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 for seven years (1998-2002. 2004-2005) during the winter-spring flooding season. 33 species of fish were captured in the flood waters, the river, and an intersecting slough. 18 species were present all years in all three habitats. The fishes fell into five groups according to how they used the floodplain: (1) floodplain spawners, (2) river spawners, (3) floodplain foragers, (4) floodplain pond fishes, and (5) inadvertent users. Eight of the abundant species were natives, while the rest were aliens. There was a consistent pattern of floodplain use, although it was modified annually by the timing and extent of flooding. The first fish to appear on the floodplain were floodplain foragers, inadvertent users, and juvenile Chinook salmon (river spawners). The next fish to appear were adult floodplain spawners, principally Sacramento splittail and common carp, although small numbers of foragers and inadvertent users from were also present. Juvenile splittail and common carp quickly grew large enough to dominate floodplain fish samples, along with juvenile Sacramento sucker and pikeminnow (river spawners).

Adult floodplain spawners left when inflow decreased; their juveniles persisted only as long as new flood pulses kept water levels up and temperatures low. Most juveniles left the floodplain either with the pulses or with declining inflows. Usually the floodplain disconnected from the river by mid-May. In two large shallow ponds of residual water, juvenile centrarchids and non-native annual fishes dominated catches by June. Essentially, eurytopic and rheophilic native fishes plus common carp dominated the floodplain fish fauna early in the season while limnophilic alien fishes dominated late in the season. Abundant native fishes were those that used the floodplain for rearing of juveniles. Most alien fishes had resident populations in permanent waters associated with the floodplain (river, sloughs, and ditches) and were not dependent on the floodplain for persistence. Restoration of floodplains to favor native fishes requires knowledge of complex interactions among physical and biological factors.

KEY WORDS

Restoration, non-native species, exotic species, splittail, carp, Chinook salmon, Sacramento River, Cosumnes River.

INTRODUCTION

There is growing recognition that naturally-functioning floodplains provide many benefits that historically have not been appreciated, including direct economic benefits, ecosystem services, and habitat for a wide diversity of species (Bayley 1995, Tockner and Stanford 2002). 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., Michner and

Hauber 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. 2004, Crain et al. 2004). However, our understanding of how fishes use Central

Valley floodplains is limited, as is our understanding of how to manage the floodplains to

favor native fishes. Most Central Valley rivers have large dams on them which regulate

flow and reduce the frequency of potential flooding events and most Central Valley

floodplains are separated from their rivers by levees. An exception is the Cosumnes

River, which has no major dams on its main channels (Moyle et al. 2003) and a

floodplain which is in the process of being restored through breaching of levees. 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 was the focus of

this study as a model for floodplain restoration in Central California, because of its small

size, accessibility, and habitat diversity. It is also useful as a 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 floodplains?

2. How does fish use of the floodplain change with season and flow?

3. What characteristics of flooding and floodplains favor native fishes?

4. Do large numbers of fish become stranded when the floodplain drains?

5. Is the pattern of fish use of floodplains similar to that of riverine fishes in other

   parts of the world?

6. How do we re-create fish-friendly floodplains?

To answer these questions, we examined floodplain use by (1) larval fishes, (2) young-of-

year juveniles, (3) adults and older juveniles. Floodplain use by larval fishes is covered in

Crain et al. (2004), so this study focuses on juvenile and adult fishes.

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., Robinson et al. 2002, Grift et al 2003). A

more floodplain-specific classification of guilds of floodplain fishes is presented here,

based on information in Moyle (2002) and Sommer et al. (2001a, b, 2004), as well as the

present study (Table 1). We classify floodplain fishes as follows: (1) floodplain spawners, (2) river spawners, (3) floodplain foragers, (4) floodplain pond 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 is at equilibrium 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 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. Common carp and goldfish are examples 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).

