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Use of a Restored Central California Floodplain by Larvae of Native and Alien Fishes

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Abstract.—We sampled larval fish in 1999 and 2001 on a restored floodplain along the lower Cosumnes River, California, from the onset of flooding to when the sites dried or when larval fish became rare. We collected more than 13,000 fish, of which prickly sculpin *Cottus asper* made up the majority (73%). Eleven species made up 99% of the catch. Three native fishes (prickly sculpin, Sacramento sucker *Catostomus occidentalis*, and splittail *Pogonichthys macrolepidotus*) and two alien species (common carp *Cyprinus carpio* and bigscale logperch *Percina macrolepida*) were associated with higher inundation and cool temperatures of early spring. In contrast, five alien taxa, sunfish *Lepomis* spp., largemouth bass *Micropterus salmoides*, crappie *Pomoxis* spp., golden shiner *Notemigonus crysoleucas*, and inland silverside *Menidia beryllina*, were associated with less inundation and warmer water temperatures. One native species, Sacramento blackfish *Orthodon microlepidotus*, was also associated with these conditions. Species did not show strong associations with habitat because of different spawning times of adults and expansion and contraction of flood waters. Most species could be found at all sites throughout flooded habitat, although river and floodplain spawning fishes usually dominated sites closest to levee breaches. Highest species richness was consistently found in two sloughs with permanent water because they both received drainage water from the floodplain and had a complement of resident species. Splittail, a floodplain spawner, was found primarily in association with submerged annual plants. Our results suggest that a natural hydrologic cycle in spring is important for providing flooding and cool temperatures important for many native larval fishes. Alien fishes are favored if low flows and higher temperatures prevail. Restoration of native fish populations that use floodplains for rearing should emphasize early (February–April) flooding followed by rapid draining to prevent alien fishes from becoming abundant.

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Introduction

Floodplains are important spawning and nursery habitats for many fishes (Welcomme 1979; Bayley 1995; Sparks 1995). Seasonal spawning and rearing habitat is made available when terrestrial vegetation becomes inundated by flood waters. Floodplains are important nursery habitats because they provide abundant invertebrates for food (Holland and Huston 1985), sanctuary from unfavorable temperatures and high velocity river currents (Holland 1986), and cover from predators (Paller 1987). Many of the habitats available to fishes change seasonally in relation to the floodplain hydrograph, resulting in successional shifts in the use of floodplains by fishes (Winemiller 1989).

In California, the importance of floodplain habitats to fishes has not been appreciated until recently, although native fishes are adapted to seasonal inundation of valley floodplains, a major event prior to water development (Sommer et al. 2001). Rain and snowmelt occur mainly in winter and spring and native riverine fishes spawn during periods of high flow from February to early May (Marchetti and Moyle 2000; Moyle 2002). Historically, the high flows provided both access to upstream spawning areas and created extensive flooded habitat for rearing. Today, dams and diversions have altered the natural flow regimes in most California rivers, with most high flows captured in reservoirs (Moyle 2002). Floodplains have become separated from rivers through channelization and levee construction and heavily developed for agricultural and urban uses (Mount 1995; Rasmussen 1996). The combination of altered flows and reduced habitats has been a major factor in the decline of the native fish fauna of California (Moyle 2002). An additional problem has been the invasion of many alien fishes that are favored by the altered habitats (Moyle 2002). This high degree of habitat loss has greatly enhanced the significance of remnant floodplain habitat (Sommer et al. 2001), such as that found along the lower Cosumnes River in central California.

The Cosumnes River is the largest stream flowing into California's Central Valley without a major dam on its main stem (Florsheim and Mount 2002). Because the Cosumnes River still maintains its natural hydrograph during winter and spring, a major floodplain restoration effort along the lower river has been undertaken by The Nature Conservancy and various state and federal agencies (Florsheim and Mount 2002). Levees were breached in five places to allow seasonal flooding of a mosaic of habitat types, including rice, oak woodland, willow and cottonwood riparian forest, grasslands, marshlands, and sloughs.

We initiated a study in February 1999 to examine use of the restored floodplain habitat by native and alien larval fishes. Our goals were to (1) compare fish use of different habitats within the floodplain, (2) assess temporal trends in abundance of native and alien species, and (3) characterize the environment in relation to use by larval fish. Special attention was paid to the use of floodplain habitat by native fishes for spawning and rearing, especially splittail *Pogonichthys macrolepidotus* because it is a a species of special concern (Moyle 2002) and is floodplain-dependent (Sommer et al. 1997, 2001, 2002).

Study Site

The Cosumnes River Preserve (CRP) is located in south Sacramento County bordering the Cosumnes River. It is a large (5,261 ha) mosaic of floodplain and surrounding upland habitat (Florsheim and Mount 2002). The preserve has some of the best remaining examples of Central Valley freshwater wetlands, cottonwood-willow riparian corridors, and valley oak riparian forests. The preserve also contains managed farmlands and diked waterfowl ponds, together with annual grasslands interspersed with vernal pools. The CRP is located just upstream (0.5 km) of the confluence of the Cosumnes River and the Mokelumne River (Figure 1). The CRP encompasses three major, tidally influenced freshwater sloughs, Middle Slough, Tihuechemne Slough, and Wood Duck Slough. During high flows, a large portion of flood water exits through Middle Slough into the northern Sacramento–San Joaquin Delta. Wood Duck Slough penetrates the middle of the floodplain and also serves as a conveyor of overland flow during periods of high inundation. Tihuechemne Slough

