	5.0–14.4	1.6 C	<0.1–2.2	7.2 B	5.4–9.4
Basin area (km^2) ¹	1484	28–19023	3752	2963–4822	3287	2587–4053	2790	2705–2877

¹Variable was log-transformed for analysis.

Table 4. Mean and range for selected fish community metrics for site groups resulting from TWINSpan analysis of fish species percentage abundances at sites in the lower San Joaquin River drainage, California. TWINSpan groups: see Figure 2 for sites in each group. Mean = geometric mean for log-transformed variables. **Bold letters** indicate significant differences among site groups (one-way analysis of variance). Values with the same letters were not significantly different (Fischers LSD multiple comparison test).

Variable	TWINSpan site groups							
	San Joaquin mainstem		Lower large tributary		Upper large tributary		Stanislaus River	
	Mean	Range	Mean	Range	Mean	Range	Mean	Range
External anomalies (%)	17.4 AB	10.3–26.6	21.7 A	12.7–33.3	6.2 B	1.3–16.1	3.0 B	1.1–4.8
Omnivorous fish (%) ¹	51.5 A	17.8–87.1	6.4 B	2.1–14.2	44.6 A	27.6–72.6	16.0 AB	7.1–34.9
Intolerant fish (%) ¹	<0.1 A	0–0.4	0.2 A	0–2.1	9.8 B	1.4–21.0	32.8 B	21.4–50.0
Introduced fish (%) ¹	98.3 A	89.0–100.0	99.1 A	97.9–100.0	12.5 B	0–53.2	29.0 AB	11.0–73.8

¹Variable was log-transformed for analysis.

Table 5. Principal component loadings for habitat and water quality variables from principal components analysis of physical data from sites in the lower San Joaquin River drainage, California. **Bolded values** were considered high ($\geq|0.70|$).

Variable	Principal component				
	1	2	3	4	5
Phosphorus, total (mg l ⁻¹ as P) ¹	-0.91	(²)	(²)	(²)	(²)
Specific conductance (μS cm ⁻¹) ^{1,3}	-0.90	(²)	(²)	(²)	(²)
Orthophosphate (mg l ⁻¹) ¹	-0.87	(²)	(²)	0.32	(²)
Agricultural + urban land (%) ¹	-0.84	0.41	(²)	(²)	(²)
Agricultural land (%) ¹	-0.83	0.39	(²)	-0.30	(²)
Phosphorus, dissolved (mg l ⁻¹ as P) ¹	-0.81	(²)	(²)	0.32	(²)
Nitrate + Nitrite (mg l ⁻¹ as N) ¹	-0.76	(²)	-0.39	(²)	(²)
Ammonia (mg l ⁻¹ as N) ¹	-0.75	0.31	(²)	(²)	(²)
Alkalinity (mg l ⁻¹ as CaCO ₃)	-0.70	(²)	0.50	-0.35	(²)
Elevation (m) ¹	0.73	0.41	(²)	(²)	(²)
Instream cover (% area) ¹	0.76	(²)	(²)	0.40	(²)
Mean dominant substrate	0.83	(²)	(²)	(²)	(²)
Mean width (m) ^{1,3}	0.29	-0.94	(²)	(²)	(²)
Basin area (km ²) ¹	(²)	-0.92	(²)	(²)	(²)
Discharge (m ³ s ⁻¹) ¹	(²)	-0.82	-0.50	(²)	(²)
Sinuosity ¹	-0.26	-0.71	-0.34	(²)	(²)
Gradient (%) ^{1,3}	0.65	0.55	(²)	(²)	(²)
Mean depth (m) ^{1,3}	(²)	(²)	-0.52	-0.63	(²)
Mean velocity (m s ⁻¹) ³	(²)	(²)	-0.69	(²)	0.43
Open sky (%) ³	(²)	-0.65	0.49	(²)	-0.46
Oxygen, dissolved (mg l ⁻¹) ³	(²)	(²)	0.56	-0.46	0.60
Oxygen saturation (%) ³	(²)	(²)	0.62	-0.30	0.69
pH ^{1,3}	-0.68	-0.36	(²)	0.37	(²)
Water temperature (°C) ³	-0.56	(²)	0.30	0.45	(²)
Proportion of variance explained	0.40	0.19	0.12	0.08	0.07

¹Variable was log-transformed for analysis.

