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Patterns In The Use Of A Restored California Floodplain By Native And Alien Fishes

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ABSTRACT

Fishes were sampled on the restored floodplain of the Cosumnes River in Central California in order to determine patterns of floodplain use. The floodplain was sampled for seven years (1998-2002, 2004-2005) during the winter-spring flooding season. The fishes fell into five groups: (1) floodplain spawners, (2) river spawners, (3) floodplain foragers, (4) floodplain pond fishes, and (5) inadvertent users. Eight of the 18 abundant species were natives, while the rest were aliens. There was a consistent pattern of floodplain use, modified by timing and extent of flooding. The first fishes to appear were floodplain foragers, inadvertent users, and juvenile Chinook salmon (river spawners). Next were floodplain spawners, principally Sacramento splittail and common carp. At the end of the season, in ponds of residual water, non-native annual fishes, mainly inland silverside and western mosquitofish, became abundant. Adult spawners left when inflow decreased; their juveniles persisted as long as flood pulses kept water levels up and temperatures low. Juvenile splittail and carp quickly grew large enough to dominate floodplain fish samples, along with smaller numbers of juvenile Sacramento sucker and pikeminnow (river spawners). Such juveniles left the floodplain either with pulses or in drainage water. Relatively few fishes that used the floodplain for spawning or rearing became stranded, except late season alien fishes. Most alien fishes had resident populations in adjacent river, sloughs, and ditches and were not dependent on the floodplain for persistence. This indicates that Central Valley floodplains managed to favor native fishes should have the following characteristics: (1) extensive early season flooding, (2) complete drainage by the end of the flooding season, (3) few areas with permanent water, (4) a mosaic of physical habitats, (5) regular annual flooding but with high variability in flood regime.

KEYWORDS

Restoration, non-native species, alien species

SUGGESTED CITATION

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INTRODUCTION

California, like most other regions of the western world, has placed levees between its rivers and their floodplains, to free land for farms and cities. Not surprisingly, floodplain ecosystems and flood-dependent species have declined greatly, often confined to small remnant populations (Williams 2000, Tockner and Standford 2002). There is growing recognition that naturally-functioning floodplains provide many benefits, including direct economic benefits, ecosystem services, and habitat for a wide diversity of species (Bayley 1995, Tockner and Stanford 2002, Pinter 2005). In highly industrialized countries, however, most rivers have been denied use of their floodplains through a combination of control of flows by dams, extensive levee systems, and other riverine alterations (Jungwirth et al. 2002, Magilligan et al. 2003). As a consequence, there is interest worldwide in rehabilitating functioning floodplains, often with fish and fisheries as a key indicator of success (e.g., Michener and Haeuber 1998, King et al. 2003, Grift et al. 2003).

In California, where rivers are highly altered and have historically been denied use of their floodplains, rehabilitation of floodplains for their combined ecological and economic benefits has only recently received serious attention (Sommer et al. 2001a). Restoration of ecologically-functioning floodplains is an important goal of an ambitious ecosystem restoration program for the Sacramento-San Joaquin (Central Valley) watershed (http://calwater.ca.gov/). One of the key reasons for restoration is to enhance native fish populations, including those of Chinook salmon *(Oncorhynchus tshawytscha)* and Sacramento splittail *(Pogonichthys microlepidotus)* (Sommer et al. 2001b, Sommer et al. 2002, Crain et al. 2004). However, our understanding of how fishes use Central Valley floodplains is limited, as is our understanding of how to manage floodplains to favor native fishes. Most Central Valley rivers have large dams on them that regulate flow, reducing the frequency of flooding events, and most Central Valley floodplains are separated from their rivers by levees. An exception is the Cosumnes River, the focus of this study, which has no major dams on its main channels (Moyle et al. 2003) and has a floodplain that is being restored through breaching of levees (Booth et al. 2006). The Cosumnes River has a hydrograph typical of rivers in a Mediterranean climate, with high flows occurring mainly in winter (January–March), followed by low (or no) flows in summer (June–October). The restored floodplain of the Cosumnes River is a model for floodplain restoration in Central California, because of its small size, accessibility, and habitat diversity. It is also useful for comparison with the nearby but much larger Yolo Bypass, a flood control channel with many attributes of a natural floodplain (Sommer et al.2001a, 2004).

The purpose of this study was to document the use of the Cosumnes River floodplain by fishes. Key questions we addressed were:

1. What kinds of fishes use the Cosumnes River floodplain?
2. How does fish use of the floodplain change with season and flow?
3. What characteristics of flooding and floodplains favor native fishes?
4. Does stranding kill large numbers of floodplain fishes?
5. Is the pattern of fish use of floodplains similar to that in other parts of the world?

To answer these questions, we examined floodplain use by young-of-year and adults and older juveniles over seven years. Floodplain use by larval fishes is covered in Crain et al. (2004). Finally, we use the information from our study and others to recommend ways of creating floodplains favorable to native fishes in California.

BACKGROUND: HOW FISH USE FLOODPLAINS

Fishes use floodplains in many different ways, although the widely used classification system developed for European rivers divides them into just three categories: (1) species with a strong dependence on the river *(rheophilic fishes)*, (2) species that live mainly in backwaters and floodplain lakes *(limnophilic fishes)*, and (3) species that occur in both broad habitat types *(eurytopic fishes)* (e.g., Grift et al 2003). Rheophilic fishes are typically the “white fishes” and limnophilic fishes are the “black fishes” used to characterize tropical floodplain fishes (e.g., De Graaf and Marttin 2003), where "white fishes" are mostly pelagic species and "black fishes" are mostly benthic species with high tolerance of high temperatures and low dissolved oxygen (Dudgeon 2000). Eurytopic fishes are labeled "grey fishes." Galat and Zweimuller (2001) assessed the importance of floodplain habitats by dividing fish into three categories: fluvial specialist species, fluvial dependent species, and microhabitat generalists. Their fluvial specialists are basically rheophilic species that are found only in flowing water, while the fluvial dependent species are a subset of rheophilic and limnophilic species that require rivers for some stage of their life history. Their microhabitat generalists include eurytopic species plus less specialized limnophilic species.

The above classification systems were largely developed in reference to highly altered European rivers. In this paper, we use a classification system that breaks the spectrum of use of seasonal floodplain habitats into more categories to better reflect complexity of use; it is based on information in Moyle (2002) and Sommer et al. (2001a, b, 2004), as well as the world literature (cited in context). We classify floodplain fishes (Table 1) as follows: (1) floodplain spawners, (2) river spawners, (3) floodplain foragers, (4) floodplain pond/lake fishes, and (5) inadvertent floodplain users.

Floodplain Spawners

These are eurytopic fishes that use the floodplain for spawning and for rearing of early life history stages. Typically, they migrate onto the floodplain when the water is rising or stable and then spawn on flooded substrates. The embryos stick to the substrate, usually vegetation, hatch in a few days and then rear until they reach an actively swimming juvenile stage (usually at ca. 25 mm total length (TL)). Juveniles leave the floodplain as the water recedes, which usually coincides with the time when they reach 40-60 mm TL. Floodplain spawners can be either *obligate* spawners or *opportunistic* spawners. The Sacramento splittail (see Table 1 for scientific names) is an example of an obligate floodplain spawner (Moyle et al. 2004); year class strength is highly correlated with the number of days of flooding (Sommer et al. 1997). Ribeiro et al. (2004) found that splittail juveniles exhibited better growth and condition in floodplain habitats than in riverine habitats. Likewise, Jurajda et al. (2001) found that the abundance of three species of fish in the Morava River (Czech Republic) was strongly dependent on the inundation of vegetated floodplain. In tropical river systems, many of the most abundant species (or at least those important to fisheries) spawn only in flooded areas, following predictable, annual flooding events (Welcomme 1979, Dudgeon 2000, Hogan et al. 2004).

Common carp *(Cyprinus carpio)* and goldfish *(Carassius auratus)* are examples of opportunistic floodplain spawners. While they do not require floodplain conditions for spawning, greatest success of spawning seems to coincide with extensive flooding (King et al. 2003). Many of the fishes of the Mississippi-Missouri river system historically were opportunistic floodplain spawners, taking advantage of long-term floods when temperatures were high enough for spawning (15-25°C, April-June) resulting in higher abundance and diversity in the rivers (Raibley et al. 1997, Galat et al. 1998). These species include fishes now present in California, such as largemouth bass and bluegill. In general, it appears that opportunistic floodplain spawners are most typical of temperate regions where the extent of flooding is unpredictable on an annual basis, while obligate floodplain spawners are most typical of tropical rivers with more predictable flood regimes. In both regions, opportunistic spawners are typically more abundant following years of extensive flooding.

River Spawners

River spawners are species in which the adults spawn upstream of floodplains, usually on gravel riffles, thereby allowing their young to use the floodplain for rearing in large numbers. Their young enter the floodplain as larvae or small juveniles. These mostly rheophilic fishes are common, but the importance of floodplain rearing to their populations is poorly known, because they also rear on stream edges and other habitats. However, locating spawning areas upstream of floodplains is presumably a deliberate rearing strategy for many of these species, to allow their young to take advantage of the abundant food and diverse habitats on floodplains. In European, east-

Table 1. Fishes collected as YOY and adults in the Cosumnes River floodplain, river, and sloughs, 1998-2002 - the years when sampling was most thorough. Species in boldface were abundant enough to use in statistical analyses. The * indicates alien species. Numbers are the number of years in which each species was collected in each habitat. User groups are described in the text. E = eurytopic, L= limnophilic, R= rheophilic. Fish not assigned to a group were not collected on the floodplain but have the potential to be inadvertent users because of presence in adjacent sloughs. Months for possible floodplain spawning are 0 = none, 2 = February, 3 = March, 4 = April, 5= May, 6 = June, 7= July. Timing is based on Crain et al.(2004) and observations during the study.