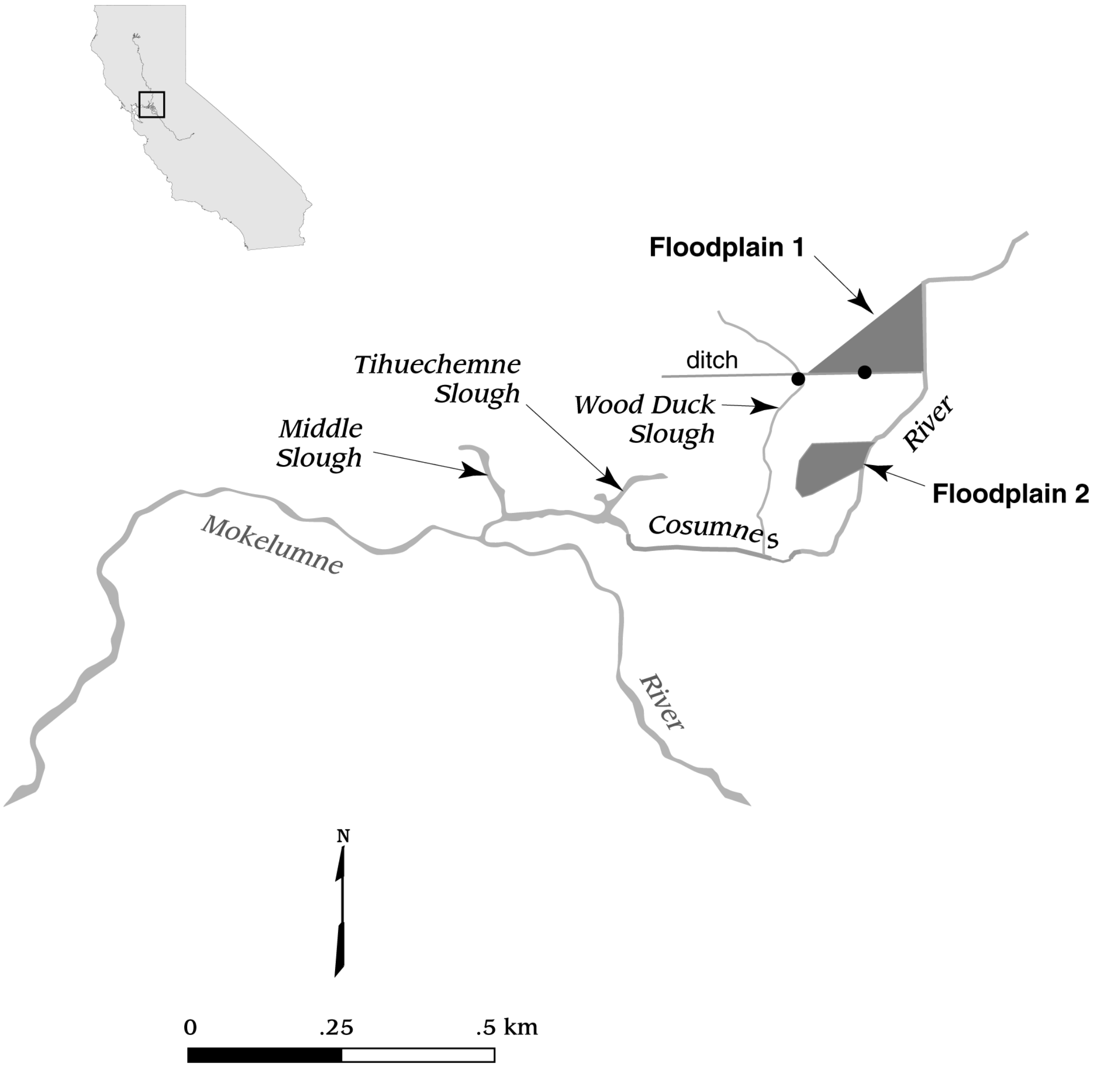


FIGURE 1. Cosumnes River floodplain study site, showing locations of principal sampling areas.

sits between Wood Duck Slough and Middle Slough. Like Wood Duck Slough, it bisects the floodplain and conveys overland flow during high flow events. It was not sampled because access to it was very difficult during high flooding.

The extent of flooding is highly variable from year to year (Figure 2). In 1999, the river was connected to the floodplain for 135 d and in 2001 for 88 d (W. Trowbridge, University of California, Davis, unpublished data). Five sampling sites were chosen on the basis of habitat availability and accessibility during flood events (Figure 1): (1) Middle Slough, (2) Wood Duck Slough, (3 and 4) two floodplain sites near levee breaches, and (5) Cosumnes River adjacent to the floodplain. Another site, only sampled in 1999, was in a ditch that ran perpendicular between the floodplain sites and acted as a catch basin when floodplain waters receded.

Methods

Field methods

Sampling was conducted in 1999 and 2001. It began with the onset of flooding and termi-

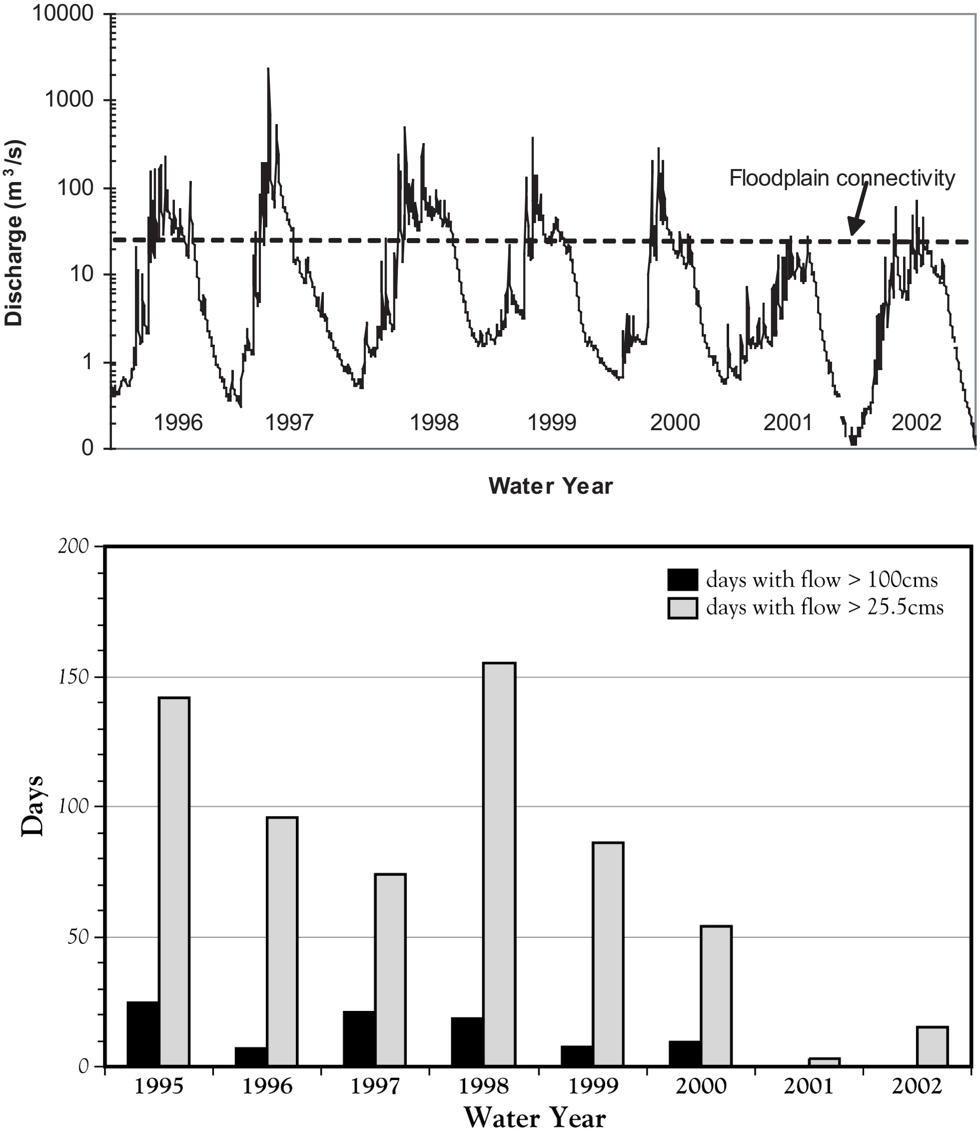


FIGURE 2. Top: Hydrograph for the Cosumnes River (1996–2002), showing flows at which the floodplain becomes connected to the river. Bottom: Number of days floodplain was connected to the river (pale bars, 1995–2002) and number of days of major floods that actively changed floodplain topography (dark bars).