²Loading of less than 0.30.

³Variables included in the canonical correspondence analysis.

Table 6. Results of canonical correspondence analysis relating fish communities to environmental variables for sites in the lower San Joaquin River drainage, California.

Environmental variable	Eigenvalue	Canonical coefficient		
		axis 1	axis 2	axis 3
Specific conductance	0.72	1.14 ¹	0.51 ¹	0.46
Mean depth	0.36	0.05	1.02 ¹	-0.27
Gradient	0.30	0.23 ¹	0.55 ¹	1.13 ¹
Percent of species variance explained		21.1	10.9	7.6
Percent of species-environment relation explained		53.2	27.7	19.1

¹T-value for the canonical coefficient was greater than 2.1 indicating that the variable made an important contribution to a canonical axis (ter Braak 1987).

first two CA axes indicated that the differences among reaches at a site were generally smaller than differences between sites (Figure 4a). Except for reach B at MR1, reaches are similarly clustered and the choice of any reach would not substantially change interpretation of the associations among sites. Reach B differed primarily because of a higher percentage of common carp and lower percentage of inland silverside.

In contrast, differences among years were more substantial. The 1995 results were different from the other 2 years. The major differences in 1995 were the presence of native species, including Sacramento blackfish, Sacramento squawfish, Sacramento sucker, and Sacramento splittail, at the Merced and Tuolumne River sites, and the presence of large percentages of young-of-year goldfish and common carp at the Stanislaus River sites (Figure 4b). The 1993 and 1994 results were most different for SJ1 and MR1. A boat electrofisher was not available in 1993, and the combination of backpack fishing and seining utilized in 1993 was only partially effective at these sites. This was one of the reasons that the 1994 data were emphasized in the previous analyses.

Discussion

Fish communities and environmental variables

Many studies of fish community structure focus on situations where introduced species are absent or do not dominate the fish community. In the latter context, introduced species are correctly perceived as invaders, usually having detrimental effects on the native fish community. However, studies of actively

invading species and fish communities dominated by introduced species can lead to valuable insights into the ecological processes associated with the success of introduced species and possible means to ameliorate them (Brown & Moyle 1997, Moyle & Light 1996a,b). The results of this study are particularly interesting because several of the fish communities observed were composed almost entirely of introduced species.

Some aspects of fish community structure in the lower San Joaquin River drainage were consistent with previous studies of summer fish community structure in California streams, but others have not previously been described. The upper large tributary sites were characterized by a native fish community that has previously been described as characteristic of the Sierra Nevada foothills, including the east-side rivers sampled in this study but above the major foothill dams (Moyle & Nichols 1973, Moyle 1976, Brown & Moyle 1993). The results of this study indicate that this native fish community can persist in the human-modified stream reaches below the major foothill dams, but the downstream range of the community appeared to be limited based on the 1993 and 1994 data, particularly in the Merced and Tuolumne rivers. The appearance of individuals of the species comprising the upper large tributary community at downstream sites in 1995 suggests that the downstream limit of the community may fluctuate with flow. Also, although the native community is still present, introduced species may be present at the same sites in low to moderate percentage abundances.

The limitation of native species to the upper tributary areas may be related to habitat and water quality conditions. For example, hardhead, Sacramento squawfish, and Sacramento sucker all spawn in riffles, and the upper tributary sites were the only sites