Floodplain Species	User groups		Floodplain, Yrs	River, Yrs	Slough, Years	Spawning months
Pacific lamprey, *Lampetra tridentata*	Inadvertent	R	5	5	5	0
American shad, *Alosa sapidissima**	Inadvertent	R	2	5	0	0
Threadfin shad, *Dorosoma petenense**	Inadvertent	L	4	5	5	0
Hitch, *Lavinia exilicauda*	River spawner	E	4	4	3	0
Sacramento blackfish, *Orthodon microlepidotus*	FP spawner	L	**5**	5	5	4-6
Sacramento splittail, *Pogonichthys macrolepidotus*	FP spawner	E	**5**	5	5	3-5
Sacramento pikeminnow, *Ptychocheilus grandis*	River spawner	R	5	**5**	**5**	0
Golden shiner, *Notemigonus chrysoleucas**	Forager	L	5	**5**	**5**	3-6
Fathead minnow, *Pimephales promelas**	Inadvertent	L	1	0	0	0
Goldfish, *Carassius auratus**	FP spawner	L	3	3	3	4-6
Common carp, *Cyprinus carpio**	FP spawner	E	5	5	5	3-6
Sacramento sucker, *Catostomus occidentalis*	River spawner	R	5	5	5	0
Brown bullhead, *Amieurus nebulosus**	Not present	L	0	0	1	0
Black bullhead, *A. melas**	Inadvertent	L	3	5	5	0
White catfish, *A. catus**	Inadvertent	E	1	5	5	0
Channel catfish, *Ictalurus punctatus**	Not present	E	0	5	5	0
Chinook salmon, *Oncorhynchus tshawytscha*	River spawner	R	5	5	4	0
Rainbow trout, *O. mykiss*	Inadvertent	R	1	3	0	0
Wakasagi , *Hypomesus nipponensis**	Inadvertent	L	1	0	0	0
Inland silverside, *Menidia beryllina**	Pond	L	5	5	5	4-7
Western mosquitofish, *Gambusia affinis**	Pond	L	5	5	5	4-7
Prickly sculpin, *Cottus asper*	River spawner	R	5	5	5	0
Tule perch, *Hysterocarpus traski*	Not present	E	0	2	0	0
Bluegill, *Lepomis macrochirus**	Forager	L	5	5	5	5-7
Redear sunfish, *L. microlophus**	Forager	L	5	5	5	5-7
Green sunfish, *L. cyanellus**	Not present	E	0	2	0	0
Warmouth, *L. gulosus**	Not present	E	0	0	2	0
Black crappie, *Pomoxis nigromaculatus**	Forager	L	5	5	5	4-7
Largemouth bass, *Micropterus salmoides**	Forager	E	5	5	5	0
Redeye bass, *M. coosae**	Not present	R	0	5	0	0
Spotted bass, *M. punctulatus**	Not present	E	0	5	5	0
Bigscale logperch, *Percina macrolepida**	River spawner	R	5	5	5	0

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ern North American, and tropical rivers, such fishes often rear in floodplain lakes (Galat et al. 1998, Dudgeon 2000, Navodaru et al. 2002). It is likely that the most abundant and persistent river spawning fishes on floodplains are those that benefit from rearing there. Thus, Sommer et al (2001b, 2005) and Jeffres (2006) demonstrated that juvenile Chinook salmon rearing on California floodplains grew faster and achieved larger sizes than fish rearing in the main river. However, Ribeiro et al. (2004) found that Sacramento suckers *(Catostomus occidentalis)* grew faster in riverine habitats than in floodplain habitats. A key adaptation to the successful use of the floodplains by the juveniles of this group is the ability to leave the floodplain as it drains and thereby avoid significant stranding.

Floodplain Foragers

Floodplain foragers are eurytopic and limnophilic fishes that actively move on to the floodplain to take advantage of abundant food, usually late in the flood cycle as the water becomes warmer. Typically, they are larger juveniles or yearlings of fishes that are resident in lakes, sloughs, ponds in or other habitats adjacent to floodplains. North American examples include golden shiner, largemouth bass *(Micropterus salmoides)*, bluegill *(Lepomis macrochirus)*, and redear sunfish *(L. microlophus)*. Such species may have substantially faster growth rates on floodplains than in non-floodplain habitats (Gutreuter et al. 1999), as well as higher survival rates (Raibley et al. 1997). In years when there is extensive prolonged flooding, adults of these species may move onto the floodplains to spawn, along with floodplain pond fishes. In California, these fishes are mostly alien species that use floodplains in their native habitats and appear be able to avoid stranding by returning to lakes and sloughs as water recedes.

Floodplain Pond/Lake Fishes

Floodplain pond/lake fishes are small limnophilic species present in lakes, sloughs, and permanent ponds that establish large populations in seasonal floodplain ponds. They could be regarded as a subset of floodplain foragers except that they reproduce in shallow floodplain ponds in most years and, with high survival and growth rates, can quickly dominate pond ecosystems, where they attract piscivorous birds. They are typically not dependent on floodplains per se for long-term persistence but are often temporarily more abundant in floodplain habitats than in the more permanent adjacent habitats. California examples of such short-lived, rapidly growing species are inland silversides *(Menidia beryllina)* and western mosquitofish *(Gambusia affinis)* (Moyle 2002). Such fishes are typical of shallow floodplain habitats in many parts of the world and apparently can sustain high productivity (even with heavy fishing pressure) because of their ability to take advantage of food-rich environments (e.g., De Graaf 2003b). Floodplain pond fishes are often stranded in ponds that dry up.

Inadvertent Users

Inadvertent floodplain users are a high percentage of the species collected on floodplains but are a small number of individuals (e.g., Borcherding et al. 2002). Most are limnophilic or rheophilic species that enter floodplains from adjacent lakes, ponds, and sloughs or from upstream but show no adaptations for floodplain use. They have a variety of fates. If they are larvae or small juveniles washed in from upstream, they either just pass though or settle out to die or become stranded. Large adults of species such as channel catfish *(Ictalurus punctatus)* that move too far from the river or home ponds are likely to become stranded in the receding water. Many of these fishes only enter the flooded areas close to their permanent habitats so are often capable of returning to their ponds or sloughs as the water recedes. In an Australian river, all fish species except the alien common carp fit into this category because the flooding is too unpredictable and of too short a duration for adaptations for floodplain use to develop (King et al. 2003).

STUDY AREA

The Cosumnes River Preserve (CRP), located in southern Sacramento County, California, is a large mosaic (5,261 hectares) of floodplain and uplands. 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, although these were not sampled on a regular basis as part of this study. The edge of the CRP sits just above (0.5 km) the confluence of the Cosumnes River and the Mokelumne River and encompasses three major tidally-influenced freshwater sloughs, Middle Slough, Tihuechemne Slough, and Wood Duck Slough (Figure 1). During non-flood periods, the tidal range in these sloughs is about 15-30 cm/day. During high flows, Middle Slough acts as an overflow channel and a large portion of the overland flow exits through it into the Cosumnes River and then the north Delta (upper San Francisco Estuary) via the Mokelumne River. Wood Duck Slough bisects the middle of the floodplain area and also acts as a conveyor of overland flow during high inundation. Sampling sites on the slough and river were typically shallow (0.5 -1.5 m deep) edge habitat, supporting low densities of aquatic and emer-

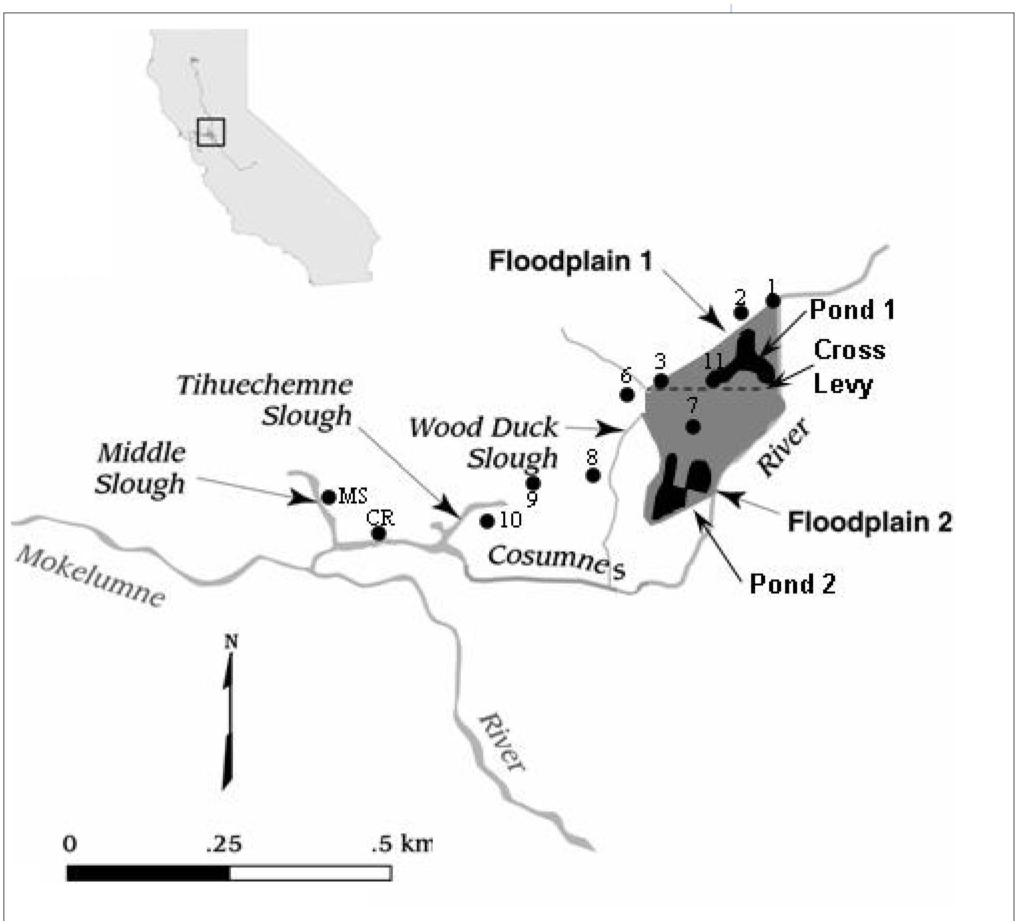

Figure 1. Map of study area. Sites of the main sampling areas are numbered 1 through 11, centering around ponds that were left after flooding ceased. During flooding, water entered breaches in these areas and flowed out through Wood Duck and other sloughs, depending on the extent of flooding. During high flow events virtually the entire area shown in the map was flooded, but during small events flooding was confined to grey areas. Actual location of sampling sites varied with the extent of flood waters, but remained in the general vicinity of the numbers.

gent vegetation. Their most important characteristics were accessibility and lack of dense vegetation, so they could be sampled with a 10 m bag seine.

When flooding occurred during the study period, water flowed through breaches in levees that separated the river from the CRP (Florsheim and Mount 2002, Booth et al. 2006). The first and largest breach delivered water into a leveed area (Floodplain 1, Figure 1) that centered around a shallow (1-2 m) depression (Pond 1); the pond so created was 1-2 ha in extent, depending on the amount of flooding. The water from this pond either flowed back into the river through another breach about 100 m downstream from the first breach or flowed parallel to the river into a second floodplain area (Floodplain 2), to which it was connected through another levee breach. Floodplain 1 was covered with diverse annual vegetation that was mostly dead during the early flooding season, although various grasses and small herbaceous plants grew on the floodplain as the water receded later in the season (and were often flooded by later events). Pond 1 often held water well into the summer; its clay bottom was consequently relatively free of vegetation during the flooding season.

The Floodplain 2 area also centered around a pond (Pond 2), 1-2 ha in extent, from which the flood waters flowed back into the river either directly through a breach or through a ditch connecting the pond to Wood Duck Slough. During high flow events, water inundated the fields and forests surrounding the ponds and there was overland flow in many directions, connecting ponds, ditches, and sloughs throughout the CRP.

Pond 1 was originally constructed as a source of earth for a levee and to hold water for waterfowl. It is adjacent to the two uppermost levee breaches. During this study, it became partially filled with sand carried in by the river (Forsheim and Mount 2003). In most years of the study, it held water though July and then dried up. When disconnected, maximum depth was about 1.5 m, and it became progressively shallower as it dried. Pond 2 was also constructed for waterfowl and had a narrow channel connecting it to Wood Duck Slough. An earthen dam constructed on the slough (to provide water for irrigation of fields of neighboring farms)

Table 2. Extent of flooding, Cosumnes River Preserve, 1998-2002. The timing of first flooding is the week in which water first flowed through the upper levee breach and on to the floodplain. The timing of the last connection is when water ceased flowing through the breach for the last time. The number of floods is the number of high-flow events that brought more water on to the floodplain following a disconnection. % flooding refers to approximate percentage of floodplain on the Cosumnes River Preserve covered with water at the maximum extent of flooding, compared to 1998, the wettest of the eight years.