nated when sites dried or larval fish became rare in samples. In 1999, samples were collected on a weekly basis at Middle Slough and the Cosumnes River from 9 February to 30 July, at Wood Duck Slough from 23 February to 30 July, at the floodplain site opposite the upper breaches from 23 February to 11 May, at the ditch site from 16 March to June 22, and at the floodplain site opposite the lower breaches from 9 March to 25 May. In 2001, all sites were sampled from 20 February to 5 July, except the lower breach floodplain site, which was started on 1 March. At each site, light traps were used to sample fish larvae following the design of Kissick (1993) with the following modifications (Marchetti and Moyle 2000):

openings leading into the traps had 5-mm-wide slots on each side, traps were equipped with extra foam for floatation, and the light source was a waterproof flashlight powered by two D cell batteries. For each sample date in both years, a single light trap was placed at each site at least 1 h after sunset. Traps were placed in succession so that each trap could be picked up after 60 min of illumination. At each site surface water temperature (°C), pH (1999 only), and conductivity (mS) were measured using a Hanna HI991300 portable meter. Water transparency was measured to the nearest cm with a Secchi disk during daylight prior to sampling. The presence or absence of current was determined using a small dip net; any ballooning of the net caused by flow indicated the presence of current. River discharge data were obtained from a fixed gauge operated by the U.S. Geological Survey at Michigan Bar, approximately 58 km upstream. Depth was measured to the nearest cm. Percent coverage of substrate type (silt, mud, clay, sand, gravel, and cobble) and vegetation (annual plants, trees, woody debris, aquatic macrophytes, emergent macrophytes, and filamentous algae) were estimated in a 1-m perimeter surrounding the light trap. Samples were preserved in a 5% solution of buffered formalin.

Larval fish identification

Larvae were identified following the keys in Wang (1986). Identification of voucher specimens was completed by J. C. S. Wang (National Environmental Services, Inc.) to confirm our identifications. Larval sunfish *Lepomis* spp. and crappie *Pomoxis* spp. could not be identified to species. However, based upon our juvenile and adult fish sampling (authors' unpublished data), the *Lepomis* spp. group probably included bluegill *Lepomis macrochirus* and redear sunfish *Lepomis microlophus*, and the *Pomoxis* spp. group probably included black crappie *P. nigromaculatus* and white crappie *P. annularis*. For convenience, hereafter, these groups will be referred to as sunfish and crappie. All other larvae were identified to species except for two smelt pro-larvae collected in 2001. The smelt were assumed to be wakasagi *Hypomesus nipponensis* because we collected juveniles later that year (authors' unpublished data).

Statistical analysis

Light trap catch data were summarized as number of fish captured per h of illumination (CPUE). We analyzed data with principal components analysis (PCA), detrended correspondence analysis (DCA), and canonical correspondence analysis (CCA), using the Canoco 4.0 software program (ter Braak and Smilauer 1998). Patterns in CPUE among sites and years were examined using PCA. Monthly succession of larval species occurrences was explored graphically and with DCA; DCA was used because an initial PCA exhibited a pronounced "arch effect" indicating a unimodal response gradient. We used CCA to describe the relationships between species abundances and environmental variables. Species that comprised less than or equal to 0.005% of the total catch were excluded from analyses. Environmental data collected as percentages were square root-transformed, while all other environmental and CPUE data were ln(x + 1)-transformed prior to analyses; all environmental data were standardized to a mean of zero and SD of one.

Results

Catch summary

We collected 7,709 larval fish in 1999 and 5,808 in 2001 (Table 1). The abundances of four species—threadfin shad *Dorosoma petenense*, American shad *Alosa sapidissima*, western mosquitofish *Gambusia affinis*, and wakasagi—were less than 0.005% of the total catch and were eliminated from statistical analyses. Prickly sculpin *Cottus asper* was the most abundant species, accounting for 73% of the total number of individuals. Other common taxa were sunfish (6%), common carp *Cyprinus carpio* (4%), Sacramento sucker *Catostomus occidentalis* (4%), bigscale logperch *Percina macrolepida* (3%), crappie (3%), and inland silverside *Menidia beryllina* (3%). Each of the remaining species (Sacramento blackfish *Orthodon microlepidotus*, splittail, largemouth bass *Micropterus salmoides*, and golden shiner

TABLE 1. Average CPUE (number larvae/illumination hour) and annual percent composition of larval fish species caught in 1999 and 2001. Native species are denoted by (N). Percentages of all species were rounded to the nearest whole number. Number of species indicates the total number of fish species caught in that year. Months are those in which spawning took place (2 = Feb., 3 = Mar., etc.); asterisk indicates months of highest CPUE.

Variable	1999	2001	Total	
Total light trap hours	116	104	220	
Average CPUE	66	56	62	
Number of species	12	14	14	
Species[a]	CPUE (%)	CPUE (%)	CPUE (%)	Months
Prickly sculpin (N)	54 (84)	35 (62)	45 (73)	2, 3^*,4,5
Sacramento sucker (N)	2.3 (3)	2.4 (4)	2.3 (4)	4^*, 5
Sacramento blackfish (N)	1.0 (2)	0.5 (1)	0.8 (1)	4^*, 5^*, 6
Splittail (N)	0.6 (1)	0.5 (1)	0.8 (1)	3, 4^*, 5^*
Sunfish[b]	1.0 (1)	6.4 (12)	3.5 (6)	5, 6^*, 7
Largemouth bass	0.2 (<1)	0.7 (1)	0.4 (1)	4, 5^*, 6, 7
Crappies[c]	1.4 (2)	1.7 (3)	1.5 (3)	3, 4^*, 5^*, 6^*, 7^*
Common carp	3.2 (5)	1.7 (3)	2.5 (4)	3, 4^*, 5^*, 6
Golden shiner	1.1 (2)	0.4 (1)	0.7 (1)	3, 4^*, 5, 6
Bigscale logperch	1 (2)	3.2 (6)	2.1 (3)	3^*, 4, 5
Inland silverside	0.4 (1)	3 (5)	1.6 (3)	4, 5^*, 6, 7

[a] Rare species not included in this analysis: threadfin shad, American shad, western mosquitofish, and wakasagi.

[b] Sunfish includes bluegill and redear sunfish.

[c] Crappies include white crappie and black crappie.

Notemigonus crysoleucas) comprised about 1% of the catch.

Comparisons among sites

The highest diversity of fishes was found in Middle Slough where all 11 species were present (Figure 3). The two floodplain sites and the ditch intersecting those two sites all had 8 species (4 native) in 1999. In 2001, Floodplain 1 had 6 species (2 native) and Floodplain 2 had 10 (4 native). Wood Duck Slough had 10 species (4 native) in 1999 and 9 species (2 native) in 2001. The river site had 8 species (2 native) in 1999 and9 (2 native) in 2001. Catches in all sites were dominated by prickly sculpin in both 1999 and 2001, except the 1999 river site, which was dominated by sunfish (Figure 3).

The PCA of larvae CPUE for site and year suggested differences related to both factors. The first three components accounted for 80% of the variance explained by PCA (Table 2). Visual inspection of a biplot of species and site scores (Figure 4) indicated that sites were very different between the 2 years; only Wood Duck Slough was similar in species composition between years. Three groups of fish had positive correlations: (1) common carp and splittail; (2) Sacramento blackfish, golden shiner, and crappie; (3) sunfish, Sacramento sucker, and inland silverside (Figure 4).