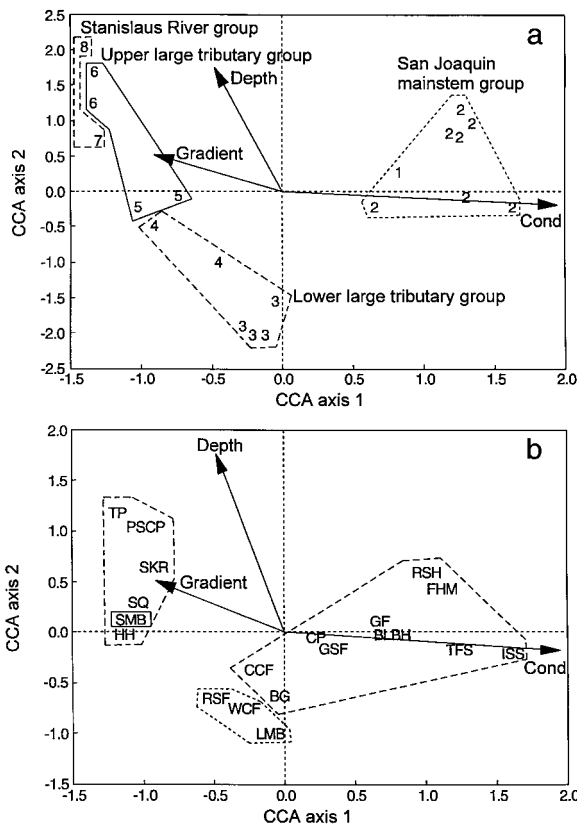


Figure 3. a – Plot of site scores on the first two canonical correspondence analysis axes. Level-2 TWINSpan site groups are enclosed by lines. Numbers refer to level-3 TWINSpan site groups (see Figure 2 for sites included in each group). b – Plot of species scores on first two canonical correspondence analysis axes. Level-2 TWINSpan groups are enclosed by lines. See Table 2 for species names. For both plots the arrows represent the correlation of physical variables with the axes (Cond = specific conductance). Arrows parallel to an axis indicate a high correlation and perpendicular to an axis indicate a low correlation.

with suitable spawning habitat. However, all these species were present in the valley floor fauna before human modification of the system (Schultz & Simons 1973), and all can be found in the lower Sacramento River. The rarity of appropriate spawning habitat in the mainstem San Joaquin River and the lower reaches of the tributaries suggests that any individuals of these species found lower in the system would most likely be downstream migrants. Under present environmental conditions, the introduced species of the lower large tributary site group and the San Joaquin mainstem group may compete with, and prey upon, any downstream migrant native fishes. Predation seems the more

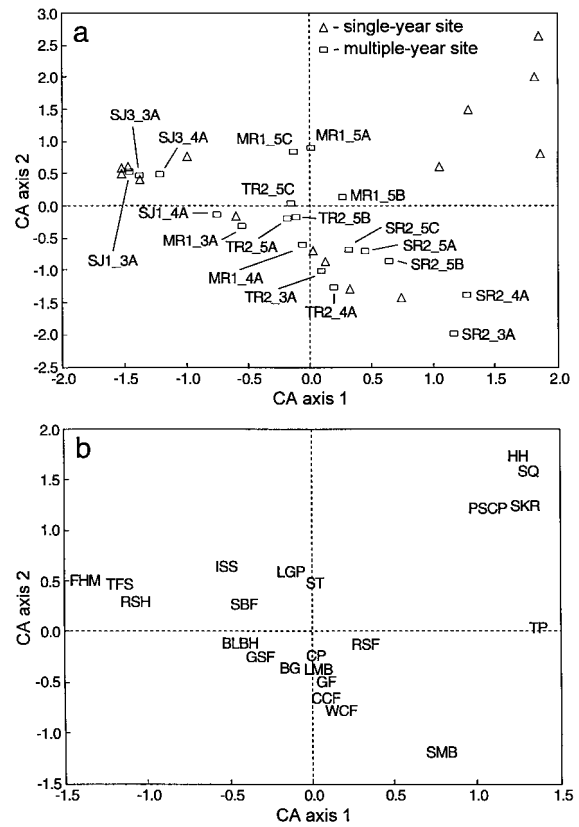


Figure 4. Plots of site (a) and species (b) on the first two correspondence analysis axes derived from the multiple-year, multiple-reach data set for sites in the lower San Joaquin River drainage, California. See Table 1 for full site names. The number and letter associated with a site indicates year (3 = 1993, 4 = 1994, and 5 = 1995) and reach (A, B, or C in 1995 only) sampled. Only reach A was sampled in 1993 and 1994. Sites sampled in only one year are not labeled. See Table 2 for species names.

likely explanation because previous studies from California and elsewhere have documented the profound effects predators can have on the microhabitat choice and distribution of prey species (Brown & Moyle 1991, 1997, Brown & Brasher 1995, Schlosser 1987, Power 1985). No studies have documented the resource limitation necessary for competition to occur.