Year	Week/Month, first flooding	Week/Month, last connection	No. days connected	No. of floods	% flooded	Pond #1 dry in late summer?
1998	2wk/Dec	4wk/June	158	3	100	No
1999	3wk/Jan	4wk/May	104	7	100	No
2000	4wk/Jan	3wk/May	63	7	20	Yes
2001	4wk/Feb	4wk/Apr	6	1	5	Yes
2002	5wk/Dec	2wk/Apr	22	5	10	Yes
2003	3wk/Dec	4wk/May	37	3	15	Yes
2004	1wk/Jan	1wk/Mar	15	3	10	Yes
2005	5wk/Dec	5wk/May	121	7	65	Yes

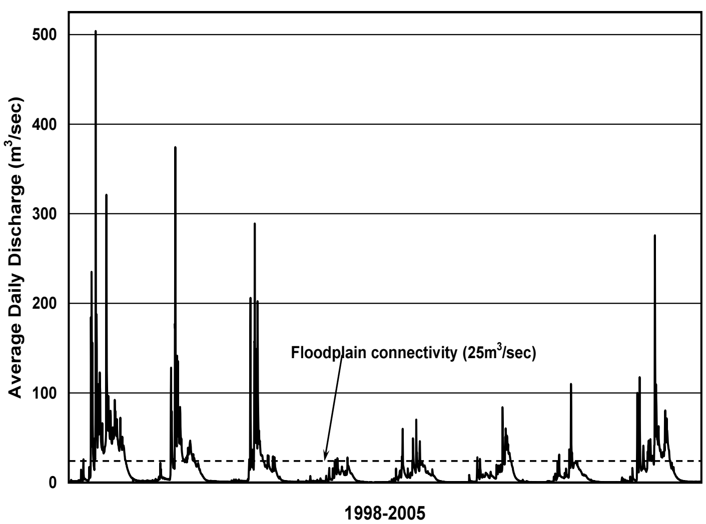

Figure 2. Hydrograph of the Cosumnes River at the USGS gauging station at Michigan Bar, 1998-2005. The dotted line indicates flows at which water entered the floodplain from the river.

usually backed water up into the pond in late summer. Pond 2 thus rarely dried up completely, but its irregular fluctuations supported fairly dense growths of annual plants around its edge. The pond was usually small and shallow (<1m deep) by late summer, with beds of aquatic macrophytes. Maximum depth was around 2 m when flooded.

Flooding occurred every year on the CRP, but the extent varied among years (Booth et al. 2006; Table 2, Figure 2). Flooding generally began following the first hard winter rains with the last connection between river and floodplain occurring any time from early March to mid-May. The number of days of connection varied from 6 (2001) to 158 (1998). 1998 was a very wet year, and flooding was nearly continuous from mid-February through late June. In both 1998 and 1999, most of the CRP flooded during peak events and water remained in ponds on the floodplain throughout the summer. During other years, typically only the sections of the CRP nearest the river flooded, mainly below a low levee designed to reduce flooding of rice paddies. In the drier years (2001, 2002, 2004), the periods of flooding were short because connections between the river and floodplain were intermittent and highly variable in timing (Table 2). Flooding was largely confined to filling the two ponds and nearby surrounding areas of annual vegetation.

Primary production in flooded areas was mainly driven by periodic connection and disconnection of the floodplain to the river channel (Ahearn et al. 2006). Peak chlorophyll-a levels on the floodplain occurred after inflow to the floodplain ceased, but flooding was still extensive. The distribution of chlorophyll-a was controlled by the residence time of water and local physical and biological conditions, which were primarily a function of the depth of water. When river flows increased and reconnected to the floodplain, complex mixing would result along with replacement of older floodplain waters. Where floodplain waters were not remixed or replaced, localized hypoxia occurred, creating unfavorable conditions for fish (Jeffres 2006).

Overall, the complex mixing and distribution of waters over the flooding season helped to create a diverse and productive floodplain ecosystem (Ahearn et al. 2006).

Because of high algal (primary) production, secondary production (zooplankton and aquatic insects) also was high during the early portion of the flooding regime (Grosholz and Gallo 2006). As soon as larval and juvenile fish became abundant (April, May), large zooplankton species became less abundant (presumably from fish predation) while smaller zooplankton maintained similar levels to early flooding levels. Late in the season large zooplankton again became abundant as larval fish (now small juveniles) switched their diet to aquatic insects and migrated off the floodplain into the river channel (Grosholz and Gallo 2006).

METHODS

Sample Sites

During each year, sampling began as soon as water entered the floodplain and continued until after flooding stopped, although extent of post-flooding sampling varied by year (Table 3). Sampling was most extensive in 1998-2002, mostly at one to two week intervals, and produced most of the data used in analyses for this study. Sampling in 2004 and 2005 was largely confined to short periods following flood events and the results are presented mainly for comparative purposes; we wanted to make sure the patterns observed in the first five years of the study were predictable. Because of the differences in sampling effort, the results of the 2004 and 2005 sampling are presented only in Appendix Table A1.

Table 3. Years and months in which different sampling programs were present on the Cosumnes River Preserve. Results of larval fish sampling are reported in Crain et al. (2004).

Year	Larval fish	Seining	Electrofishing
1998	None	March-June	None
1999	Feb-August	Feb- August	None
2000	April-July	Feb-July	Feb-June
2001	Feb-July	Feb-July	Feb -May
2002	None	Feb-June	Feb -May
2003	None	None	None
2004	None	Feb-May	None
2005	None	Feb-June	None

Sampling focused on the floodplains surrounding the two ponds. When flood waters entered the study area, these ponds became the centers of two areas that were separated by another levee and a ditch. The levee had two breaches through which the water flowed from the Pond 1 area to the Pond 2 area. As flooded areas expanded in size and depth, the areas we sampled also expanded, especially because areas suitable for seining progressively shifted back and forth across the floodplain. We had basically 10 sampling sites (Figure 1) that were used as water levels rose and fell. Thus sites 7 and 11 were used mainly at low water levels, while 1, 2, and 6 were used during high water events. Sites 8-10 were located in forested areas and were sampled sporadically only in extreme flood events. Fish were considered stranded on the floodplain when sampling was only possible at sites 7 and 11 and when the two ponds stopped draining into the river.

For comparison with the floodplain samples, we also sampled edge sites on Middle Slough and on the Cosumnes River in 2000, 2001, and 2002 (Figure 1). Both sites were downstream from the flooded areas and represented principal routes of movement of fish off the floodplain as well as sites with permanent populations of fish. The same general sites could be fairly consistently sampled although actual locations for seining moved up and down the banks as the flood waters rose and fell. The year 2000 was the wettest of three (Table 2) and had 63 days of connection (inflow) to the river; this was close to the mean number of connection days (66, n = 8), so this year was used to illustrate patterns of fish movement on and off the floodplain.

Sampling Methods

The two major methods for sampling juvenile and adult fishes were seining and electrofishing. Seining was with a 7 mm mesh, 10.5m x 1.5m seine with 1x1x1 m bag and was the principal sampling method in all years. At each site, the net was set a minimum distance of 10 m from shore and stretched to its full length. Seiners pulled the net to shore in a standard fashion that enabled the area sampled to be estimated.

Sampling effort varied according to the amount of habitat available for sampling; we generally made seine hauls until we were satisfied we had adequately sampled the available area. As a result, the number of hauls made was higher in years of extensive flooding than in drier years.

Once the net was on shore, fish were removed and placed live in buckets. All fish were identified to species and measured (SL), until 50 individuals of each species were measured. For purposes of analysis "adult/yearling" fish for all species but inland silverside and western mosquitofish were considered to be individuals >60 mm SL, while young-of-year (YOY) were fish <60 mm SL. The few inland silverside, mosquitofish, and small (< 60 mm SL) bluegill that were present on the floodplain in February through mid-April were placed in the adult/yearling class regardless of size because there was no evidence of spawning by these fish in this period (Crain et al. 2004). After mid-April, all silversides and mosquitofish were counted as YOY. All salmon were counted as YOY because they grew rapidly on the floodplain to > 60 mm SL (unpublished data).

Fish that were not measured were counted by species and length category (YOY or adult/yearling) and returned to the water. Location of sample sites varied from time to time and year to year, depending on the extent of flooding, which regulated our ability to sample most areas. However, we consistently sampled areas in general localities (Figure 1). Sampling was done weekly. At each site, temperature (°C), conductivity (µs), and water clarity (Secchi depth, cm) were measured. In 2000 and 2002, continuous temperature recorders (Hobotemps) were located near most seining sites. Physical data is summarized in Appendix Table A3.

Habitat type sampled was recorded as floodplain, slough, slough margin, river, river margin, pond, old-growth riparian forest, recent forest (<30 years old), or farm field, although only the floodplain, pond, slough margin, and river margin categories were systematically sampled for use in the principal study. Floodplain and pond data were lumped together for the final analysis because floodplain habitat became pond habitat at the end of the flooding season each year. Other areas were qualitatively checked for fish as the situation allowed, usually by electrofishing. Substrate was recorded as presence of the dominant type: soft mud, mineral mud (sand and mud), sand-silt, sandy-gravel, gravel, cobble-rock, and clay. Six categories of cover for fish were each classified on the following scale: 0 = none, 1= some (<50%), 2 = dense (>50%) in the sampling area. The categories of cover were (1) annual vegetation (grasses, cockle burrs, herbaceous plants etc.), (2) woody debris, (3) woody vegetation (bushes and trees), (4) aquatic vegetation (floating and submerged recorded separately), (5) filamentous algae, and (6) emergent vegetation.

Electrofishing was performed in 2000, 2001, and 2002 with a shallow draft 5 m boat upon which was mounted a 5.0 GPP Smith-Root electrofishing array, including two 2-m long booms with a SA-6 umbrella anode arrays and bar array type cathode. The boat electrofisher sampled fish effectively at depths of 0.5-2.0 m. Current used for shocking was adjusted for conductivity but was normally 600 volts and 4 amps. Electrofishing was most effective for capturing fish over 10 cm TL but smaller fish were also captured. Fish (mainly common carp) over 45 cm often escaped by swimming out of the electrical field before they could be captured. Fish were captured by a person standing in the bow of the boat with a long-handled (1.5-2 m) dip net. All fish were placed in a large container of water after being captured. Fish were then measured (SL) and returned to the water. Electrofishing time varied from 2 to 5 minutes at each station because the focus was on sampling a fairly uniform section of habitat (e.g., marsh edge, open water, patches of vegetation). Because of fluctuating water levels, station locations were variable, but efforts were made to sample all types of habitat accessible by the boat in a haphazard manner. At each station, the same habitat variables were measured or estimated as for seining.

Classification

Fish were classified initially as rheophilic, eurytopic, or limnophilic based on information in Moyle (2002). Assignment to one of the five new categories was based on the following criteria:

(1) Floodplain spawner. This designation required evidence of annual spawning on the floodplain as a

reproductive strategy (Moyle 2002), followed by rearing of early life history stages on the floodplain (Crain et al. 2004, Table 1) and departure from the floodplain as inflow declined.