Comparisons among months

There was a temporal pattern in larval fish catch by month (Figure 5). In February, only prickly sculpin were present. Bigscale logperch appeared in March together with common carp, splittail, and golden shiner (Figure 5). In April, all species were present, with splittail exhibiting highest abundance in 1999. In May, some early spawners (prickly sculpin and bigscale logperch) were less abundant. Splittail abundance was higher in May of 2001 than in 1999 (Figure 5). In late May, Sacramento blackfish, sunfish, crappie, golden shiner, largemouth bass, and inland silverside

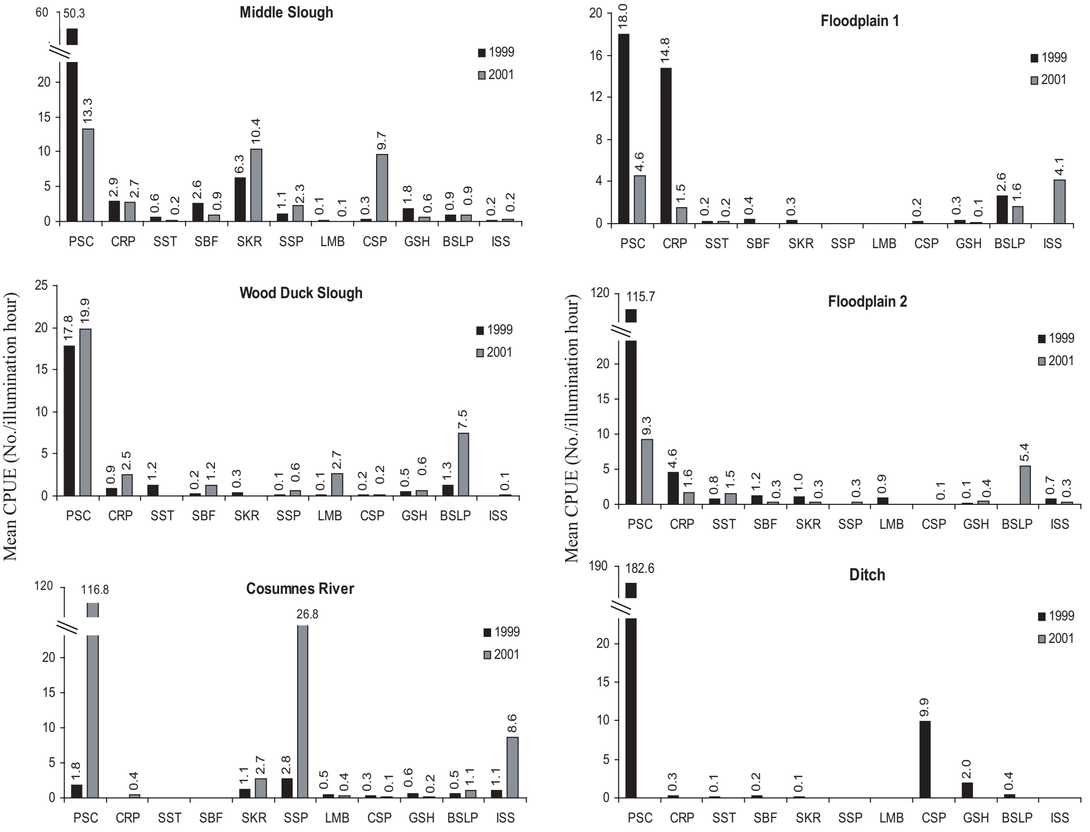


FIGURE 3. CPUE of larval fishes for 1999 and 2001. Species codes are as follows: PSC, prickly sculpin; SKR, Sacramento sucker; SBF, Sacramento blackfish; SST, Sacramento splittail; SSP, sunfish; LMB, largemouth bass; CSP, crappie; CRP, common carp; GSH, golden shiner; BSLP, bigscale logperch; ISS, inland silverside.

became increasingly common in the catches (Figure 5). Sunfish and inland silverside dominated June catches in both years, although numbers were higher in 2001. In July, sunfish and crappie were the most abundant taxa in 1999, while inland silverside were dominant in 2001 (Figure 5).

The DCA of species abundance by month and year supported this pattern of temporal change (Figure 6). The first two axes of the DCA explained 58% of the variance in the species abundance data (Table 3). The first axis gradient length of 3.94 standard deviations indicated that species found in February and early March were not present in June and July (Figure 6). This patterns is supported by the graphical relative abundance data (Figure 5), although common carp and golden shiner appeared earlier in 2001.

Environmental variables and species composition

The forward selection mode in the CCA resulted in the retention of six variables in the 1999 model and five in the 2001 model (Table 4). In 1999, flow, temperature, sand and clay substrate, and terrestrial and emergent vegetation were selected (Figure 7). In 2001, flow, temperature, mud substrate, macrophytes, and filamentous algae were selected (Figure 7). River flow and temperature explained the largest amount of variation among species abundances in both years, although the other environmental variables were also important. Because the first and second axes cumulatively explained the most variance (28% and 24%, respectively), the third and fourth axes were

TABLE 2. PCA component loadings for fish species data summarized by site and year. Native species are denoted by (N). An asterisk indicates a heavy loading with the component.

Species or correlation	Component loadings 1	 2	 3
Prickly sculpin (N)	0.94*	–0.31	–0.09
Common carp	–0.18	–0.55*	–0.74*
Splittail (N)	–0.17	–0.37	–0.19
Sacramento blackfish (N)	0.23	–0.46	–0.49*
Sacramento sucker (N)	0.48*	0.35	–0.36
Sunfish	0.46	0.84*	–0.12
Largemouth bass	0.01	0.05	–0.23
Crappies	0.43	–0.39	0.75*
Golden shiner	0.33	–0.36	0.47
Bigscale logperch	–0.52*	–0.06	–0.22
Inland silverside	0.24	0.82*	–0.09
Eigenvalue and explained variance			
Eigenvalue	3.70	2.80	1.40
Culmulative percent of variance explained	37.20	65.20	79.00

