

Fish assemblages of perennial floodplain ponds of the Sacramento River, California (USA), with implications for the conservation of native fishes

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Abstract To assess the likelihood of enhancing native fish populations by means of floodplain restoration projects, habitat characteristics and fish assemblages of seven perennial floodplain ponds in Yolo Bypass, the primary floodplain of the Sacramento River, California (USA), were examined during summer 2001. Although all ponds were eutrophic, based upon high chlorophyll *a* or dissolved nutrient concentrations, relatively large shallow ponds generally exhibited higher specific conductivity and dissolved phosphorus concentrations than small deep ponds, which exhibited greater water transparency and total dissolved nitrogen concentrations. Using multiple gear types, 13 688 fishes comprising 23 species were collected. All ponds were dominated by alien fishes; only three native species contributing < 1% of the total number of individuals and < 3% of overall biomass were captured. Fish assemblage structure varied among ponds, notably between engineered vs. natural ponds, and was related to specific conductance, total dissolved solids and water transparency.

KEYWORDS: alien species, floodplain restoration, Sacramento-San Joaquin Delta, Yolo Bypass.

Introduction

River-floodplain systems are highly dynamic yet productive environments. Biotic interactions and productivity of these systems are strongly linked to flood pulse processes (Junk, Bayley & Sparks 1989). Spatial and temporal variability in hydrology during the flood pulse creates a heterogeneous habitat within the floodplain that can lead to high biotic diversity (Junk *et al.* 1989) and increased production of fish (Bayley 1991) and invertebrates (Gladden & Smock 1990). Flood pulse dynamics, therefore, can have a significant influence on the year class strength of fishes (Welcomme 1979; Sommer, Baxter & Herbold 1997).

Studies in the Sacramento River basin, California (USA), demonstrated that seasonally inundated floodplains are an important habitat for spawning and rearing of native fishes (Sommer *et al.* 1997; Sommer, Nobriga, Harrell, Batham & Kimmerer 2001a). However, little is known about the functional role of perennial aquatic floodplain habitats such as ponds or wetlands. In some systems, such as connected off channel ponds along the Mississippi River (USA), these

habitats serve as important nurseries for young fishes (Sabo, Kelso, Bryan & Rutherford 1991; Sabo & Kelso 1991). In tropical floodplain and temperate oxbow lakes, isolated water bodies often develop localised fish assemblages strongly influenced by habitat features (Rodriguez & Lewis 1997; Tejerina-Garro, Fortin & Rodriguez 1998; Winemiller, Tarim, Shormann & Cotner 2000; Suarez, Petrere & Catella 2001). Localised extinction of species intolerant of abiotic conditions or biotic interactions (such as predation or competition) were identified as an important mechanism structuring such fish assemblages (Halyk & Balon 1983; Rodriguez & Lewis 1997).

This study examined the functional role of perennial floodplain ponds for fishes in a regulated and highly invaded temperate river-floodplain system, the Sacramento River's Yolo Bypass (Sommer, Harrell, Nobriga, Brown, Moyle, Kimmerer & Schemel 2001b). The goals for this paper were to determine: (1) if fish assemblages varied among perennial ponds in the Yolo Bypass floodplain; and (2) if variation in assemblage structure among ponds was related to pond-level physical habitat features. Because of Yolo Bypass's

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demonstrated importance for native fishes, floodplain rehabilitation has been identified as a potential approach to enhance native fish populations in the San Francisco Estuary catchment (CALFED 2000). Understanding fish assemblage dynamics in perennial floodplain ponds can aid resource managers in making decisions regarding floodplain rehabilitation actions.

Study area

The 24 000-ha Yolo Bypass (Fig. 1) is the largest floodplain of the Sacramento-San Joaquin Delta, a region dominated by alien fish species (Bennett & Moyle 1996; Feyrer & Healey 2003). The 61-km long floodplain is inundated during winter and spring in about 60% of years. During high flow events, Yolo Bypass can have a discharge of up to $14\,000\text{ m}^3\text{ s}^{-1}$, representing 75% of total Sacramento River basin flow. Under typical flood events, water spills into Yolo Bypass at Fremont Weir when Sacramento basin flows

surpass approximately $2000\text{ m}^3\text{ s}^{-1}$. At higher basin flows ($>5000\text{ m}^3\text{ s}^{-1}$), Sacramento Weir also spills. When flood waters recede, the basin empties through a permanent tidal channel along the eastern edge of Yolo Bypass. The floodplain is relatively well drained but, several isolated ponds remain perennially inundated.