(2) River spawner. These were fishes known to require riverine conditions (usually gravel riffles) for spawning (Moyle 2002) and whose larvae or small juveniles appeared on the floodplain in abundance and appeared to rear there, as indicated by their presence through much of the flooding period. They generally were able to leave the floodplain as water levels dropped.

(3) Floodplain forager. Fish in this category were typically common on the floodplain throughout the flooding season and usually appeared in small numbers soon after the first flood event. While they did not require floodplains for completion of their life history (Moyle 2002), they appeared to take advantage of abundant food resources in the temporary habitat. While individuals were often stranded, it appeared that most returned to the habitat (sloughs) in which they were found for the rest of the year.

(4) Pond fish. This category was reserved for small, short lived fishes that could build up large populations in floodplain ponds even after the ponds became isolated from the river. Most died as the ponds dried up or were consumed by predatory birds (e.g., white pelicans, herons) that were attracted to the ponds.

(5) Inadvertent users. Species in this category were uncommon and highly erratic in occurrence on the floodplain. They presumably were species that got carried on to the floodplain by accident and had no particular adaptations for persisting there.

Statistical Analyses

The data sets will be available on-line through the Interagency Ecological Program web site (http://baydelta.ca.gov/). Monthly succession of YOY species was first explored graphically. We then analyzed the relationship between species abundance (total number of individuals of each species) and environmental variables (Julian day, temperature, conductivity, water clarity, habitat types, substrate types, cover types) using Canonical Correspondence Analysis (CCA), using the data from all years. Separate analyses were run on YOY fishes and adult fish because of differences in floodplain use between the two groups. Species that comprised less than 1% of the total number of fish caught were excluded from the analysis. All environmental data was ln(x + 1) transformed prior to analysis. The species counts were ln(x + 1) transformed, and rare species were down-weighted within the CANOCO 4.5 program (ter Braak and Smilauer 2002). Using the forward selection mode in CCA, a model with six variables was developed for YOY fishes and a model with five variables for adult fishes. Significance of the first

Table 4. Percent abundances of young-of-year of the most common species on the Cosumnes River floodplain during three periods: 1. February-March, 2. April-May, 3. June-July. The * indicates alien species. No samples were taken in period 3, 1998.

	1998			1999			2000			2001			2002		
Period	1	2	3	1	2	3	1	2	3	1	2	3	1	2	3
N	157	1671	-	15	1600	4845	2	15534	4936	109	27545	6273	3	5480	373
Seine hauls	107	84	-	30	29	19	53	52	16	39	40	16	40	37	7
Species	%														
Splittail	87	82	-	0	4	8	0	34	3	0	66	5	0	71	0
Golden shiner*	0	0	-	0	3	11	0	19	12	0	<1	4	0	8	13
Common carp*	0	0	-	0	23	40	0	38	6	0	28	2	0	3	4
Sacramento sucker	0	13	-	0	48	10	0	4	1	0	5	0	0	8	0
Chinook salmon	8	2	-	100	6	0	100	0	0	100	0	0	100	0	6
Inland silverside*	0	0	-	0	0	14	0	1	31	0	0	82	0	4	51
Western mosquitofish*	0	0	-	0	0	17	0	2	41	0	0	7	0	5	26
Black crappie*	0	0	-	0	14	0	0	2	6	0	<1	0	0	0	0
Other species	5	3	-	0	2	<1	0	<1	<1	0	<1	<1	0	1	<1

two canonical axes was tested using Monte Carlo permutations built into the Canoco 4.5 program.

RESULTS

Over seven years of sampling, 32 species of fish were captured in the floodplain, slough, and river. During the five years of intensive sampling, 15 species occurred in all years in the river, sloughs, and floodplain (Table 1). However, only 12 species were consistently abundant enough (more than 1% of fish collected) to contribute to analyses of trends and habitat use as YOY or as yearlings/adults (Table 1). Four of the abundant species were natives, while eight were aliens. YOY fish were captured primarily in the seining samples, while large adult fish were taken mainly in the electrofishing samples. Both types of sampling captured yearling fish and small adults. Most of the fish captured in the floodplain at the end of the study (May-June) were in isolated ponds and were stranded there; most did not make it through the summer either as the result of predation, the ponds drying up, or harsh physical conditions (unpublished observations).

Young-of-Year

Floodplain

Over seven years of sampling, there was a fairly predictable succession of YOY fishes, although there was variation in the timing of their appearance and disappearance. In general, native fishes predominated early in the flooding season, while alien species predominated at the end. This succession is obvious when catch data are lumped together for two-month intervals (Table 4) but is also clear in the progression of fish in monthly (Figure 3) and weekly data summaries (Appendix Tables A2-A6). In February and March, rheophilic Chinook salmon dominated catches, although splittail (eurytopic) appeared in some late March samples (Table 4, Figure 3). Splittail YOY typically dominated catches in April and early May, except in 1999 when they were largely absent from the floodplain. Other YOY that usually appeared at this time were common carp (eurytopic) and Sacramento sucker (rheophilic). During May, splittail became less abundant (except in 1998, an exceptionally wet year), suckers and common carp increased in abundance, and juvenile golden shiners and other alien species started to make their appearances. In June, small numbers of splittail persisted in wet years (1998, 1999) but most left the floodplain before it became disconnected from the river (Table 4).

Following disconnection, the water warmed up and alien, limnophilic species increasingly dominated the YOY catches (Figures 3, 4, 5). By late June and July, inland silverside and western mosquitofish, both with very short generation times (Moyle 2002), were the most abundant fishes in isolated floodplain ponds, which often became dry or only a few cm deep by August, killing all or most of the fish remaining.

Despite this general pattern, there were differences in timing and abundance of YOY fishes from year to year (Table 4, Appendix Tables A2-A6). Some species, such as

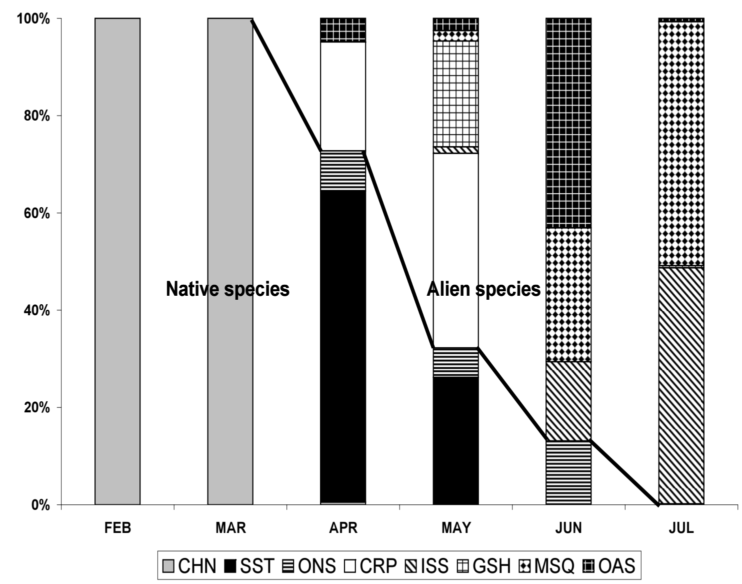

Figure 3. Monthly changes in the percent abundance of the most abundant juvenile fishes on the Cosumnes River floodplain, for the year 2000. Patterns were similar in other years, but 2000 was chosen to represent more or less average number of connection days (66, n = 8) during the study period. The line connects the dividing line between native and alien species for each month. CHN = Chinook salmon, SST = splittail, ONS= other native species, CRP = common carp, ISS = inland silverside, GSH = golden shiner, MSQ = western mosquitofish, and OAS = other aliens.

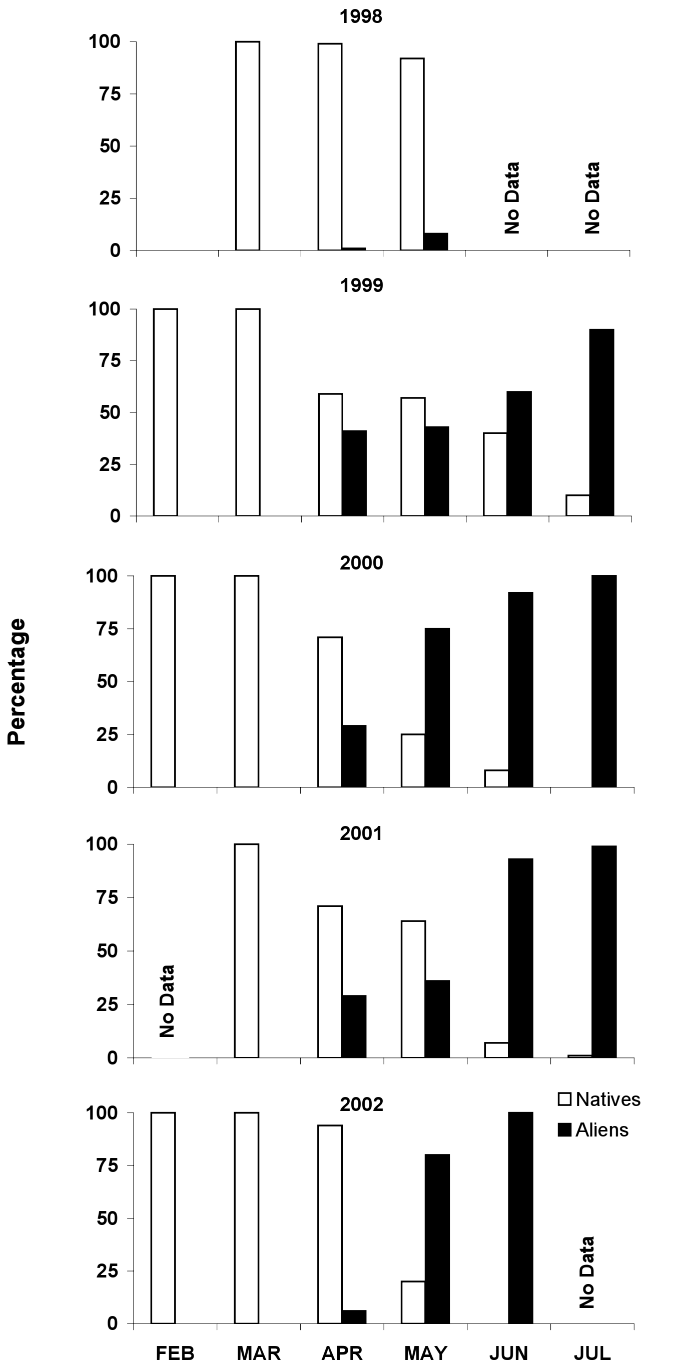

Figure 4. Percentages of juvenile native and alien fishes in seine hauls, by month, Cosumnes River floodplain, 1998-2002.