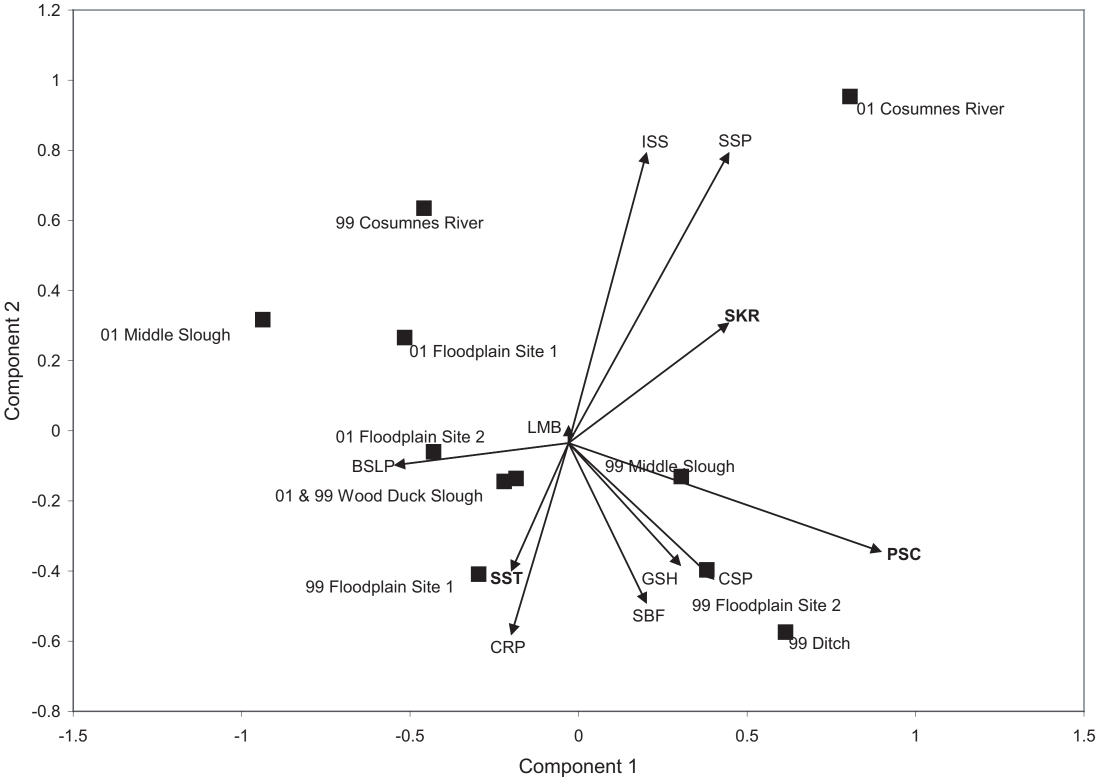


FIGURE 4. Principal component analysis biplot of larval fish CPUE defined by site and year. Species codes are same as Figure 3. Native species are in bold type.

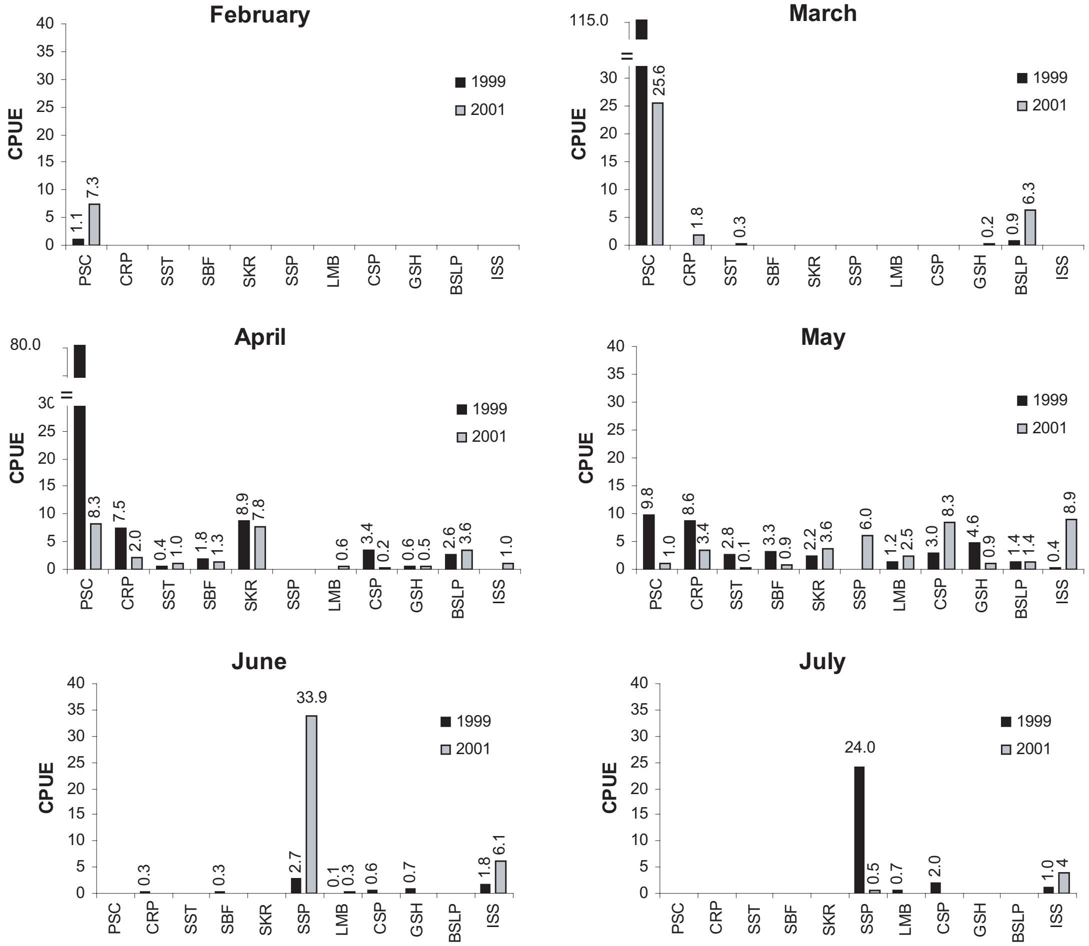


FIGURE 5. Bar graph of species CPUE by month for 1999 and 2001. Species codes are the same as Figure 3.

not interpreted (Table 4). Monte Carlo tests showed that the first axis (1999, $F = 15.9$, $P = 0.005$; 2001, $F = 13.1$, $P = 0.005$) and the full model (1999, $F = 7.0$, $P = 0.005$; 2001, $F = 5.5$, $P = 0.005$) were statistically significant.

Although river flow is an indirect measure of inundation of the floodplain, it was directly related to flows at the slough and river sites. Temperatures were lower on the floodplain when there was connectivity to the cool river water (Table 5). Conversely, when the river was disconnected from the floodplain, there was a dramatic warming effect on water temperature (Table 6). The timing and magnitude of flow was very different for the 2 years, changing the number of days that the river was connected to the floodplain (Figure 2). Because of the dramatic difference in river flow between years, average temperature in 2001 (19.7°C) was significantly higher than in 1999 (17.9°C; t-test, $t = 2.66$, df = 71, $P < 0.001$). Vegetation type was also related to inundation magnitude. In 1999, floodwaters covered a large amount of terrestrial and emergent vegetation. In 2001, flood waters receded very quickly into low areas, most of which were ponds or wetlands with beds of aquatic macrophytes.

The CCA species scores, when plotted in relation to environmental gradients (Figure 7), showed patterns that reflect the different conditions on the floodplain in a wet (1999) and