Unlike the upper elevation sites, there are limited data describing the fish communities of the valley floor area. Some of the native species characteristic of this area before species introductions include hitch, Sacramento blackfish, Sacramento perch *Archoplites interruptus*, Sacramento splittail, Sacramento sucker, tule perch, and the now extinct thickettail chub *Gila crassicauda* (Schulz & Simons 1973, Moyle 1976).

Other native species associated with the area include hardhead, Sacramento squawfish, and prickly sculpin. Saiki (1984) recognized differences in species distribution and abundance that closely correspond to the first TWINSPAN division of native species from introduced species and indicated that species distributions appeared to be associated with water quality parameters. The present study demonstrates clear groupings of sites in the valley floor on the basis of the presence of characteristic species.

The San Joaquin mainstem site group was characterized by a group of introduced species (fathead minnow, inland silverside, red shiner and threadfin shad) that are fairly recent invaders of the San Joaquin River. All were introduced to California after 1950 (Moyle 1976, Dill & Cordone 1997) with red shiner being the most recent invader (1980s) (Jennings & Saiki 1990). These species share a number of life history characteristics that may explain their great abundance in the lower San Joaquin River system. All are short-lived, but fecund for their size, and have long reproductive seasons; thus, it is unlikely that any short-term environmental disturbances would severely affect reproductive success of the species. Such disturbances can include fluctuations in discharge, fluctuations in general water quality, and short-term, high concentrations of dissolved pesticides (Brown et al. 1999). The native species and other introduced species generally have more restricted spawning seasons, making them more vulnerable to these disturbances because a single event could result in the loss of the majority of a species' annual reproductive effort.

The similarity of fish communities in the small western and southern tributaries to the mainstem San Joaquin River was somewhat unexpected because of the relatively harsh conditions in these tributaries. Of the four such streams included in the study, all but Salt Slough are intermittent during part of the year because discharge is dependent on water releases or irrigation return flows. In particular, Orestimba Creek and Spanish Grant Drain are often reduced to isolated pools during certain periods of the year, primarily autumn and winter, when irrigation return flows are not occurring. Under these circumstances, the high percentage abundances of red shiner and fathead minnow also were expected because these species are native to physically harsh, disturbed streams (Moyle 1976). Moreover, the absence of threadfin shad and inland silverside from the two sites was not surprising because those species, though tolerant of harsh environmental conditions, are native to larger, more permanent bodies of water. It is

possible that small species like fathead minnow, green sunfish, and red shiner can maintain resident populations in these streams as long as they do not dry completely, but the presence of other fishes suggests that invasions from permanent waters may also be important. In particular, the presence at Spanish Grant Drain of several young-of-year striped bass, a large adult channel catfish, adult white catfish, and abundant large goldfish and common carp suggests that immigration from the mainstem San Joaquin River or from upstream water supply canals may play an important role in maintaining fish populations in these systems.

All of the small tributaries were sampled only in 1993 while the data for the other sites were from 1994 but it is unlikely that this greatly affected the results. Flows in the small tributaries are completely managed and are primarily affected by agricultural practices which are relatively stable over time. Also flows in the larger streams were similar in the two years suggesting ecological conditions were likely comparable between the two years (see below for more detail).