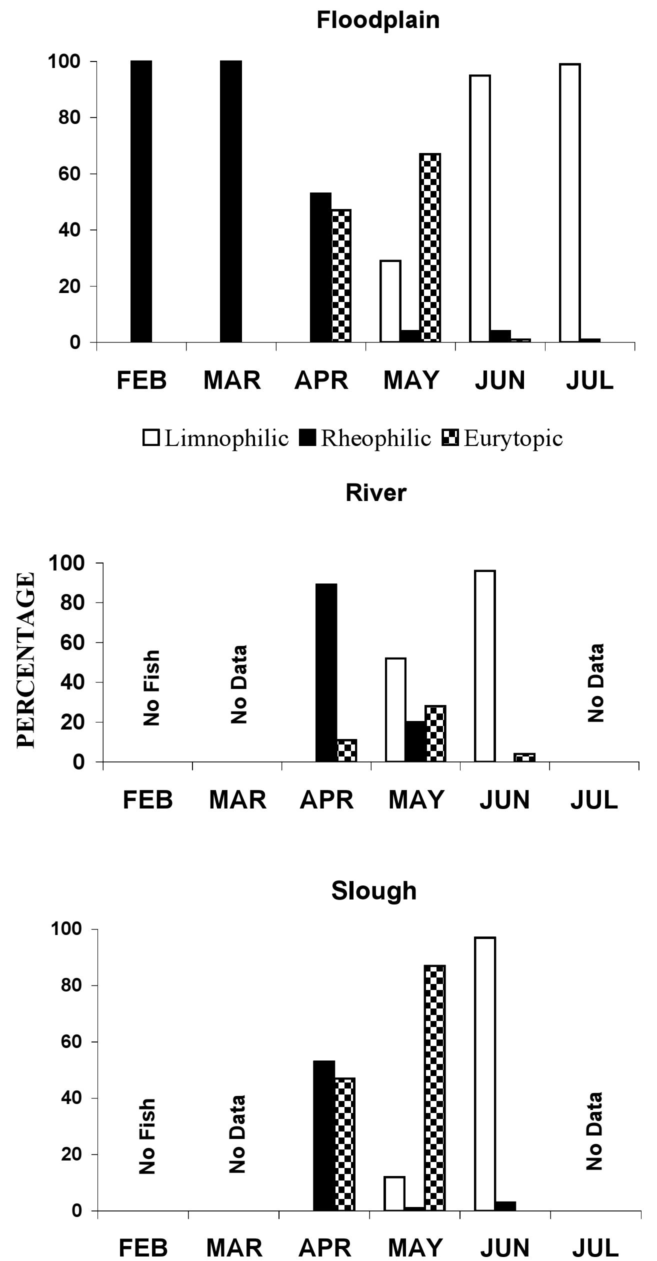

Figure 5. Percentages of rheophilic, limnophilic, and eurytopic fishes taken in seines in floodplain (N = 52 hauls, 24.263 fish), river (N = 11 hauls, 347 fish), and slough (N= 10 hauls, 1,860 fish) habitats, year 2000. No sampling was done in river and sloughs in February and March.

golden shiner, were common in some years but uncommon in other years. Other species, such as rheophilic Sacramento pikeminnow, were fairly consistently found from year to year but only in low numbers.

The pattern of occurrence for many fishes reflected the length of time the floodplain was connected to the river. In 1998, 1999, and 2005, which had long periods of connection, YOY Chinook salmon persisted on the floodplain through April; they were gone by late March in the other years. In 1998, splittail YOY appeared in March (indicating spawning on the floodplain a month earlier) and were still present in large numbers when sampling ended in late May. In 1999, YOY splittail first appeared in May and persisted through June but only in low numbers, despite apparently highly favorable conditions. This pattern of a strong spawning year followed by a weak one, even under favorable conditions, was noted in the Yolo Bypass as well (Moyle et al. 2004). During 2000-2002 and in 2005, splittail YOY were found mainly in April and May, although adults appeared on the floodplain as early as February.

Sloughs

YOY captured in Middle Slough in March were primarily Chinook salmon. In April and May YOY were mainly splittail, suckers, and carp, usually with sharp peaks of abundance (eurytopic fishes, Figure 5), suggesting that these were fish leaving the floodplain when water either was flowing across the floodplain or draining pond 2. The lengths of the fish in the river and sloughs were also coincident with those of larger fish on the floodplain (Ribeiro et al. 2004). YOY of limnophilic species dominated the catches in later months.

River

In the Cosumnes River, the pattern of YOY succession was similar to that of the sloughs although it reflected both fish leaving the floodplain and fish coming down from upstream areas. Thus the shift from riverine fishes to other fishes tended to be stronger (Figure 5). Some alien fish present in our river samples were species rarely found on the floodplain (e.g., American shad, channel catfish).

Overall Patterns

The patterns just discussed show strong seasonal changes in YOY species in the floodplain, river, and slough and indicate that most native fishes left the floodplain, took up temporary residence in the river and sloughs and then left the region, or were eaten by predators. In the CCA model for the seven most abundant YOY fishes, the variables selected were: Julian date, maximum depth, annual vegetation, submerged vegetation, conductivity, and organic mud substrate (Figure 6, Table 5). Because the first and second axis together explain the most variance (24% and 3% respectively), the third and fourth axis were not interpreted. Monte Carlo tests run for YOY fish groups resulted in the first axis and the full model being significant (axis 1, F ratio = 31.7, p = .002, full model, F ratio = 3.5, p = .002). Julian date was the most explanatory variable because of the strong shift in abundance of different fish species through the flooding season. Late season YOY fishes (western mosquitofish, golden shiner, inland silverside, black crappie, and Sacramento blackfish) tended to be found in shallow water associated with ponds, while common carp and splittail were found in cooler, deeper water with lots of submerged annual vegetation, associated with sustained flooding (Figure 6). Sacramento sucker YOY, being washed in from the river, tended to be found in clear cold water early in the flooding season.

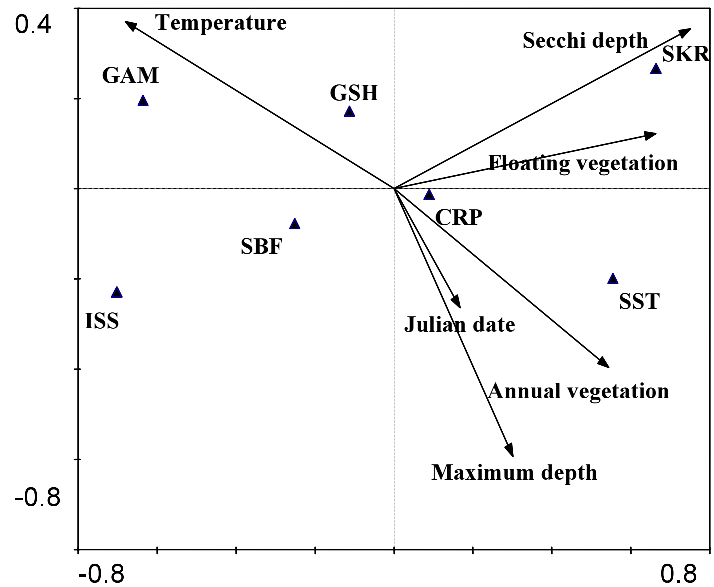

Figure 6. Canonical correspondence ordination diagram showing the relationships of YOY fish to environmental gradients. Species codes are SBF = Sacramento blackfish, SST = Sacramento splittail, GSH = golden shiner, CRP = common carp, SKR = Sacramento sucker, ISS = inland silverside, and MSQ = western mosquitofish, BCR = black crappie.

Table 5. Results of CCA analysis for relationships between catch of young-of-year fish (top) and adult fish (bottom). The canonical coefficients represent the contribution of individual environmental variables to the definition of ordination axes.

Young of Year			coefficients	
Axes	Axis 1	Axis 2	Axis 1	Axis 2
Eigenvalues:	.290	.040		
Species-environment correlations:	.843	.524		
Cumulative percentage variance				
of species data:	24.1	27.4		
of species-environment relation:	72.5	82.4		
Maximum depth			.052	.352
Floodplain			.083	.396
Organic Mud			.003	.442
Annual vegetation			.091	-.199
Submerged vegetation			-.189	-.420
Conductivity			-.170	-.201
Julian Date			-.949	.383
Adults				
Axes	Axis 1	Axis 2	Axis 1	Axis 2
Eigenvalues:	.255	.209		
Species-environment correlations:	.664	.616		
Cumulative percentage variance				
of species data:	9.2	16.7		
of species-environment relation:	48.4	88.0		
Floodplain pond			-.356	.507
Mineral mud			.100	.784
Filamentous algae			-.222	-.071
Conductivity			-.670	-.205
Secchi depth			-.311	.230

Adults and Yearlings

Using seining and electrofishing together, we captured 22 species of adult fish on the floodplain. The seines mostly caught smaller species (golden shiners, western mosquitofish) or yearling fish, especially centrarchids, usually in fairly small numbers. The electrofisher was set up to capture larger fish because we were looking for spawning adults, but by number our catches tended to be dominated by fish 8-20 cm SL, mainly golden shiners and centrarchids (Table 6). Despite these differences in catch, the basic pattern observed every year with both kinds of gear was similar to that of YOY. Small numbers of fish appeared in our floodplain samples in February; such fish presumably came in as early as December, with the first flooding. They were mostly species resident in sloughs (e.g., golden shiners, bluegill, western mosquitofish) or fish washed in from the river (prickly sculpin, yearling Sacramento pikeminnow). Recently transformed Pacific lampreys moving downstream were caught with the early high flows both in our regular samples and in fyke nets set in floodplain channels (unpublished data). In late February and March, ripe adult splittail, common carp, and goldfish moved into flooded areas and were usually present through April (Table 6). Adult Sacramento suckers also moved in at this time, apparently in process of moving upstream to spawn. Adult common carp and goldfish frequently became stranded with falling water under fluctuating conditions, but adult splittail usually moved off the floodplain before they became trapped, as indicated by the low numbers found in April (Table 6).

During flooding periods in April and May, numbers of yearling and adult fishes steadily increased as more fish moved from the rivers or out from the ponds. Thus adult suckers, mostly fish spent from spawning, came in from the river, as did immature Sacramento pikeminnows (8-12 cm SL), and, in some years, mature blackfish and hitch. Fairly large numbers of golden shiners and various sizes of centrarchids moved out from the ponds and sloughs to forage if water temperatures exceeded 20°C for an extended period of time (unpublished data).

The CCA model for adults and yearlings included secchi depth, floodplain pond, filamentous algae, mineral mud, and conductivity (Figure 7, Table 5). Because the first and second axes together explain the most variance (9% and 7%, respectively), the third and fourth axes were not interpreted. The model was significant for both the first axis and the full model, with (axis 1, F ratio = 11.7, p = .002; full model, F ratio = 1.8, p = .002). The model showed that black crappie, western mosquitofish, bluegill, and inland silverside were associated with shallow ponds late in the season, although inland silversides were most abundant at stations where the bottom was predominately mud (i.e., little vegetation). Yearling Sacramento pikeminnows and golden shiners, in contrast, appeared to be responding to early flooding, characterized by lower conductivity and lower water clarity.

Table 6. Adult and yearling fish captured by electrofishing on the Cosumnes River floodplain, February-April, 2000-2002. Chinook salmon were YOY. % is the percentage of the total number of fish for all three years.