Seven perennial ponds in Yolo Bypass were studied (Fig. 1). Except for one site that could not be accessed because of private property restrictions, these sites represent all major perennial floodplain ponds within Yolo Bypass. Three sites (YB1, YB2, YB3) are located in the Yolo Basin Wildlife Area, the largest contiguous area of non-agricultural floodplain habitat, which is managed by the California Department of Fish and Game, primarily for waterfowl. These three engineered ponds possess low gradient smooth depth profiles and a soft mud and silt substratum. The remaining four sites (FW1, FW2, FW3, FW4) are natural ponds located in the northern reach of Yolo Bypass near Fremont Weir in upland habitat. Two of these ponds, FW1 and FW2, are located in an old oxbow channel of the Sacramento River that is only connected to the river when Yolo Bypass floods. Each possess a low-gradient, smooth depth profile and firm mud substratum with small amounts of gravel present at FW2. Historical maps of the region show that the basins of FW3 and FW4 were created by a combination of historical river meanders prior to the construction of Yolo Bypass in the early 1900s, but may have been further shaped by subsequent flood events. Pond FW3 has a firm mud substratum and a smooth but high-gradient depth profile extending from the riparian zone to the pond bottom. Pond FW4 possesses a relatively shallow but highly variable depth contour; the substratum is primarily hard mud with embedded cobble, with soft mud and silt at some locations.

Prior to this study, Yolo Bypass most recently flooded during spring 2000 and then partially flooded in spring 2001. Each study pond was inundated for approximately 45 days in 2000, while only four ponds (YB1, YB2, YB3, FW4) were inundated for approximately 25 days in 2001. None of the ponds had desiccated since they were last connected with flood waters. This study was conducted from August to October 2001 and all sampling was completed between 07:00 and 14:00 hours.

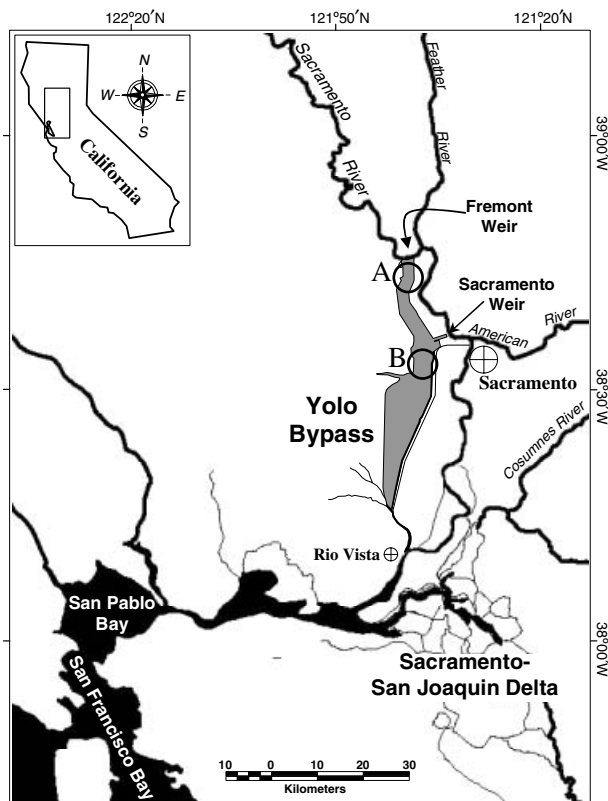


Figure 1. The Sacramento River's Yolo Bypass and location of seven perennial floodplain ponds studied during summer 2001. Ponds FW1 ($38^{\circ}46'45''$, $121^{\circ}40'20''$), FW2 ($38^{\circ}46'15''$, $121^{\circ}40'15''$), FW3 ($38^{\circ}46'38''$, $121^{\circ}30'50''$) and FW4 ($38^{\circ}45'45''$, $121^{\circ}38'55''$) were located within region A, while ponds YB1 ($38^{\circ}34'5''$, $121^{\circ}38'24''$), YB2 ($38^{\circ}33'15''$, $121^{\circ}35'26''$) and YB3 ($38^{\circ}32'28''$, $121^{\circ}35'23''$) were located in region B.