River spawners are species that spawn upstream of floodplains, usually on gravel riffles, and then use the floodplain for rearing. These mostly rheophilic fishes are common but the importance of floodplains to their populations is poorly known, because they also rear on stream edges and other habitats. Sommer et al (2001b) demonstrated that juvenile Chinook salmon rearing in the Yolo Bypass grew faster and achieved larger

sizes than fish rearing in the main river. However, Ribeiro et al. (2004) found that Sacramento suckers grew faster in riverine habitats than in floodplain habitats. A key to the success of these species is that they have the ability to leave the floodplain as it drains and thereby avoid stranding. The presence of adults and yearlings of river-spawning native fishes on the Cosumnes River floodplain suggests that these fishes also benefit from foraging on the floodplain, especially following spawning.

Floodplain foragers are eurytopic and limnophilic fishes that move on to the floodplain to take advantage of abundant food. Typically, they are most abundant in local sloughs and ditches and spawn after the flood has receded. They enter the floodplain as either juveniles or adults and seem to have a relatively low incidence of stranding, although some may spawn in floodplain ponds if the water stays long enough. Examples include golden shiner, bluegill, and redear sunfish. Such species may have substantially faster growth rates on floodplains than in non-floodplain habitats (Gutreuter et al. 1999).

Floodplain pond fishes are limnophilic species present in local sloughs and permanent ponds that become abundant, through rapid growth and reproduction, in shallow floodplain ponds as the water recedes. They are the fishes that most commonly become stranded in large numbers when ponds become isolated. Examples are inland silversides and western mosquitofish.

Inadvertent floodplain users are a high percentage of the species collected on floodplains but are a small number of individuals. They enter floodplains from ponds and sloughs on the floodplains or from upstream. They have a variety of fates. If they are larvae or small juveniles washed in from upstream, they either just pass though

(lampreys) or settle out to die or become stranded (prickly sculpin). Large adults of

species such as largemouth bass or channel catfish that move too far from the river or

home ponds are likely to become stranded in the falling water. Many of these fishes

(e.g., black crappie) 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.

STUDY AREA

 The Cosumnes River Preserve (CRP) is located in southern Sacramento County,

California. It 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.   The CRP edge sits just above (.5 km) the confluence of

the Cosumnes River and the Mokelumne River (Figure 1). The preserve encompasses

three major tidally-influenced freshwater sloughs, Middle Slough, Tihuechemne Slough,

and Wood Duck Slough. 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. When flooding occurs, water flows through breaches in

levees that separate the river from the CRP (Florsheim and Mount 2003). The first and

largest breach delivers water into a shallow (1-2 m) depression (Pond 1 in our studies)

that is 1-2 ha in extent, depending on the amount of flooding. The water from this pond

either flows back into the river through another breach about 100 m downstream from the first breach or flows parallel to the river into a second pond (Pond 2), also 1-2 ha in extent, from which it can flow back into the river through another breach or through a ditch connecting the pond to Wood Duck Slough. During high flow events, water inundates the fields and forests surrounding the ponds and there are overland flows in many directions, connecting ponds, ditches, and sloughs throughout the CRP.

Flooding occurred every year on the CRP but the extent varied among years (Table 2, Figure 2). 1998 was a very wet year and flooding was nearly continuous from early January through late June. Most of the CRP flooded during peak events. Water remained in ponds on the floodplain throughout the summer. 1999 and 2005 were similar to 1998 except that connection between the river and floodplain began in late January and was lost in early June. In 2000 and 2003, there was fairly average precipitation and spring flows, so flooding began in late January and was continued through mid- May, with occasional breaks in connectivity. Only the lowest sections of the CRP flooded, mainly below a low levee designed to reduce flooding of rice paddies. 2001, 2002, and 2004 were dry years with flooding beginning in late January; the period of flooding was 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.

Floodplain sampling focused on two ponds. 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 and became partially filled with sand carried in by the river during the course of the study (Forsheim and Mount 2003). In most years 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 annually on the slough (to provide water for irrigation of fields of

neighboring farms) usually backed water up into the pond in late summer, so it rarely

dried up completely, although it was usually small and shallow (<1m deep) by late

summer. Maximum depth was around 2 m. When flood waters entered the study area,

these ponds became the centers of two flooded areas separated by another levee and a

ditch, but connected by 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 flood plain.