Species	Year	Total #	%	Feb.	Mar.	Apr.
Threadfin shad	2000					
	2001					
	2002	3	<1		3	
Hitch	2000	6	1	1	1	6
	2001	4	<1	0	2	2
	2002	8	1	0	7	1
Sacramento blackfish	2000	3	<1	2	0	1
	2001	10	1	2	6	2
	2002	5	<1	0	1	4
Sacramento splittail	2000	12	2	8	3	1
	2001	30	4	13	14	3
	2002	19	3	3	11	5
Sacramento pikeminnow	2000	23	10	6	10	17
	2001	6	2		5	1
	2002	17	4	1	14	2
Golden shiner	2000	51	7	22	11	18
	2001	34	5	10	17	7
	2002	114	16	8	83	12
Goldfish	2000	11	3	1	3	7
	2001	12	4		8	4
	2002					
Common carp	2000	20	3	3	6	11
	2001	53	7	9	40	4
	2002	103	14	8	23	12
Sacramento sucker	2000	78	11	11	31	36
	2001	11	2	3	3	5
	2002	17	2	1	10	6
Black bullhead	2000	2	<1		2	
	2001	2	<1		2	
	2002	2	<1	1	1	
Chinook salmon	2000					
	2001	1	<1	0	1	0
	2002					
Inland silverside	2000	2	<1	0	2	0
	2001	95	13	9	82	4
	2002	1	<1	0	1	0
Western mosquitofish	2000	2	<1	0	2	0
	2001	1	<1	1	0	0
	2002	1	<1	0	1	0
Prickly sculpin	2000	3	<1	1	2	
	2001	12	4		12	
	2002	4	1	2	1	1
Bluegill	2000	56	17	33	18	5
	2001	24	7		21	3
	2002	98	25	7	69	22
Redear sunfish	2000	16	5	13	1	2
	2001	4	1		2	2
	2002	41	10	6	31	4
Black Crappie	2000	13	2	5	2	0
	2001	8	1	0	2	6
	2002	19	3	4	13	2
Largemouth bass	2000	12	4	1	1	10
	2001	11	3	1	7	3
	2002	28	7	1	19	8
Bigscale logperch	2000	5	1		1	4
	2001	7	2	1	3	3
	2002	8	2	3	3	2

Stranding

To examine the problem of stranding of fish on drying floodplains, we looked at the number of fish left in the two main ponds after the floodplain completely stopped draining (Table 7). This occurred roughly 5-6 weeks after the last inflow to the floodplain ceased. In the four years with adequate data (sampling ceased in 1998 before draining stopped), the majority of stranded fish were alien species: inland silverside, western mosquitofish, golden shiner, and common carp. The inland silversides and western mosquitofish developed large populations in the isolated ponds from natural reproduction of stranded adults (Moyle 2002). YOY of native cyprinids, including splittail, were stranded in only small numbers in most years. The comparatively large numbers of splittail stranded in 2001 seemed to reflect the intermittent conditions of inflow to the floodplain. The periodic disconnection resulted in fish being concentrated in shrinking ponds

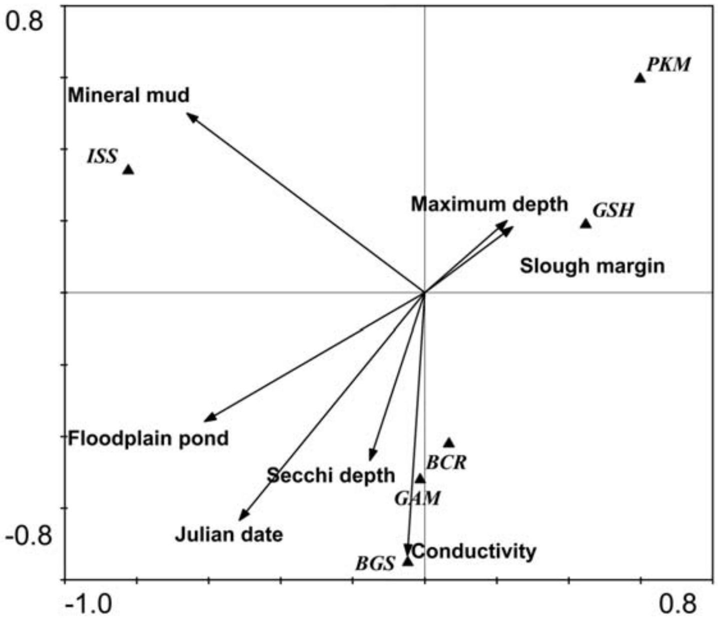

Figure 7. Canonical correspondence ordination diagram showing the relationships of catches of adult and juvenile fishes to environmental gradients. Species codes are the same as in Figure 6, with the addition of: PKM = Sacramento pikeminnow, BGS = bluegill, and CHN = Chinook salmon.

and having few and relatively short opportunities to escape to the river. Even in 2001, however, only a small percentage of splittail YOY became stranded (Table 7).

Relatively few adult fish were found in the ponds after disconnection (unpublished data). While 8-10 species of fish were present in these ponds and surrounding floodplain during flooding, most of the larger fish disappeared as the ponds became isolated and the water became progressively warmer, shallower, and more turbid. Some of this was due to predation; large flocks of white pelicans were observed feeding in the ponds in some years, and carcasses of common carp and catfish eaten by otters were common on pond edges.

The ability of floodplain-adapted fish to avoid stranding is illustrated by the events in Pond 1 in 2000 (Appendix Table A4). When the pond level dropped prior to disconnecting from the river in early May, we captured large numbers of YOY splittail and common carp. Most these YOY were gone by the following week, apparently leaving with the draining water. For the next three weeks, catches of YOY were low and variable, mainly a few splittail. As daytime temperatures rose (from roughly 20°C to 25°C daily maximum), YOY of golden shiners, western mosquitofish, and inland silversides increasingly made up the catch. By July, almost all the catch consisted of inland silversides and western mosquitofish.

Table 7. YOY fish caught in isolated ponds on the Cosumnes River floodplain, after all connection to the river was lost. The date used for stranding is six weeks after all inflow into the floodplain had stopped. Percent stranded is the percentage of individuals from the catch for the entire flooding season that were captured after the stranding date. Composition is the percent of each species present in all samples taken after the stranding date. Native species are in bold.

Species	Year	Stranding date	N	Stranded (%)	Composition (%)
	1999	July 1			
Hitch			86	81	2
Sacramento blackfish			359	80	7
Sacramento splittail			50	11	1
Golden shiner			425	73	9
Common carp			1551	56	31
Inland silverside			1601	90	32
Western mosquitofish			843	86	17
	2000	July 1			
Inland silverside			774	46	49
Western mosquitofish			800	34	50
	2001	June 1			
Sacramento splittail			322	2	5
Golden shiner			227	65	4
Common carp			123	2	2
Inland silverside			5060	97	79
Western mosquitofish			407	55	6
Prickly sculpin			77	41	1
Black crappie			75	39	1
	2002	May 20			
Sacramento blackfish			78	51	7
Sacramento splittail			64	2	6
Golden shiner			177	36	15
Common carp			30	15	3
Inland silverside			372	97	32
Western mosquitofish			364	90	32
Prickly sculpin			28	28	2
Bigscale logperch			26	96	2

DISCUSSION

What Kinds Of Fish Use The Floodplain?

Of the 32 species we collected over seven years in floodplain, river, and slough habitats, 25 were found on the floodplain. Nine of the floodplain species were inadvertent users although most of these species were common in the river or sloughs (Table 1 and Crain and Moyle, unpublished data). The only inadvertent user consistently collected was Pacific lamprey, which was found every year as transformers migrating out to sea. The 16 species captured on a regular basis were about equally divided among rheophilic, eurytopic, and limnophilic species, although rheophilic species dominated at the beginning of flooding season and limnophilic species dominated at the end (Figure 5). Four species were floodplain spawners and YOY of one native species, splittail, were among the most abundant fish in most years. Splittail were also the only obligate floodplain spawner we found. The other three, common carp, goldfish, and Sacramento blackfish, generally spawn on submerged vegetation but do not seem to require flooded areas *per se*.

There were six species of river spawners whose juveniles moved (or were carried) on to the floodplain and reared there for several weeks (Table 1). Five species (golden shiner, bluegill, redear sunfish, black crappie, and largemouth bass) apparently moved on to the floodplain, mostly as yearlings, as floodplain foragers; they were often found fairly early in the season and were widely distributed on the floodplain. Adults of these species occasionally spawned in temporary floodplain ponds late in the season. In their native habitats, these species are opportunistic floodplain spawners during extended periods of flooding in early summer. Two limnophilic pond/lake species with short generation times, inland silverside and western mosquitofish, typically dominated the shallow, seasonal floodplain ponds and were often stranded as the ponds dried up.

What this diversity of floodplain users shows is that different species use floodplains for different reasons, but relatively few species (e.g., splittail) depend on floodplains for persistence. It is also evident that many of the species found in numbers on floodplains, especially native species, have behavioral adaptations that allow them to take advantage of floodplains while also avoiding being stranded by receding water. Not surprisingly, the two groups of native fish that use the floodplain most extensively are floodplain spawners and river spawners that use the floodplain during peak flooding periods (February through mid-April). For YOY of floodplain-adapted species such as splittail and Chinook salmon, the floodplain represents habitat that promotes rapid growth, presumably resulting in increased survival when they migrate to other habitats (Sommer et al. 2002, Ribeiro et al. 2004). The species that use the floodplain as inflow diminishes and water temperatures rise later in the season (mid-April through June) are mainly alien species that move onto the floodplain to forage and, if the water persists, to spawn.

How Does Fish Use Of The Floodplain Change With Season And Flow?

There was a fairly consistent pattern of floodplain use by fish over the five-year period of intensive study, although the basic pattern was modified on an annual basis by the extent and timing of flooding. The first fish to appear on the floodplain, typically in February, were a few individuals from ponds and ditches (e.g., golden shiner), some inadvertent species (e.g., Pacific lamprey), and juvenile Chinook salmon, moving in from the river. The next fish to appear were adult floodplain spawners, principally splittail and common carp, which spawned on flooded annual vegetation, although small numbers of species resident in ponds and neighboring sloughs were continuously present. YOY splittail and carp quickly became large enough to dominate floodplain fish samples, along with YOY suckers and pikeminnows moving in from the river. The adult spawners disappeared from the floodplain as inflow decreased and the water became clearer and warmer. YOY persisted on the floodplain as long as occasional new pulses of flood water kept water levels up and temperatures down, but most YOY native fishes left the floodplain either with the pulses or with declining inflows. Most were gone by mid-May but some persisted through June if conditions favored their presence. Usually, the floodplain became disconnected from the river by mid-May. In two large shallow ponds of residual water (Ponds 1 and 2), western mosquitofish, inland silverside, and, to a lesser extent, YOY centrarchids dominated catches by June. The first two species can reproduce and reach maturity quickly, so can build up large populations in a short period of time. The centrarchids were mainly bluegill, redear sunfish, black crappie, and largemouth bass, which were abundant in adjacent sloughs and presumably colonized floodplain ponds through individuals moving in via ditches or through spawning by stranded fish. In many years, the ponds dried up by August. If the ponds persisted, the fish that persisted in them were mainly western mosquitofish and inland silversides (unpublished observations).

What Characteristics Of Flooding And Floodplains Favor Native Fishes?