The major difference between the San Joaquin mainstem sites and the lower tributary sites was the absence of fathead minnow, inland silverside, red shiner, and threadfin shad at the lower large tributary sites. The remaining San Joaquin mainstem species and all the species considered characteristic of the lower tributary sites were present in both groups, but at different percentages. It is unlikely that differences in water quality can account for the absence of the four species because they were found in the most extreme environment. It seems unlikely they could not survive under more benign conditions. It is possible that the four species are more vulnerable to predation in the smaller, clearer tributary streams. Inland silverside and threadfin shad are planktivores and also may be limited by food availability if the relatively swift tributaries produce few zooplankton.

One of the most interesting contrasts to emerge from the analysis is the separation of the two middle Stanislaus River sites from both the upper large tributary and lower large tributary site groups. These sites were distinctive because of large percentages of introduced smallmouth bass and native tule perch. The Stanislaus River sites did not appear physically distinct, but were similar to, or intermediate between, the upper and lower tributary site groups (Table 3); however, the values reported for physical variables are based on instantaneous measurements. Continuous records of discharge, specific conductance and temperature from

June through August 1993 and 1994 indicate that the Stanislaus River (SR2) had greater daily discharge, lower maximum daily specific conductance, and lower maximum daily temperature than the other two rivers (Mullen et al.⁶, Anderson et al.⁷, U.S. Bureau of Reclamation unpublished data). The higher summer base flow and lower temperatures are likely important variables in explaining the differences in fish communities. Smallmouth bass are more stream-oriented and prefer cooler water than the other introduced species present in the system. Tule perch, a live bearer, is also a stream-oriented fish, but requires abundant cover for the near-term females and newborn young to escape predators. The Stanislaus River near Riverbank (SR3), where tule perch were the most abundant, was characterized by large areas of submerged aquatic vegetation. Though submerged aquatic vegetation was present in the other rivers, the vegetated areas tended to be small and patchy, probably because summertime water level fluctuations and generally low discharge restricted submerged plants to deeper areas.

The composition of the fish community associated with each site group was clearly related to physical characteristics of the environment (Table 3, Figure 3). The CCA analysis stressed the importance of specific conductance, but, as the PC analysis demonstrated, this variable was largely acting as a surrogate for a number of correlated variables. Depending on the choice of surrogate variables or order of entry of variables to the model, if all variables had been used, a variety of plausible CCA models were possible. Specific conductance was chosen because it is measured easily and accurately with commonly available equipment. Also, past studies (Saiki 1984) and the PCA analysis (Table 5) indicated that this variable is a good indicator of agricultural land use.

The fish communities probably were not responding to a specific aspect of a site, such as a single water quality or habitat quality variable, but to the general environmental quality of the aquatic ecosystem. This attribute of fish communities has been exploited by

many researchers in the development of various refinements of the Index of Biotic Integrity (Karr 1981). Once scoring systems and standards for such an index can be established for a particular geographic region, sampling of fish communities can be a fast and inexpensive indicator of environmentally impaired locations. When such sites are identified, detailed studies of water chemistry and physical conditions then can be initiated to identify the specific problem.

The overall conclusion of this study is that fish community structure in the lower San Joaquin River drainage is responsive to environmental conditions, including conditions associated with human-caused disturbances, particularly those associated with agriculture and water development. The results are also consistent with the hypothesis that the introduced species compete with, or prey upon the native species; however, the evidence is circumstantial and experimental work is necessary to evaluate these hypotheses.

Spatial and annual variability

Differences between reaches sampled at sites MR1, TR2, and SR2 were relatively small compared with differences between years at those sites, primarily because of the large differences between 1995 and the prior sampling years. The results suggest that sampling of a single representative reach of a stream provides an adequate representation of a larger segment as long as appropriate sampling techniques are used. Other studies also suggest that single-reach sampling is adequate for most purposes (Paller 1995, Simonson & Lyons 1995, Pusey et al. 1998).