Methods

Physical variables

Each pond was mapped with a global positioning system. Pond perimeter (m) and surface area (ha) were

calculated with the aid of a geographic information system. Shoreline development, a relationship between pond perimeter (P) and surface area (A), was calculated as $P/(4\pi A)^{0.5}$. Mean depth (m) was estimated as the average of a series of soundings taken with a weighted measuring tape along the shortest and longest axes of a pond. Volume was estimated as the product of mean depth and surface area. The major habitat types along the riparian perimeter of each pond were visually estimated in terms of proportional coverage of open shoreline, willows, tules, or submerged and overhanging wood. To assess stratification, water temperature ($^{\circ}\text{C}$), specific conductance (μS), dissolved oxygen (mg L^{-1}) and salinity (psu) were measured in series along the longest axis (at a depth of approximately 1 m) and also down a vertical depth profile at the deepest point of each pond. All water quality parameters were measured at the time and place when fishes were sampled. Standard US Environmental Protection Agency laboratory methods were used for determining the concentration of total dissolved solids, total dissolved phosphorus, PO_4 , total dissolved nitrogen, NH_4 ; and fluorometry was used to estimate chlorophyll a concentration.

Fish assemblages

Due to the variety of habitats encountered and in attempt to sample all possible fish species in each pond, three different sampling gears – beach seine, gill net and electric fishing – were used. All fishes captured were measured for fork length (mm), weighed wet (0.1 g) on an electronic balance, and released alive.

A 15×1.5 m beach seine with 3.2-mm mesh was used. All seine hauls were conducted perpendicular to the shore. Three to 10 seine hauls were conducted along unique transects in each pond until no new species or substantial changes in the proportional abundance of species were observed. Every pond except FW3 was seined; seining was not feasible at this pond because of extremely steep banks and dense underwater structures, such as woody debris and submerged trees.

Gill nets measured 60×2.4 m with random mesh panels of 51–102-mm stretch mesh. They were deployed in all possible locations throughout each pond, including nearshore and offshore zones, and areas adjacent to wood structure where possible. Two to eight gill nets were set for approximately 1 h in each pond, except FW3 because of dense wood structure, and YB2 and YB3 because of shallow water.

Electric fishing was used to sample ponds or regions of ponds that could not be effectively sampled with

beach seines because of woody debris or the absence of a landing beach. Electric fishing was conducted with a Smith Root Model GPP pulsed DC unit powered by a 5.5-hp generator mounted on a 3.3-m aluminium boat. Two separate electric fishing passes were conducted along transects at FW1 and FW2 that possessed dense wood structure and steep banks. At FW3, four separate passes along the entire shoreline perimeter were conducted; electric fishing was the sole sampling gear employed at FW3 because of dense wood structure and steep banks. In pond FW4, a single pass along four separate transects was conducted in different regions that possessed steep rock or mud banks and wood structure.

Data analysis

Principal components analysis (PCA) was used to ordinate ponds based upon their habitat characteristics. The PCA is a multivariate statistical technique that facilitates the interpretation of complex data sets by reducing the number of inter-correlated variables in a data set to a reduced set of independent variables (Legendre & Legendre 2000). The data matrix for this analysis was not of full rank as descriptor variables (perimeter, surface area, riparian habitat complexity, mean depth, volume, Secchi depth, maximum observed temperature, lowest observed dissolved oxygen concentration, mean specific conductance, mean salinity, total dissolved nitrogen, NH_4 , total dissolved phosphorus, PO_4 , total dissolved solids and chlorophyll a) outnumbered the cases (each individual pond). Therefore, correlation analysis was used to identify highly correlated variables ($r \geq 0.80$) and reduce the number of descriptor variables to equal the number of cases. Legendre & Legendre (2000) pointed out that an interpretation of the first two eigenvectors of such an analysis rarely yields invalid ordination interpretations. Therefore this analysis was used to construct a biplot of pond and habitat variable scores on the first two PCA eigenvectors to evaluate how ponds varied amongst each other according to physical variables.