Essentially, native fishes plus common carp dominated the floodplain fish fauna early in the season while alien fishes dominated (almost completely) late in the season (Figures 3, 4). Native fishes that are abundant each year are those that have YOY that can use the floodplain for rearing but leave before the river disconnects from the floodplain. Most alien fishes have resident populations in permanent waters associated with the floodplain (sloughs, ditches, ponds) and are not dependent on the floodplain for persistence (i.e., they are widespread in many other habitats in the region). Thus, native fishes mostly used the floodplain when temperatures were cool (daily maximum<20°C) and flooding was more or less continuous. Most of the natives were resident only in the rivers or migrated onto the floodplain from other areas. The sloughs and ditches were dominated almost completely by alien fishes. Native fishes appeared in our slough samples mainly when YOY were leaving the floodplain. This same pattern was true for fishes in the river below the floodplain, although there were some additional river species present that were rarely found on the floodplain.

An interesting exception to these general patterns is Sacramento blackfish, a large cyprinid that favors many of the same conditions as alien species. It was relatively uncommon in the Cosumnes River and its sloughs but spawned occasionally on the floodplain, fairly late in the flooding season. It is presumably a remnant of the native slough fish fauna (now displaced by alien species), including the extinct thicktail chub *(Gila crassicauda)* and the extirpated Sacramento perch *(Archoplites interruptus)* (Moyle 2002). Recent studies of the Sacramento perch indicate that it spawns on vegetation in early spring, suggesting it may have once used floodplains for spawning and rearing (C. Woodley, unpublished data).

Does Stranding Kill Large Numbers Of Floodplain Fishes?

The shallow ponds that remained at the end of the flooding season, with no or little connection to the river or sloughs, contained large numbers of small fish which often attracted flocks of fish-eating birds. The vast majority of these fish, however, were short-lived pond species (especially inland silverside and western mosquitofish) that achieved large populations through reproduction in the ponds. Remarkably few native fishes were collected in these ponds after all connections were lost, although in most years we did capture a few individuals in them, especially splittail and Chinook salmon, usually shortly after the floodplain had stopped draining. Both adults and YOY of all native species seemed to have the capacity to find their way off the floodplain before it disconnected, although in 2001 exceptionally rapid, intermittent, and early disconnection stranded more splittail than usual.

In most years, except for silversides and mosquitofish, relatively few adult alien fishes were stranded on the floodplain. We often observed large carp in isolated floodplain ponds, albeit in small numbers compared to the numbers we had observed and captured on the floodplain itself while the flood was in progress. The trapped fish were quickly captured by otters and other predators, as indicated by half-eaten carcasses along the shoreline of the ponds. In 1999, large numbers of YOY carp, apparently resulting from spawning of stranded adults, also were abundant. During electrofishing, most large alien fish from the sloughs, especially centrarchids, were captured fairly close to permanent water, suggesting that they rarely wandered far onto the floodplain and thus were less prone to stranding. However, during years in which flood waters spread widely (1998, 1999), we observed small numbers of both slough and river fish stranded throughout the flooded area as the water receded.

Is The Pattern Of Fish Use Of Floodplains Similar To That In Other Parts Of The World?

King et al. (2003) present a conceptual model of the importance of floodplains to riverine fish faunas that suggests that floodplains are most important to fish when (1) temperatures and flows are tightly coupled, (2) the annual flood pulses are predictable in timing, (3) annual flooding lasts for extended periods (months), and (4) the area of inundation is large. In large tropical rivers of Africa, South America, and Asia, temperatures show little variability, flooding has a strong predictable seasonal pattern over vast areas, and floodplains can be inundated for months at time. Not surprisingly, many fish species are adapted for using floodplains for spawning, rearing, and foraging and the floodplains are the focus of major movements of fish in and out of them (Welcomme 1979, Goulding 1980, De Graaf 2003a,b, Hogan et al. 2004). At the opposite end of the floodplain use spectrum are the rivers of Australia. In particular, in the Murray-Darling system, the continent's largest river, flooding is highly erratic in frequency and size and is largely decoupled from water temperature (King et al. 2003). Consequently, no native fishes seem specifically adapted to using floodplains although many species will take advantage of them for foraging and rearing on a limited basis (King et al. 2003, King 2004).

European rivers seem to occupy an intermediate position in the importance of flooding to fish, although most existing floodplains are small remnants of the originals, so their historic importance may have been higher (Tockner and Stanford 2002). Flooding historically occurred on an annual basis but not necessarily in a predictable fashion, often having multiple, often short, peaks during the course of a spring or summer. As a result, the ability of floods to reconnect isolated floodplain lakes to the river is regarded as one of their important attributes from a fish perspective (e.g., Borcherding et al. 2002). There seem to be few fishes that require newly flooded areas for persistence, although many rheophilic species may be in decline because of the lack of flooded areas and other shallow water habitat for rearing of their young (Buijse et al. 2002). Limnophilic and eurytopic fishes may use floodplains for spawning and rearing, but the most important function of flooding may be redistributing fish to permanent habitats, especially floodplain lakes (Jurajda et al. 2001).

In the major rivers of central and southern North America (mainly the Mississippi River and its tributaries), the flooding pattern was historically fairly similar to that of tropical systems. These rivers had an extended period of flooding in the spring, although it was more erratic in timing and extent than that of tropical rivers (Sparks et al. 1998). Many fish species, consequently, seemed to be most abundant and/or exhibited higher growth rates in years of extensive flooding (Gutreuter et al. 1999). This was especially true of sunfishes (Centrarchidae) and catfishes (Ictaluridae), which require at least six weeks of inundation to build nests, spawn, and care for their young (Sparks et al. 1998). The diverse fauna of minnows (Cyprinidae) and darters (Percidae) also take advantage of flood events, with each species having somewhat different responses (Starrett 1951, Grossman et al. 1982). Today, the flood regime in most of these rivers is more like that of Europe because of extensive modification of the watersheds and river channels (Sparks et al. 1998) although most of the centrarchids and ictalurids are still common in permanent lakes, ponds, and channels, many of them artificially created and maintained.

Central California floodplains represent an intermediate model of fish use because while the timing of flooding, following mountain snowmelt in the spring, is or was fairly predictable, the extent and duration of flooding is not. Thus there is just one floodplain dependent species, Sacramento splittail, although there are others (e.g., Chinook salmon) for whom survival and growth is enhanced when floodplains are available for rearing and foraging (Sommer et al. 2001b, Feyrer et al. 2004, Ribiero et al. 2004). Most fishes, however, appear to use floodplains on an ad hoc basis. Unfortunately, in California, as in many other areas with temperate, Mediterranean, and arid climates, floodplains have been largely divorced from their rivers for so long that historic patterns of use are not present, or potential floodplain dependent species (e.g., Sacramento perch) have been extirpated. The increasing presence of alien fishes in permanent floodplain habitats also confuses our understanding of historic patterns.

Assuming that loss of riparian forests is a good measure of floodplain loss, then over 90% of functioning floodplain has been lost in California (Bay Institute 1998). Given the importance of floodplain habitat to splittail and Chinook salmon, and likely importance to other native species, the long-term decline in abundance of native fishes and fisheries may be at least in part related to the loss of floodplain habitat. In particular, there was likely a positive feedback between salmon production and riparian systems in California. Merz and Moyle (2006) have shown that marine nutrients from spawning salmon likely have a positive effect on riparian plants (including crop plants) and wildlife in California rivers, even at the present time. Thus, increasing floodplain habitat to benefit salmon and other fishes may have other positive ecosystem consequences.

CONCLUSIONS

This study, along with those from the Yolo Bypass (e.g., Sommer et al. 2001a), demonstrates that native fishes are adapted for taking advantage of the annual flood regime and the vast historic floodplains of the Central Valley. Presumably the availability of floodplains for spawning and for rearing of juvenile fishes was an important factor in creating large populations of fishes that were important in the diets of the Indian tribes of the Central Valley and for the large commercial fisheries that were present in the nineteenth century for species as diverse as Chinook salmon, Sacramento perch, and thicktail chub (Moyle 2002). Conservation of the native fish fauna, as well as restoration of fisheries, thus seems to require re-creation of floodplain habitats, although because of the presence of alien species, these habitats will have to be creatively designed and intensively managed.

However, restoring even small floodplain systems demonstrably benefits a variety of fishes, especially native fishes such as Chinook salmon and splittail. The natives are clearly adapted for the seasonal pattern of flooding (Sommer et al. 2004). They move onto the floodplain as soon as it floods and mostly leave with the receding waters, avoiding being stranded except where artificial structures and ponds prevent it (Sommer et al. 2005). By and large, alien fishes arrive on the floodplain later than the natives and are more likely to become stranded. This pattern results in a definite succession of fishes in floodplain habitats. Re-creation of fish-friendly floodplains must recognize and take advantage of this pattern.

Guidelines For Restoring Native Fishes To Floodplains

Re-creation of floodplains with a high degree of ecological function is not easily accomplished, especially given the likelihood of conflicting goals for species and habitats. For example, our studies have indicated that native fish do best in open floodplain areas covered with annual vegetation, while a frequent goal of “restoration” projects is to bring back dense riparian forests. It also has to be recognized that some historic features of California floodplains, such as permanent ponds and oxbow lakes, by and large favor alien species. So from a native fish perspective, those features are no longer necessarily desirable features in floodplains. Here we provide some guidelines for restoring floodplains friendly to native fishes, based on studies on the Cosumnes River Preserve (this study, Florsheim and Mount 2002, Crain et al. 2004, Ahern et al. 2006) and the nearby Yolo Bypass (Sommer et al. 2001, 2004, 2005, Feyrer et al. 2004).

1. Provide early season flooding. The most favorable timing of flooding for native fishes is from early January though April. The flooding can come in pulses, but continuous inundation of at least some areas is important (high residence time of water). This timing allows first for the build up of algal and invertebrate populations in floodwaters as food for fish (Ahern et al. 2006) and then for a succession of YOY of different species for rearing (Sommer et al. 2004).

2. Create a floodplain that drains completely. A floodplain topography that promotes rapid draining reduces stranding of native fish. Most stranding occurs in pits or behind structures that create ponds that do not drain. The Yolo Bypass shows remarkably little stranding of salmon and other fishes, for example, because it is designed to drain as quickly as possible to allow for farming. Most stranding occurs where artificial structures obstruct the drainage pattern (Sommer et al. 2005).

3. Reduce permanent water habitats. Permanent water on Central Valley floodplains, whether ponds or sloughs, supports mainly alien resident fishes, which may be significant predators on juvenile native fishes or otherwise alter the system in unfavorable ways (Angeler et al. 2002, Feyrer et al. 2004). Thus it is desirable to reduce such habitats as much as possible or to find ways to make them more favorable for native fishes.

4. Maintain a mosaic of habitats. Open areas covered with annual terrestrial plants that have a fairly high residence time of water appear to be most favorable for spawning and rearing of native fishes. There is some evidence that farmed areas (e.g., rice stubble) may be nearly as suitable for spawning and rearing as areas with natural plant cover. Given that untended floodplain areas tend to be rapidly colonized by trees, floodplains managed for natural values will need to have an actively maintained mosaic of terrestrial habitats that include large open areas. Very limited sampling in flooded forest areas, for example, revealed few fish, compared to nearby open areas (unpublished data).

5. Maintain both high variability in flood regime and regular annual flooding. High year to year variability in the extent and duration of flooding is both natural and should be desirable to maintain habitat mosaics. Where flooding can be regulated, providing at least some flooded area every year is desirable, especially for the rearing of juvenile Chinook salmon.