For comparison with the floodplain samples, we also sampled sites on Middle

Slough and on the Cosumnes River in 2000, 2001, and 2002. Both sites were downstream

from the flooded areas, so 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.

METHODS

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 1999-2002; sampling in 2003-2005

was largely confined to short periods following flood events.

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. 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 fish 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 (Y0Y) were fish <60 mm SL, with the exception of a few small bluegill which were present on the floodplain in February and March samples (prior to spawning). All salmon were counted as juveniles because they grew rapidly on the floodplain to > 60 mm SL (unpublished data).

Remaining fish were counted by species and length category (YOY or adult/yearling). Most fish were released back into the water although small samples of fish were killed with a blow on the head (the preferred method for euthanasia; Robb and Kestin 2002) and preserved in formalin for use in dietary studies. 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.

Habitat type sampled was recorded as floodplain, slough, slough margin, river, river margin, old forest, new forest, farm field, or pond. 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. Cover for fish was classified on a 3 point scale with 0 = none, 1= some (<50%), 2 = dense (>50%) in the sampling area. Categories of cover included annual vegetation (grasses, cockle burrs, herbaceous plants etc.), woody debris, woody vegetation (bushes and trees), aquatic vegetation (floating and submerged recorded separately), filamentous algae, and emergent vegetation.

Electrofishing was performed in 2001, 2002, and 2003 with a shallow draft 5 m boat upon which 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, propelled by a15 HP 4-stroke outboard motor, sampled fish effectively at depths of 0.5-2.0 m. The current used for shocking was adjusted automatically for conductivity but was normally 600 volts and 4 amps. Shocking was most effective for 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) dipnet. 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, various habitat

variables were measured or estimated: using the same habitat characteristics as for

seining.

      Statistical analyses. Seining and electrofishing capture data and the associated

environmental measurements were entered on an Excel spread sheet for analysis. The

data sets are available on-line through the Interagency Ecological Program web site

(http://baydelta.ca.gov/). Monthly succession of YOY species was explored graphically.

We analyzed the relationship between species abundance and environmental variables

using Canonical Correspondence Analysis (CCA). Separate analyses were run on YOY

fishes and adult fish because of differences in floodplain uses 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, C.J.F. and Smilauer, P. 2002) Using the

forward selection mode in CCA, a model with six variables was developed for YOY

fishes and a model with seven variables for adult fishes. For YOY fishes, the variables

selected were: maximum depth, annual vegetation, aquatic vegetation, temperature, water

clarity, and Julian date. The model for the adults included, maximum depth, floodplain

pond, slough margin, mineral mud, conductivity, water clarity, and Julian date. Because

the first and second axis together explain the most variance (24 % and 20% 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 = 29.06, p =

.002, full model, F ratio = 2.90, p = .002). The model for adult fish was also significant

for both the first axis and the full model, with (axis 1,F ration = 16.1, p = .002, full

model, F ratio = 2.18, p = .002).

RESULTS

Over the eight years of sampling, 33 species of fish were captured in the

floodplain, slough and river. During the five years of intense sampling, 18 species

occurred in all years in all three habitats, although only 12 were consistently abundant

enough to contribute to analyses of trends and habitat use, as YOY or yearlings/adults

(Table 1). Four of the abundant species were natives, while eight were aliens. YOY fish

were caught primarily in the seining samples, while large adult fish were caught mainly

in the electrofishing samples. Both types of sampling captured yearling fish and small

adults.

Young-of- year.

Floodplain. Over the eight years of sampling, there was a fairly predictable

succession of YOY fishes, although there was also 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 the catch data are lumped together for two-month intervals (Tables 4, 5) but is also

clear in the progression of fish in monthly (Figure 3) and weekly data summaries (not

shown). In February and March, rheophilic chinook salmon dominated the catches,

although splittail (eurytopic) appeared in some late March samples (Table 4, Figure 3).