Correspondence analysis (CA) was used to examine fish assemblage variation among ponds. Correspondence analysis is an indirect ordination technique based upon reciprocal averaging that can be used to assess assemblage similarity along primary gradients (Legendre & Legendre 2000). For this analysis, data were combined from each gear type and summarised for each pond as a binary response of presence or absence. The limitation of incorporating binary data in CA is that resultant scores are not weighted by species

abundance but solely by presence or absence. However, this method has often been used successfully in ecological studies (ter Braak 1985; Hawkes, Miller & Layher 1986; Jackson & Harvey 1989; Robinson & Tonn 1989). The CA was run with the CANOCO software program (ter Braak & Smilauer 1998). Inspection of plots of site (pond) scores and species scores on the first two CA axes formed the basis for interpretation of assemblage variation among ponds. Four species – prickly sculpin, *Cottus asper* (Richardson), striped bass, *Morone saxatilis* (Walbaum), black bullhead, *Ameiurus melas* (Rafinesque) and goldfish, *Carassius auratus* (L.), – were excluded from this analysis because of their extremely rare occurrence. To investigate which habitat characteristics had the greatest influence on fish assemblage structure in ponds, correlation analysis was used to compare CA axis I and II scores vs all possible environmental variables mentioned above. Correlations were considered significant at $P \leq 0.05$.

Results

Physical variables

Each pond was eutrophic based upon high chlorophyll *a* or nutrient levels (Horne & Goldman 1994) but varied in most other habitat features (Table 1; Fig. 2). Axis I explained 54.5% of the variation in pond

structure and differentiated shallow ponds that possessed a large surface area, high specific conductance and high dissolved phosphorus concentrations (YB3, YB2, FW4, YB1) from deep ponds that possessed a small surface area, relatively high water transparency and dissolved nitrogen concentration (FW3, FW2, FW1). Axis II explained 29.7% of the variation in pond structure and primarily differentiated ponds by chlorophyll *a* concentration. The only pond that exhibited vertical stratification was FW3. This pond was the deepest and located in a ravine that provided protection from wind.

Fish assemblages

A total of 13 688 fishes comprising 23 species was collected (Table 2). The overall numerical catch was dominated by alien species, including inland silverside, *Menidia beryllina* (Cope), threadfin shad, *Dorosoma petenense* (Gunther), mosquitofish, *Gambusia affinis* (Baird and Girard), and bluegill sunfish, *Lepomis macrochirus* (Rafinesque). The total catch accounted for 231 kg of fish biomass. Of this amount, common carp, *Cyprinus carpio* (L.), contributed 64%, white crappie, *Pomoxis annularis* (Rafinesque), 11%; no other species accounted for >4%. Inland silverside, numerically the most abundant species, accounted for <1% of total biomass. Only three native species were collected [Sacramento blackfish, *Orthodon*

Table 1. Environmental habitat features during summer 2001 for seven perennial floodplain ponds in Yolo Bypass

Variable	FW1	FW2	FW3	FW4	YB1	YB2	YB3
Perimeter (m)	1247	701	224	2808	539	2129	2350
Surface area (ha)	24.5	15.3	2.2	71.4	13.1	88.2	104.3
Shoreline development	2.3	1.6	1.4	3.0	1.3	2.0	2.1
Mean depth (m)	4.7	7.3	12.2	1.8	2.5	1.8	1.8
Volume $\times 10^5$ (m ³)	1.15	1.11	0.27	1.29	0.33	1.59	1.88
Estimated proportional riparian coverage (%)							
Bare shoreline	95	90	10	94	98		
Willows				2		98	70
Submerged or overhanging wood	5	10	90	2			
Tules				2	2	2	30
Secchi depth (cm)	19	20	40	15	12	21	23
Maximum temperature (°C)	25.3	25.1	24.7	22.6	22.6	24.3	26.9
Lowest dissolved oxygen (mg L ⁻¹)	3.8	2.9	0.1	5.6	4.4	7.8	3.9
Mean specific conductance (μ S)	336	314	498	917	917	1042	1140
Mean salinity (psu)	0.2	0.2	0.3	0.5	0.5	0.5	0.6
Total dissolved nitrogen (mg L ⁻¹)	0.01	0.01	0.07	0.01	0.01	0.01	0.01
NH ₄ (mg L ⁻¹)	0.01	0.01	0.29	0.01	0.01	0.01	0.02
PO ₄ (mg L ⁻¹)	0.01	0.01	0.06	0.01	0.05	0.28	1.0
Total dissolved phosphorus (mg L ⁻¹)	0.22	0.11	0.13	0.17	0.22	0.35	1.1
Total dissolved solids (mg L ⁻¹)	203	182	278	591	638	674	809
Chlorophyll <i>a</i> (μ g L ⁻¹)	86.3	38.0	7.4	69.2	25.3	18.7	26.9