6. Create experimental habitats. Development and management of special habitats for native fishes should be tried on an experimental basis, to increase fish numbers and diversity. For example, Sommer et al. (2002) demonstrated that splittail can be spawned and reared successfully in temporary floodplain ponds. Creation of drainable floodplain ponds stocked with native fishes (Sacramento perch, hitch, blackfish) that would flood every 2-3 years could help to maintain or re-establish populations of these fishes.

7. Provide long-term monitoring programs. Our study shows that the fish communities on floodplains are highly variable through time, responding to variations in the timing, amount, and duration of flooding. We are far from completely understanding how these systems work, especially if they are to be managed for conservation purposes. Thus the Cosumnes River floodplain and similar systems should be monitored on a continuing basis to look for both unanticipated gradual and sudden changes.

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APPENDIX

Table A1. Percent abundances of young-of-year of the most common species on the Cosumnes River floodplain during three periods of flooding in 2004 and 2005: 1. February-March, 2. April-May, 3. June-July. The * indicates alien species. No samples were taken in period 3, 2004.

	2004			2005		
Period	1	2	3	1	2	3
N	2	4099	-	4	391	123
Seine hauls	15	2	-	7	12	1
Species	%					
Hitch	0	0	-	0	0	39
Sacramento blackfish	0	0	-	0	0	14
Sacramento splittail	0	81	-	0	23	0
Golden shiner*	0	0	-	25	8	35
Common carp*	0	16	-	0	41	2
Sacramento sucker	0	0	-	0	12	2
Chinook salmon	0	0	-	25	<1	0
Inland silverside*	0	0	-	0	0	0
Western mosquitofish*	0	2	-	-	4	0
Black crappie*	100	0	-	0	5	4
Other species	0	<1	-	50	7	4

Table A2. Numbers of fish caught by sampling date (approximately weekly) in 1998 that made up at least 1 percent of the total catch. LMB = largemouth bass, SKR = Sacramento sucker, PSN = prickly sculpin, SST = Sacramento splittail, CRP = common carp, ISS = inland silverside, CHN = Chinook salmon, and BSLP = bigscale logperch.

1998	LMB	SKR	PSN	SST	CRP	ISS	CHN	BSLP
12/2/98	0	0	0	0	0	0	0	0
12/6/98	0	0	0	0	0	0	0	0
2/2/98	0	0	0	0	0	0	0	0
2/9/98	0	0	0	0	0	0	0	0
2/16/98	0	0	0	0	0	0	0	0
2/23/98	0	0	0	0	0	0	0	0
3/2/98	0	0	0	0	0	0	2	0
3/8/98	0	0	0	0	0	0	8	0
3/16/98	0	0	0	0	0	0	3	0
3/23/98	0	0	0	5	0	0	2	0
3/30/98	0	0	8	131	0	0	2	0
4/6/98	0	44	8	0	0	0	9	0
4/14/98	0	90	17	1090	0	0	11	0
4/23/98	0	60	0	120	0	0	16	0
4/30/98	1	23	1	166	0	0	1	15
5/7/98	0	530	5	570	20	0	3	20
5/22/98	0	43	1	148	0	74	0	3
	1	790	40	2230	20	74	57	38

Table A3. Numbers of fish caught by sampling date (approximately weekly) in 1999 that made up at least 1 percent of the total catch. GSH = golden shiner, SBF = Sacramento blackfish, HCH = hitch, MSQ = western mosquitofish, SKR = Sacramento sucker, SST= Sacramento splittail, CRP = common carp, BCR = black crappie, and ISS = inland silverside.

1999	GSH	SBF	HCH	MSQ	SKR	SST	CRP	BCR	ISS
2/12-16/99	0	0	0	0	0	0	0	0	0
2/19-26/99	0	0	0	0	0	0	0	0	0
3/4/1999	0	0	0	0	0	0	0	0	0
3/12-17/99	0	0	0	0	0	0	0	0	0
3/19-26/99	0	0	0	0	0	0	0	0	0
4/2-6/99	0	0	0	0	0	0	0	0	0
4/9-15/99	0	0	0	0	0	0	0	0	0
4/23/99	0	0	0	25	1	0	0	0	0
4/30/99	0	0	0	0	0	0	0	0	0
5/7/99	0	0	0	0	66	0	31	0	0
5/14/99	0	0	0	0	20	0	24	2	0
5/21/99	54	7	2	0	620	67	320	0	0
6/18/99	13	70	18	0	27	315	56	12	6
6/30/99	93	11	0	111	439	7	802	8	176
7/7/99	212	13	6	439	25	2	64	7	170
7/13/99	55	98	15	136	0	36	203	1	130
7/21/99	107	41	27	99	0	12	433	6	162
7/28/99	32	25	14	32	0	0	440	10	11
8/12/99	2	9	13	36	0	0	40	0	18
8/20/99	11	142	3	66	0	0	327	0	822
9/2/99	6	18	8	35	0	0	39	3	232
9/17/99	0	13	0	0	0	0	5	0	56
	585	447	106	979	1198	439	2784	49	1783

Table A4. Numbers of fish caught by sampling date (approximately weekly) in 2000 that made up at least 1 percent of the total catch. Species codes are the same as in Table A3.

2000	GSH	SBF	HCH	MSQ	SKR	SST	CRP	BCR	ISS
2/1/00	0	0	0	0	0	0	0	0	0
2/8/00	0	0	0	0	0	0	0	0	0
2/15/00	0	0	0	0	0	0	0	0	0
2/22/00	0	0	0	0	0	0	0	0	0
3/7/00	0	0	0	0	0	0	0	0	0
3/14/00	0	0	0	0	0	0	0	0	0
3/23/00	0	0	0	0	0	0	0	0	0
4/4/00	0	0	0	0	3	0	0	0	0
4/18/00	0	1	1	0	6	375	269	0	0
4/25/00	1	0	11	0	69	1234	314	0	0
5/2/00	0	0	0	0	0	1025	4000	0	0
5/9/00	38	10	145	0	96	809	51	0	0
5/18/00	2185	0	134	20	172	200	294	59	11
5/23/00	143	10	17	7	36	49	101	21	8
5/30/00	487	15	30	244	60	200	986	21	163
6/6/00	173	18	8	305	22	91	74	5	32
6/13/00	131	4	1	436	0	0	7	8	106
6/20/00	129	10	6	250	38	33	66	34	83
6/28/00	36	6	0	275	8	5	126	30	521
7/6/00	7	0	0	800	0	0	3	11	774
	3330	74	353	2337	510	4021	6291	189	1698

Table A5. Numbers of fish caught by sampling date (approximately weekly) in 2001 that made up at least 1 percent of the total catch. Species codes are the same as those found in Table A3.

2001	GSH	SBF	HCH	GAM	SKR	SST	CRP	BCR	ISS
2/15/01	0	0	0	0	0	0	0	0	0
2/21/01	0	0	0	0	0	0	0	0	0
3/5-6/01	0	0	0	0	0	0	0	0	0
3/13/01	0	0	0	0	0	0	0	0	0
3/20-21/01	0	0	0	0	0	0	0	0	0
3/27/01	0	0	0	0	0	0	0	0	0
4/3/01	0	0	0	0	0	4280	1525	0	0
4/10/01	0	0	0	2	0	2356	1734	2	0
4/19/01	0	0	0	0	0	6720	3150	0	0
4/26/01	0	0	0	0	20	2570	100	30	0
5/1/01	29	0	6	0	401	1296	11	30	0
5/8/01	0	0	0	5	455	150	295	0	0
5/18/01	16	2	0	1	252	496	18	0	0
5/24/01	17	8	0	48	0	100	359	37	125
5/30/01	60	2	0	282	0	66	78	20	12
6/5/01	1	3	0	112	0	7	44	1	3
6/13/01	186	20	0	44	0	230	58	59	936
6/20/01	38	2	2	11	0	77	15	12	3381
7/5/01	2	1		240		8	6	3	740
	349	38	8	745	1128	18356	7393	194	5197

Table A6. Numbers of fish caught by sampling date (approximately weekly) in 2002 that made up at least 1 percent of the total catch. Species codes are the same as in Table A3.

2002	GSH	SBF	HCH	MSQ	SKR	SST	CRP	BCR	ISS
1/3-7/02	0	0	0	0	0	0	0	0	0
1/14/02	0	0	0	0	0	0	0	0	0
1/22/02	0	0	0	0	0	0	0	0	0
2/4/02	0	0	0	0	0	0	0	0	0
2/15-20/02	0	0	0	0	0	0	0	0	0
2/25/02	0	0	0	0	0	0	0	0	0
3/5/02	0	0	0	0	0	0	0	0	0
3/11/02	0	0	0	0	0	0	0	0	0
3/18/02	0	0	0	0	0	0	0	0	0
3/25/02	0	0	0	0	0	0	0	0	0
4/2-8/02	1	0	1	0	331	3	3	0	0
4/15-23/02	25	5	0	0	98	3504	58	2	0
4/30-5/6/02	86	24	0	0	4	381	60	14	2
5/13/02	37	11	5	12	3	27	26	10	1
5/20/02	172	35	1	28	2	19	23	1	9
5/31/02	128	50	0	254	4	64	16	0	114
6/10/02	16	15	2	36	0	0	2	1	70
6/17/02	33	13	0	74	0	0	12	0	188
	498	153	9	404	442	3998	200	28	384

Table A7. Means (minimum-maximum) of temperature, conductivity, and secchi depths for all stations for each month 1999 through (July of 2000 and June of 2002 had only two data points, July of 2001 had only one data point) 2002.

Parameter	Year	Jan	Feb	Mar	Apr	May	Jun	Jul
	1999							
Temperature		no data	10 (7-13)	13 (10-16)	15 (12-19)	19 (16-23)	26 (22-30)	no data
Conductivity		no data	87 (73-99)	152 (91-375)	86 (61-114)	88 (68-121)	118 (107-129)	no data
Secchi		no data	25 (17-33)	31 (7-49)	45 (24-80)	72 (65-77)	9 (6-12)	no data
	2000							
Temperature		no data	12 (11-16)	14 (11-17)	19 (14-25)	22 (15-30)	27 (23-32)	23.15 (22-24.3)
Conductivity		no data	130 (87-206)	129 (11-194)	95 (59-154)	80 (56-116)	92 (49-144)	95 (94-96)
Secchi		no data	27 (11-45)	35 (5-59)	44 (27-58)	45 (15-92)	24 (11-44)	13 (7-19)
	2001							
Temperature		no data	12 (12-13)	17 (11-24)	19 (15-23)	25 (21-31)	26 (22-28)	26.4
Conductivity		no data	107 (27-127)	120 (103-190)	119 (73-190)	150 (93-344)	130 (68-202)	300
Secchi		no data	22 (13-37)	34 (13-48)	23 (9-33)	28 (11-79)	10 (8-12)	13
	2002							
Temperature		9 (7-12)	13 (13-15)	14 (10-17)	24 (17-30)	23 (17-30)	27.5 (24.0-30)	no data
Conductivity		154 (68-187)	156 (144-164)	142 (123-172)	157 (124-210)	194 (100-275)	243.5 (238-249)	no data
Secchi		60 (12-90)	56 (43-100)	38 (11-59)	64 (20-110)	40 (13-55)	8.5 (6-11)	no data