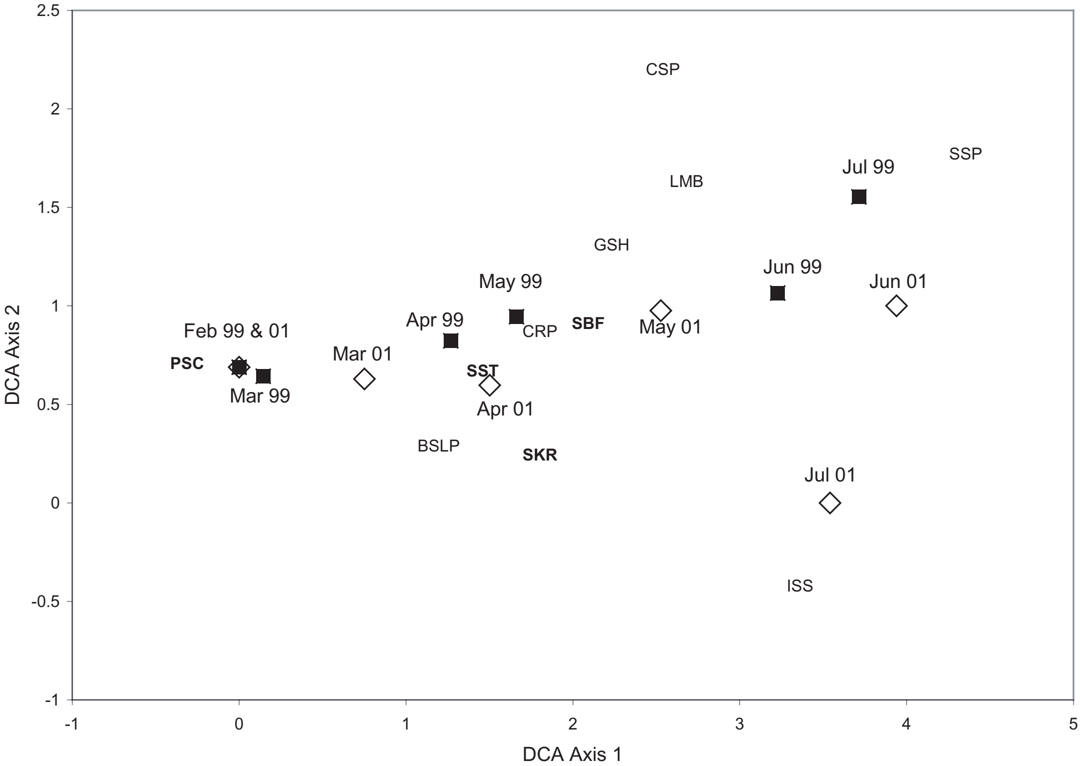


FIGURE 6. Detrended correspondence ordination plot of larval fish CPUE by month. Species codes are same as Figure 3. Native species are in bold type.

dry (2001) year. In 1999, with more extensive flooding in space and time, two species (prickly sculpin and bigscale logperch) were associated with flooded terrestrial vegetation and two species (Sacramento sucker and common carp) were associated with higher flows. Splittail larvae also showed an association with higher flows but were more closely associated with emergent vegetation. Late-season spawners (inland silverside, crappie, and sunfish) exhibited an association with warmer temperatures and clay substrates of the permanent floodplain ponds, while species with fairly broad spawning times (golden shiner, Sacramento blackfish, and largemouth bass) showed less defined patterns. In 2001, prickly sculpin, Sacramento sucker, bigscale logperch, common carp, Sacramento blackfish, golden shiner, and splittail were most abundant when flows were highest but, presumably because of the limited extent of inundation, did not show strong associations with

TABLE 3. Results of detrended correspondence analysis run on data defined by CPUE of a species by month and year. Shown are the eigenvalues, length of gradient, and percentage of variance explained by the species data by each axes.

Axes	1	2	3	4	Total inertia
Eigenvalue	0.668	0.103	0.013	0.003	1.227
Gradient length	3.94	1.55	0.95	0.91	
Percent variance	51.38	57.73	58.08	57.83	
Sum of all unconstrained eigenvalues					1.227

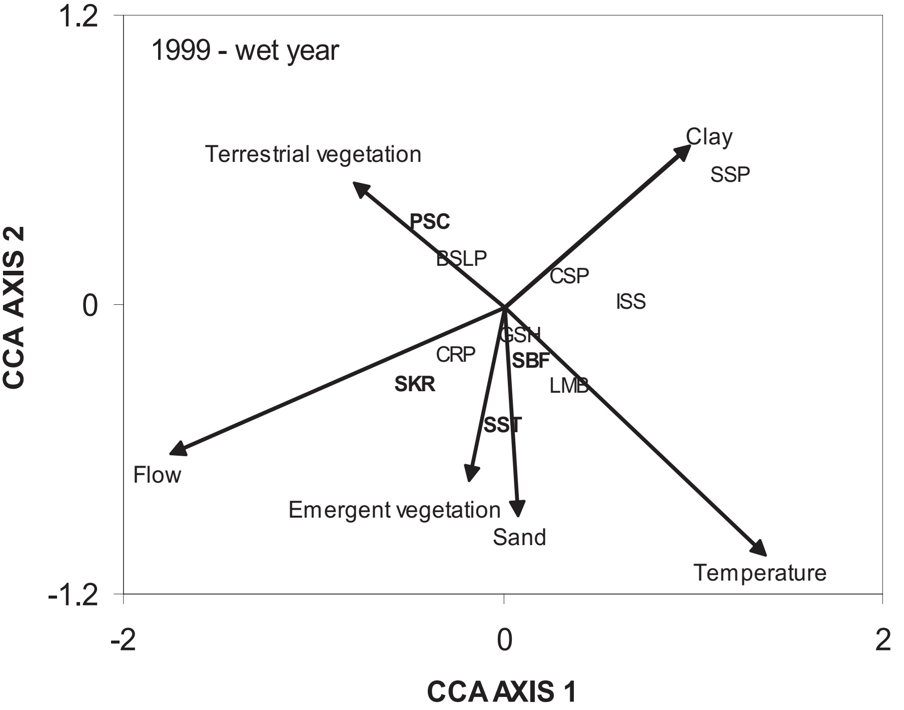
TABLE 4. Results of canonical correspondence analysis run on environmental variables and larval fish abundance data (CPUE) collected on the Cosumnes River floodplain in 1999 and 2001. Shown is the CCA summary table for the first three ordination axis, canonical regression coefficients, and interset correlations for the standardized environmental variables with the first two ordination axes.

1999				Canonical coefficients		Interset correlations	
	Axis 1	Axis 2	Axis 3	Axis 1	Axis 2	Axis 1	Axis 2
Eigenvalues	0.558	0.353	0.091				
Species–environment	0.880	0.787	0.542				
Cumulative percentage variance							
Species data	16.9	27.6	30.4				
Species–environment relation	48.2	78.6	86.5				
Flow				–0.608	–0.612	–0.777	–0.255
Temperature				0.370	–0.865	0.613	–0.417
Sand substrate				0.075	–0.255	0.033	–0.353
Clay substrate				0.235	0.291	0.440	0.259
Terrestrial vegetation				–0.206	0.230	–0.356	0.201
Emergent vegetation				–0.022	–0.197	–0.082	–0.300
2001							
	Axis 1	Axis 2	Axis 3	Axis 1	Axis 2	Axis 1	Axis 2
Eigenvalues	0.592	0.217	0.125				
Species–environment	0.915	0.713	0.584				
Cumulative percentage variance							
Species data	17.7	24.2	27.9				
Species–environment relation	57.0	77.9	90.0				
Flow				–0.844	–0.481	–0.886	–0.155
Temperature				0.215	–0.424	0.609	–0.167
Mud substrate				–0.008	–0.219	–0.045	–0.320
Macrophytes				0.180	–0.911	0.156	–0.592
Filamentous algae				–0.064	0.284	–0.124	–0.146

vegetation types (Figure 7). Inland silverside, sunfish, largemouth bass, and crappie were associated with higher temperatures present in the disconnected ponds and, to a lesser extent, the macrophyte beds that developed in the ponds.