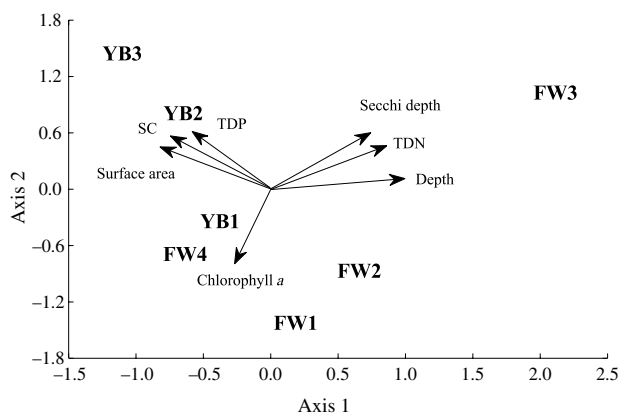


Figure 2. Principle components analysis biplot depicting habitat features (vectors) of each perennial floodplain pond. Pond labels are in bold and centred over actual scores. TDP, total dissolved phosphorus; TDN, total dissolved nitrogen; SC, specific conductance.

microlepidotus (Ayers), Sacramento sucker, *Catostomus occidentalis* (Ayers), and prickly sculpin] in just three of seven ponds, which together represented < 1% of the total number of individuals and < 3% of total biomass.

Correspondence analysis revealed differences in fish assemblages among ponds (Fig. 3). The first CA axis explained 41.7% (eigenvalue = 0.268) of the variation in assemblage structure and differentiated engineered ponds in Yolo Basin Wildlife Area from natural ponds located at Fremont Weir. Further, fish assemblages among Fremont Weir ponds were more similar to each other than those among Yolo Basin Wildlife area ponds. Specific conductance ($r = 0.77$) and total dissolved solids ($r = 0.78$) were significantly correlated with CA axis I site scores ($P < 0.05$). Species scores (Fig. 3) indicated that white catfish, *Ameiurus catus* (L.), centrarchids, Sacramento sucker and golden shiner, *Notemigonus crysoleucas* (Mitchill), were most associated with Fremont Weir ponds, and that red shiner, *Cyprinella lutrensis* (Baird and Girard), and brown bullhead, *Ameiurus nebulosus* (LeSueur), were most associated with Yolo Basin Wildlife Area ponds. Several species were found in both regions and had intermediate axis I scores.

The second CA axis explained 26.0% (eigenvalue = 0.167) of the variation in assemblage structure and differentiated FW3 from the other Fremont Weir ponds and YB1 from the other Yolo Basin Wetland Area ponds (Fig. 3). Water transparency ($r = 0.92$) was significantly correlated with CA axis II site scores ($P = 0.003$). The absence of threadfin shad, mosquitofish, bigscale logperch, *Percina macrolepidota* (Stevenson), black crappie, *Pomoxis nigromaculatus*

(LeSueur), largemouth bass, *Micropterus salmoides* (Lacépède), channel catfish, *Ictalurus punctatus* (Rafinesque), and Sacramento sucker separated FW3 from other Fremont Weir ponds. Although electric fishing was the only sampling gear used at FW3, sampling gear bias was considered not to exclude these species from capture at FW3 because they were collected in similar habitats within other ponds with the electric fishing gear. The main differences among Yolo Basin Wildlife Area ponds stem primarily from bigscale logperch, Sacramento blackfish, channel catfish and largemouth bass only being present at YB1. Additionally, red shiners were collected in YB2 and YB3, but not YB1. The presence or absence of Sacramento blackfish at YB1 could be attributable to gear selectivity as it was the only species collected by gill net that was not collected by beach seine in these ponds. The four rare species excluded from the CA were found only in Yolo Basin Wildlife Area ponds: striped bass (YB2), goldfish (YB1), prickly sculpin (YB2) and black bullhead (YB1).