The results also suggest that the differences in electrofishing techniques used in 1993 (only backpack electrofishing available) compared to 1994 and 1995 (both backpack and boat electrofishing available) had a minimal effect on the results for MR1, TR2, SR2, and SJ3. For these sites, variation between 1993 and 1994, years of similar stream discharge (see below), was similar in magnitude to variation among reaches for the multiple-reach sites. The largest difference occurred for site SJ1 which was also the largest site. However, it is impossible to determine the relative importance of true annual variation in fish communities and differences in technique. It seems likely that the results for the sites sampled only in 1993 (MS, OC, SGD, and SS) are comparable to the data for the other sites because these sites were the smallest sites sampled and, except for SS, would have been sampled by backpack

⁶ Mullen, J.R., S.W. Anderson & P.D. Hayes. 1993. Water resources data, California, water year 1993, volume 3, southern central valley basins and the Great Basin from Walker River to Truckee River. U.S. Geological Survey Water-Data Report CA-93-3, Reston. 583 pp.

⁷ Anderson, S.W., P.D. Hayes & G.L. Rockwell. 1994. Water resources data, California, water year 1994, volume 3, southern central valley basins and the Great Basin from Walker River to Truckee River. U.S. Geological Survey Water-Data Report CA-93-3, Reston. 593 pp.

electrofishing anyway because they were too small for boat electrofishing.

Differences in stream discharge among years is the most likely reason that species communities in 1995 were so different from those in the other years. Stream discharge in the lower San Joaquin drainage was much higher in water year 1995 (October 1 of previous year to September 30) compared to 1993 and 1994 (Mullen et al.⁶, Anderson et al.⁷, Hayes et al.⁸). Annual mean daily stream discharges ($\text{m}^3 \text{s}^{-1}$) in water years 1993 to 1995 were 66.6, 47.7, and 246.5, respectively, at the San Joaquin River near Vernalis (SJ1), 14.2, 8.4, and 42.6, respectively, at the Merced River at River Road (MR1), and 13.9, 10.4, and 93.5, respectively, at the Tuolumne River in Modesto (TR2). The exception was the Stanislaus River near Ripon (SR2), where stream discharge was relatively unchanged with values of 13.2, 12.7, and 16.5 $\text{m}^3 \text{s}^{-1}$ in 1993, 1994, and 1995, respectively. Stream discharge at the time of sampling followed the same pattern.

The presence of native species, including hardhead, Sacramento squawfish, and Sacramento sucker, at MR1 and TR2 in 1995 can be attributed largely to downstream transport or active migration from upper large tributary sites. Reproductive success for these species may also be higher in high flow years because of increased availability of spawning gravels in upstream areas. The presence of young-of-year splittail suggests that upstream migration of species from the Sacramento-San Joaquin Delta was occurring because the species was not collected in 1993 or 1994. Other studies indicate only sporadic presence of splittail in the lower San Joaquin River system in previous years (Saiki 1984, T. Ford, Turlock Irrigation District, unpublished data), but 1995 was an exceptional year with a large spawn of splittail in the San Joaquin River system (Sommer et al. 1997). Discharge conditions in the Stanislaus River were similar in all three years (above), but the large numbers of carp and goldfish, primarily young-of-year fish, indicate greater reproductive success of residents or perhaps upstream movement of spawning adults from the San Joaquin River. The mechanism for the apparent increase in reproductive success was presumably increased flooding of streamside vegetation by the somewhat higher 1995 flows which

would supply the needed spawning substrate for these species.

Fish community metrics

Differences among site groups for the fish community metrics tested (Table 4) suggest that an IBI could be developed for the streams of the San Joaquin Valley. Percentage of introduced fish and percentage of intolerant fish clearly differentiated the upper large tributary site group from the other groups. However, all of the intolerant species are also native species (Table 2), making the two metrics redundant. An earlier IBI applied to San Joaquin Valley foothill streams (Brown & Moyle 1992) relied heavily on native species with the percentages of native fish and native species constituting two of the four metrics applied to streams without salmonids. The earlier IBI was not particularly sensitive to moderate environmental degradation, probably because the native species can tolerate relatively degraded environmental conditions in the absence of introduced species (Brown & Moyle 1993).