Discussion

It is clear that each species had a fairly predictable response to flow and temperature variation on the floodplain, as indicated by comparisons among sites, changes in abundance through time, and characteristics of habitats in which the fishes appeared. Although monthly larval fish data show clear patterns related to flooding regime, finer scale larval fish distribution and abundance on the Cosumnes River floodplain is highly variable. Part of the variability results from the spawning sites of the different species. There were three basic types of spawners (Moyle 2002): (1) river spawners whose larvae washed into the floodplain (Sacramento sucker, prickly sculpin), (2) floodplain spawners (splittail and common carp), and (3) resident pond or slough fishes that opportunistically spawned in floodplain areas close to their adult habitats (Sacramento blackfish, golden shiner, sunfish, crappie). Thus, the appearance on the floodplain of each species depended on factors such as connectivity between river and floodplain and temperatures required for spawning.



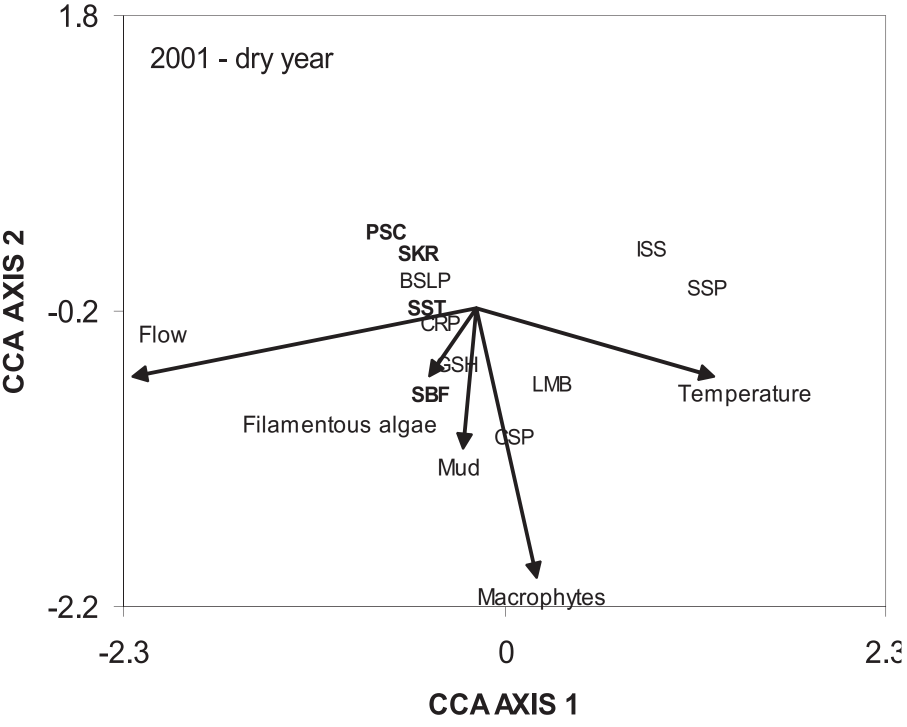


FIGURE 7. Canonical correspondence ordination diagram showing the relationships of larval fishes to environmental gradients. Species codes are the same as in Figure 3. Native species are in bold type.

TABLE 5. Physical characteristics of Cosumnes River floodplain sites sampled for larval fish in 1999 and 2001. Mean river flow (m^3/s), temperature (°C), electrical conductivity (µS), Secchi depth (cm), water depth (cm), and range of values in parentheses for all sites in both years.

Characteristic	Floodplain 1	Ditch	Wood Duck Floodplain 2	Cosumnes Slough	Middle River	Slough
1999						
River flow	35 (22–60)	24 (5–45)	31 (21–49)	29 (31–60)	46 (0.31–374)	44 (0.31–374)
Temperature	17 (13–26)	16 (11–20)	20 (10–29)	19 (12–29)	16 (9–26)	16 (9–26)
Conductivity	115 (2–247)	112 (61–191)	105 (66–234)	161 (67–741)	104 (38–248)	125 (77–256)
Secchi	51 (25–85)	77 (22–120)	49 (23–78)	34 (10–48)	54 (15–87)	47 (20–70)
Depth	51 (39–62)	66 (46–84)	50 (40–63)	56 (44–75)	55 (45–72)	61 (45-110)
2001						
River flow	9 (1–23)	No data	12 (7–18)	10 (1–26)	10 (1–26)	9 (1–26)
Temperature	22 (11–30)		21 (16–31)	20 (11–28)	20 (10–28)	20 (11–29)
Conductivity	150 (102–253)		126 (106–155)	171 (67–487)	100 (56–258)	177 (104–273)
Secchi	37 (10–71)		31 (9–47)	34 (1–72)	49 (5–81)	41 (12–90)
Depth	53 (42–63)		54 (42–72)	56 (40–103)	54 (38–80)	51 (36–84)

Comparisons among sites

There were few strong or consistent relationships among species and sites because of the continuous expansion and contraction of floodwaters. Most species could be found at all sites at one time or another (Figure 3). However, sites closest to levee breaches were dominated by larvae (mostly from native species) from river spawning fishes and by larvae of obligate floodplain spawners such as splittail. Highest species diversity was consistently found in the two sloughs because they received drainage water from the entire floodplain and also had their own complement of resident species. Some species (e.g., inland silverside and golden shiner) were found primarily in low lying floodplain ponds and in Middle Slough when these waters were warm and there was little influence from river flow.

Comparisons among months

The clear temporal separation of different groups of species suggests that early season

TABLE 6. Mean temperatures (°C) with range by site and month.

1999	Feb	Mar	Apr	May	Jun	Jul
Floodplain 1	15 (10–17)	20 (16–23)	18 (15–21)	22 (19–26)	No data	No data
Ditch	No data	13 (11–14)	15 (11–18)	17 (16–18)	19 (17–20)	No data
Floodplain 2	No data	15 (10–17)	20 (16–23)	24 (19–30)	No data	No data
Wood Duck Slough	12 (12–12)	14 (13–15)	17 (13–21)	21 (17–26)	25 (21–29)	25 (23–28)
Cosumnes River	10 (9–11)	11 (10–12)	14 (11–17)	18 (15–21)	24 (22–25)	22 (19–25)
Middle Slough	10 (9–12)	12 (10–14)	15 (12–18)	19 (16–22)	24 (22–26)	22 (21–23)
2001						
Floodplain 1	11 (11–11)	17 (14–21)	18 (16–25)	26 (20–30)	26 (24–28)	26 (26–26)
Floodplain 2	No data	17 (13–22)	19 (16–24)	26 (22–31)	No data	No data
Wood Duck Slough	11 (11–11)	17 (12–19)	17 (14–22)	23 (19–26)	25 (23–28)	27 (27–27)
Cosumnes River	10 (10–10)	16 (12–19)	16 (14–19)	22 (18–24)	26 (24–28)	27 (27–27)
Middle Slough	11 (11–11)	15 (12–20)	16 (15–16)	20 (17–23)	26 (25–29)	28 (28–28)

to late season environmental cues were important to the timing of larval emergence. Some of the potential cues include flow, temperature, and photoperiod (Robinson et al. 1998; Marchetti and Moyle 2000; Moyle 2002). Flow and temperature together explained the most variation in the abundance of species. Although the pattern is not as clear as in other nearby systems (Marchetti and Moyle 2000; Meng and Matern 2001; Feyrer 2004, this volume), in general, native larvae appeared early in the season (February–April) and aliens appeared later (April–July) (Figure 8). The fact that 1999 and 2001 were very different in terms of hydrology (Figure 2) is seen in the timing of emergence of native and alien larval fish. Common carp and splittail, for example, appeared a month earlier in 2001 than 1999.