Discussion

Alien fish species dominated perennial ponds of the Yolo Bypass floodplain and assemblage structure appeared to be influenced by habitat features that varied among ponds. Assemblage structure, as measured by CA axis scores, was primarily associated with gradients of specific conductance and water transparency. Shallow ponds with large surface areas and high specific conductance generally possessed fishes with broad environmental tolerances (e.g. bullhead catfishes, inland silverside, common carp and mosquitofish), while small deep ponds with greater water transparency generally possessed large numbers of visually-oriented fishes such as centrarchids. The relationships between fish assemblages and pond habitat features are consistent with other studies of perennial floodplain habitats. Rodriguez & Lewis (1997) and Tejerina-Garro *et al.* (1998) found that water transparency was a strong predictor of fish assemblages, especially the abundance of visually-oriented predators, in South American floodplain lakes.

This study did not directly address the importance of seasonal fluctuations in environmental conditions on fish assemblages within the ponds. Seasonal patterns of dissolved oxygen levels were demonstrated to be an important variable structuring fish assemblages in lotic habitats (Tonn & Magnuson 1982; Rahel 1984). It was likely that seasonal dissolved oxygen levels played an important role in structuring the fish assemblage at

Table 2. Total number and biomass (g, in parentheses) of fishes collected during summer 2001 in seven perennial floodplain ponds in Yolo Bypass. Data are combined for seine, gill net and electric fishing samples

Taxa	FW1	FW2	FW3	FW4	YB1	YB2	YB3	Total
Clupeidae								
Threadfin shad	187	220		1299	461	203	17	2387
<i>Dorosoma pentenense</i> (Gunther)	(158)	(625)		(963)	(411)	(232)	(52)	(2442)
Cyprinidae								
Common carp	47	18	2	36	39	16	20	178
<i>Cyprinus carpio</i> (L.)	(73920)	(19604)	(5761)	(31491)	(15443)	(1177)	(373)	(147767)
Red shiner						54	23	77
<i>Cyprinella lutrensis</i> (Baird and Girard)						(39)	(9)	(48)
Sacramento blackfish*				3	10			13
<i>Orthodon microlepidotus</i> (Ayers)				(1769)	(2317)			(4086)
Golden shiner				5				5
<i>Notemigonus crysoleucas</i> (Mitchill)				(78)				(78)
Goldfish					2			2
<i>Carassius auratus</i> (L.)					(78)			(78)
Catostomidae								
Sacramento sucker*	11			2				13
<i>Catostomus occidentalis</i> (Ayers)	(5171)			(1315)				(6486)
Ictaluridae								
Channel catfish	20	1		6	3			30
<i>Ictalurus punctatus</i> (Rafinesque)	(10357)	(318)		(2449)	(163)			(13286)
White catfish	2	2	1	1				6
<i>Ameiurus catus</i> (L.)	(177)	(331)	(51)	(3)				(563)
Brown bullhead					3	3		6
<i>Ameiurus nebulosus</i> (LeSueur)					(448)	(17)		(464)
Black bullhead					1			1
<i>Ameiurus melas</i> (Rafinesque)					(171)			(171)
Poeciliidae								
Mosquitofish				123	6	240	350	719
<i>Gambusia affinis</i> (Baird and Girard)				(33)	(5)	(22)	(36)	(96)
Atherinopsidae								
Inland silverside	728	457	70	855	3949	772	1284	8115
<i>Menidia beryllina</i> (Cope)	(112)	(108)	(184)	(89)	(132)	(164)	(131)	(920)
Centrarchidae								
Bluegill	103	87	207	301	4		10	712
<i>Lepomis macrochirus</i> (Rafinesque)	(1362)	(1341)	(1889)	(832)	(42)		(11)	(5476)
White crappie	35	18	2	273	77	1	3	409
<i>Pomoxis annularis</i> (Rafinesque)	(5176)	(2743)	(207)	(15197)	(1907)	(10)	(19)	(25251)
Green sunfish	15	22	157	19		2	4	219
<i>Lepomis cyanellus</i> (Rafinesque)	(414)	(546)	(1548)	(335)		(4)	(5)	(2852)
Redear sunfish	1	2	64	80				147
<i>Lepomis microloepus</i> (Gunther)	(103)	(72)	(479)	(922)				(1576)
Black crappie	27	6		8	27	2		70
<i>Pomoxis nigromaculatus</i> (LeSueur)	(6871)	(1327)		(875)	(381)	(9)		(9462)
Largemouth bass	29	18		15	1			63
<i>Micropterus salmoides</i> (Lacépède)	(3432)	(2393)		(2968)	(9)			(8802)
Warmouth		3	9	10				22
<i>Lepomis gulosus</i> (Cuvier)		(41)	(207)	(28)				(276)
Percidae								
Bigscale logperch	82	57		290	20			449
<i>Percina macrolepada</i> (Stevenson)	(200)	(151)		(244)	(48)			(643)
Moronidae								
Striped bass						3		3
<i>Morone saxatilis</i> (Walbaum)						(65)		(65)
Cottidae								
Prickly sculpin*						1		1