The results for the other two metrics were not as clear. The percentage of fish with external anomalies was highest at the lower large tributary sites; however, water quality and habitat quality were most extreme at the San Joaquin mainstem sites. Most of the sites sampled exceeded the 1–2% category of fish with anomalies considered indicative of degraded conditions in most IBIs (Karr 1981, Fausch et al. 1984, Leonard & Orth 1986, Hughes & Gammon 1987, Bramblett & Fausch 1991). Several of the low values for the upper tributary sites were based on visual examination of a small fraction of the fish observed because many of the fish at those sites were observed while snorkeling and could not be examined for anomalies.

The percentage of omnivorous fish was highest at the San Joaquin mainstem and the upper large tributary sites. These groups represented the extremes in the gradients in environmental conditions observed in this study (Table 3). The similar high percentages of omnivorous fish at sites with very different environmental conditions occurred because the native Sacramento sucker, an omnivore, tended to be numerous at upper large tributary sites and omnivorous carp, goldfish, red shiner, and fathead minnow were numerous at the San Joaquin mainstem sites. Values for percentage of omnivorous fish greater than 20–35% have been considered indicative of degraded conditions in other IBIs (Karr 1981, Fausch et al. 1984, Hughes & Gammon

⁸ Hayes, P.D., G.L. Rockwell & S.W. Anderson. 1995. Water resources data, California, water year 1995, volume 3, southern central valley basins and the Great Basin from Walker River to Truckee River. U.S. Geological Survey Water-Data Report CA-93-3, Reston. 508 pp.

1987, Bramblett & Fausch 1991). By this criterion, most of the upper large tributary sites would be considered degraded, and the lower large tributary sites would not. This reversal in expectation would be difficult to correct by simply rescaling the scoring criteria because the percentage was also high at the San Joaquin mainstem sites.

A more fundamental problem in developing a San Joaquin Valley IBI is the absence of reference conditions for the valley floor sites. Though this study shows clear differences among site groups, some level of difference would be expected between the upper large tributary and the San Joaquin mainstem sites on the basis of natural gradients in fish communities (Moyle 1976). Unfortunately, the native valley floor fish community has been almost completely replaced by introduced species. Should the reference condition for the IBI be based on a hypothetical reconstruction of a historic fish community that is not an attainable goal under existing land-use and water-use conditions or should the reference condition be based on an attainable condition determined by sampling additional sites over a range of water year (discharge) conditions? The latter implies an acceptance of introduced species as a permanent feature of the fish communities.

Conservation implications

The results have interesting implications for fisheries management in the region. The enhancement of chinook salmon runs in the Merced, Tuolumne, and Stanislaus rivers has always been the primary management effort in the area. Enhancement efforts have included supplementation with hatchery fish, flow manipulations to aid migration of both juveniles and adults, spawning gravel enhancement, and studies of factors affecting mortality of juveniles migrating out to sea. Efforts to enhance this economically and ecologically important native species should certainly be continued, but the results of this study suggest that enhancement of resident native species populations also is possible.

Recent ideas for conservation of California native fish communities have appropriately concentrated on identifying watersheds where the communities are relatively intact rather than on areas with only remnant populations (Moyle & Yoshiyama 1993). However, the results of this study indicate that manipulations of flow, water quality, and stream habitat have the potential to increase the range of native stream fish communities in the major tributaries and perhaps

increase use of the system by migratory species. Recent work has indicated that a natural flow regime is one of the most important factors in maintaining native California stream fish communities (Baltz & Moyle 1993, Brown & Moyle 1997). Changes in the water management of large east-side tributaries, in combination with improvements in water quality of smaller tributaries, could result in a downstream extension of native species and shift the mainstem San Joaquin fish community away from red shiner, fathead minnow, threadfin shad, and inland silverside to the community, including many game species, that presently dominates at the lower large tributary sites. The value of such species shifts would have to be balanced against the possibility of increasing predation on migrating juvenile salmon in the spring. Balancing such conflicting costs and benefits poses a considerable challenge to resource managers, particularly in areas, such as the San Joaquin-Tulare basins, where long-established human land uses have had greater or equal importance to the enhancement of natural resources.

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