Environmental variables and species composition

Temperature and flow clearly had the biggest effect on larval fish abundance and resulted in seasonal changes in the distribution and abundance of species. However, catches in light traps were also positively influenced by the presence of dense growths of annual terrestrial vegetation or aquatic macrophytes. Presumably, the vegetation was a combination of refuge from predators, shelter from high flows, and source of small invertebrates as food (Holland and Huston 1985; Holland 1986; and Paller 1987). Flooded terrestrial vegetation also served as spawning substrate for floodplain spawning fishes such as splittail and common carp (Moyle 2002). Although not quantified, our observations during this study suggest that dense stands of dead annual plants that occur in

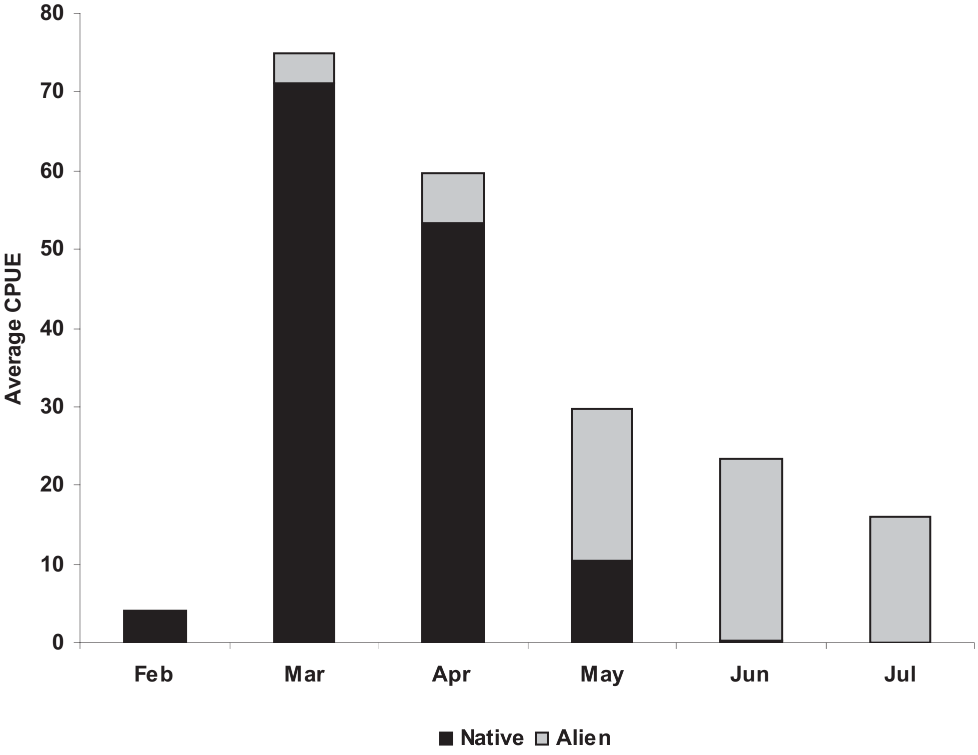


FIGURE 8. Percent native and alien species larvae by month, with 1999 and 2001 combined.

open, unforested areas are especially favorable to native species, including splittail.

A key reason for this study was to determine how native species use floodplain habitats for rearing in order to develop management strategies. The four most abundant native fishes were prickly sculpin, Sacramento sucker, splittail, and Sacramento blackfish. Prickly sculpin were the most abundant larvae at every site from February to April. Adults or juveniles were rarely found on the floodplain, so we presume that larvae must have washed in from upstream. This is supported in that greater abundance of prickly sculpin larvae occurred in 1999, when the floodplain was connected more often than in 2001. The Cosumnes River is heavily rip-rapped with boulders just upstream of levee breaches that deliver water into the floodplain. We sampled this area and found high densities of adult prickly sculpin (5–10 fish/m^2; authors' unpublished data). Prickly sculpin spawn underneath rocks and have an extended spawning season, producing large numbers of pelagic larvae (Moyle 2002). Thus, they can produce larvae that migrate onto the floodplain as long as there is connection with the river. However, the importance of floodplain as a rearing habitat for prickly sculpin is not known; it is possible that it is a "sink" for larvae because we collected relatively few juveniles during an associated weekly beach seine study and have no evidence of strong outward movement of young fish in fyke net catches set in outflow channels (authors' unpublished data).

Sacramento sucker were most abundant in the Middle Slough and river sites, but some were also found at floodplain sites. The larvae presumably originated from large numbers of adult fish that moved up river to spawn from the nearby estuary, beginning in January. While juvenile Sacramento suckers were collected later in the season, they were most abundant in the river itself and not on the floodplain (authors' unpublished data). Therefore, the overall importance of the floodplain to Sacramento sucker populations is uncertain.

Splittail, a species of special concern, used the floodplain in both years, but was most abundant in 1999. Splittail presumably spawned on the floodplain 2001, when only a portion of the floodplain was available for a limited time. Based on the initial appearance of larvae, spawning mostly took place in the last week of March or first week in April. This is about the same time that temperatures on the floodplain reached 17–20°C. Larvae grew quickly, and small juveniles usually moved off the floodplain in the last week of April or first week in May, when short pulses of cold water, from rain or snowmelt, reconnected the floodplain to the river for brief periods (authors' unpublished data).

Sacramento blackfish are different from most native species in that they spawn later in slightly warmer water. Sacramento blackfish larvae first appeared in our samples in late April, although the majority of juveniles were caught in our beach seine study in May (authors' unpublished data). This is also when the river disconnected from the floodplain, so the fish persisted only in permanent water that also contained abundant alien species.

Conclusions

Use of the Cosumnes River floodplain by native and alien fishes was related to inflowing floodwaters and accompanying water temperatures. Our results suggests that floodplains were historically important habitats for rearing of native fishes, such as splittail, although their importance to river-spawning species, such as Sacramento sucker and prickly sculpin, and native species resident in sloughs, such as Sacramento blackfish, is poorly understood. At present, floodplains appear important for native fishes mainly early in the season (February–April) because warmer temperatures and lower flows later in the season favor alien species, especially those that are permanent residents in ponds, ditches, and sloughs on the floodplain. By summer, the only fishes appearing as larvae are alien fishes, especially inland silverside and centrarchids. However, some alien species, especially common carp, have spawning habits very similar to native species and also benefit from early season flooding.

Another important observation is that larval fishes in the main floodplain were secondarily associated with flooded annual vegetation in 1999. This suggests that unforested fields of annual vegetation may be useful for larval rearing because of the abundance of food and cover. Larval fish use of forested habitats, however, has not yet been adequately studied. Presumably the historic floodplains of the Central Valley were a mosaic of forested and open habitats, so would have provided both habitats. Overall, our observations suggest that management of recreated floodplains, such as the Cosumnes River, should involve strong emphasis on (1) flooding in February–April, with rapid draining thereafter; (2) reduction in permanent habitats that support resident alien fishes; and (3) maintenance of habitat mosaics that keep large expanses of annual vegetation available for flooding.

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