Table 2. Continued

Taxa	FW1	FW2	FW3	FW4	YB1	YB2	YB3	Total
<i>Cottus asper</i> (Richardson)						(1)		(1)
Total species	13	13	8	17	14	11	8	23
Total numbers	1287	911	512	3326	4603	1299	1714	13 688
Total biomass (g)	107 444	29 599	10 327	59 518	21 553	1759	650	230 580

Native species are indicated by an asterisk.

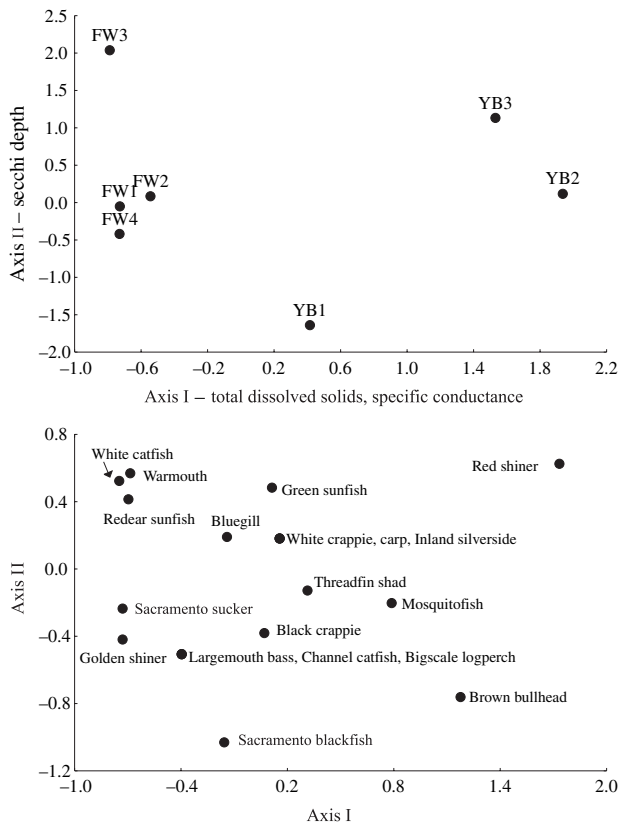


Figure 3. Plots of site (upper panel) and species (lower panel) scores for the first two axes of the correspondence analysis using fish presence-absence data combined from seine, gill net and electric fishing samples. Environmental variables given in the axis captions of the upper panel are those that were significantly positively correlated with the site scores for that axis.

FW3. Because it was stratified, the majority of this pond's volume exhibited dissolved oxygen concentrations well below 1.0 mg L^{-1} . Water column mixing during autumn turnover probably produces temporally harsh conditions of low dissolved oxygen concentration throughout the pond that only a few species can tolerate. This was supported by the collection of primarily small-sized fishes with broad environmental tolerances at FW3.

Species richness was highest at FW4 as it possessed between 30 and > 100% more species than each of the other ponds. This is probably because this pond exhibited the greatest overall diversity of microhabitats. It had the highest measurements of perimeter and shoreline development, had multiple types of substratum including rock, mud and silt, was the only pond that had several islands with varying habitat types, and was also the only pond that possessed each of the major riparian habitat types assessed – open shoreline, tules, willows, and other submerged and overhanging wood structure.

Although the study covered a relatively short time period, it is likely that fish assemblage dynamics in Yolo Bypass perennial ponds are deterministic on a time trajectory following flood events. The likely mechanism is that a diverse group of species is introduced and reshuffled among ponds during flooding, followed by a sequential loss of species incapable of withstanding the localised abiotic and biotic environments during drier months. Indirect support for the deterministic model in the Yolo Bypass was provided by the ponds in similar habitats (regions of the floodplain), which flooded in different years, possessing similar fish assemblages (Fig. 3). Rodriguez & Lewis (1994) found that fish assemblages in neotropical floodplain lakes were highly predictable in that similar assemblage properties were observed following flood events. They proposed that this regularity was strongly influenced by predation mediated by habitat characteristics among lakes, and thus that fish assemblages were structured by deterministic processes. Chapman & Chapman (1993) documented a continued occurrence of species from year-to-year in floodplain ponds of the River Sokoto, Nigeria. In a correlative example demonstrating the importance of physical habitat, Halyk & Balon (1983) found a relationship between species richness and pond area but not between species richness and time period of inundation for floodplain pools in Ontario, Canada. The applicability of the deterministic model in Yolo Bypass is currently being tested directly by continuously sampling ponds after annual flood events.

In terms of conservation, one major rehabilitation goal to enhance native fish populations in California's Central Valley was to improve connectivity between riverine and floodplain habitat, particularly in dry years (CALFED 2000). However, establishing rehabilitation goals for perennial habitats has been problematic because virtually no information exists on their ecological function. Although large, off-channel floodplain lakes in California's Central Valley historically possessed large numbers of native species (Buckingham, Dibble & Sherwood 1886; Gobalet & Fenenga 1993; Moyle 2002), the perennial floodplain ponds studied appear not to be major habitats for native fishes. This contrasts with Scheerer (2002), who found that isolated perennial floodplain ponds on the Willamette River, Oregon (USA) represented the last remaining refuges for an endangered native minnow. Nonetheless, there is evidence that seasonal floodplain inundation in Yolo Bypass greatly benefits native fishes. Juvenile chinook salmon *Oncorhynchus tshawytscha* (Walbaum) exhibited improved growth and survival when rearing on the floodplain (Sommer *et al.* 2001a); the advantages of floodplain habitat include increased food supply and rearing area. Splittail, *Pogonichthys macrolepidotus* (Ayers), a threatened endemic cyprinid, uses the floodplain for spawning and rearing, and produces strong year classes during years of extended inundation (Sommer *et al.* 1997). These and several other native fishes of the San Francisco Estuary, show a strong migratory life history pattern (Moyle 2002); with probably most emigrating seasonal floodplain habitat during winter and spring, with relatively few remaining in perennial ponds. Relatively few individuals of these species were captured in numerous isolated ponds within the Yolo Bypass (both perennial and non-perennial) sampled immediately after flood waters have receded, suggesting that they rapidly emigrate from the floodplain on the descending hydrograph (T.R. Sommer, unpublished data). Based on these observations, it was expected that seasonal floodplain inundation is likely to provide greater benefits than existing isolated perennial habitats for the extant native fish fauna. While the present value of perennial ponds for native fish is questionable, management of perennial floodplain ponds cannot be weighted solely in terms of fishes. The Yolo Bypass is located within the Pacific Flyway and is a major habitat for migrating waterfowl (Sommer *et al.* 2001b). Numerous other wildlife, including many threatened and endangered species, also occur within the region.

It is possible that habitat values of some perennial ponds could be improved for native fishes. As

evidence, differences in fish assemblages of natural (FW1, FW2, FW3, FW4) vs. engineered (YB1, YB2, YB3) ponds were observed. Negative interactions with alien species, such as predation (Turner & Kelley 1966; Bennett & Moyle 1996) or competition (Marchetti 1999) are likely to be major factors affecting native fish use of perennial floodplain ponds between inundation events. Predation is an important factor structuring fish assemblages in similar habitats (Rodriguez & Lewis 1994; Tejerina-Garro *et al.* 1998) and is considered to be the most important mechanism whereby alien species affect natives in the Colorado River system, another large regulated river system in the western USA (Marsh & Langhorst 1988; Minckley, Marsh, Brooks, Johnson & Jensen 1991; Tyus & Saunders 2000). Because predation is enhanced where the visual environment is optimal, and because native species and relatively few alien predators were captured in shallow turbid ponds, predation may be an important factor in Yolo Bypass. The significant environmental variable correlations with CA axis scores indicated that native species were found in ponds exhibiting low water transparency and low specific conductance. The PCA indicated that ponds exhibiting these characteristics had a large surface area, were shallow, had relatively high dissolved oxygen concentrations and were typically most productive as measured by chlorophyll *a* concentrations. Ponds exhibiting these characteristics should be given serious consideration in rehabilitation projects because they can support native fish populations and potentially minimise negative interactions with alien species.

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