Splittail juveniles typically dominated the catches in April and early May, except in 1999

when they were largely absent from the floodplain. Other juveniles 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 appearance. 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 the isolated floodplain ponds, which often became dry

or only a few cm deep by August.

Despite this general pattern, there were differences in timing and abundance of

YOY fishes from year to year. Some species, such as Sacramento blackfish and golden

shiner were abundant 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 very low numbers. The pattern of occurrence for many fishes reflected the length

of time the floodplain was connected to the river. In 1998 and 1999, which had long

periods of connection, juvenile chinook salmon persisted on the floodplain through April;

they were gone by late March in the other three years. In 1998, splittail juveniles

appeared in March (indicating spawning on the floodplain a month earlier) and persisted

in large numbers through June. In 1999, juvenile 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 (Sommer et al. 2000). 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 (2002).

The ability of floodplain-adapted fish to avoid stranding is illustrated by the

events in Pond 1 in 2000. As the pond level dropped prior to disconnecting 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), juveniles 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. However, stranding

by splittail and carp was not always avoided. The large numbers of juveniles captured in

2001 reflected the intermittent conditions of flow which resulted in fish being

concentrated in the periodically shrinking ponds and becoming more vulnerable to

capture and less able to escape to the river. Splittail present in early June in such years

were stranded and were gone (presumably dead) by late June.

. Curiously, carp YOY were collected in disproportionately small numbers

compared to the number of large adults observed spawning on the floodplain. Likewise,

we did not collect *any* YOY (or larval) goldfish on the floodplain, despite capturing large

ripe adult females during all years of electrofishing.

Sloughs. YOY captured in Middle Slough in March were primarily chinook

salmon and in April and May splittail, suckers, and carp, usually with sharp peaks of

abundance (Figure 3), suggesting 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. YOY
of limnophilic species dominated the catches in later months.

River. In the Cosumnes River, the patterns of YOY succession were similar to
that of the sloughs although catches of native fishes were more consistent from week to
week, reflecting both fish leaving the floodplain through the breaches and coming from
upstream areas (Figure 5). Occasionally, alien fish common in our river samples were
species not found on the floodplain or in sloughs (e.g., American shad, threadfin shad,
spotted bass).

Overall YOY patterns. The change in YOY species in the floodplain, river, and
slough relative to one another showed that most native fishes left the floodplain, took up
temporary residence in the river and sloughs and then left the region, or got eaten by
predators (Figure 5). Another view of this pattern is provided by the environmental CCA
for YOY of the seven most abundant species (Figure 6). The late season fishes, western
mosquitofish, golden shiner, inland silverside, and Sacramento blackfish, tended to be
found in warm, shallow water associated with ponds, while common carp and splittail
were found in the cooler, deeper water with lots of submerged vegetation (including
annual terrestrial plants) associated with sustained flooding. Sacramento sucker YOY,
being washed in from the river, tended to be found in clear, cold water with cover
provided by filamentous algae and plants.

Adults and yearlings

With seining and electrofishing combined we captured 29 species of adult fish on
the floodplain. The seines mostly caught the 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 on the floodplain in January and February following the first flooding events. 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 down stream 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. Adult suckers also moved in at this time, apparently in process of moving upstream to spawn. Carp and goldfish frequently became stranded with falling water under fluctuating conditions, but adult splittail usually moved off the floodplain before they became trapped.

In April and May, numbers and diversity 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 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 and perhaps spawn if water temperatures exceeded 20°C for an extended period of time.

In June and July, the most of the floodplain dried up and shallow ponds became disconnected from the river. While a diversity of fishes were present in these ponds initially, most of the larger fish disappeared as 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 carp and catfish eaten by otters were common on pond edges. Usually by July, the ponds were dominated by inland silversides, which reproduce rapidly in such conditions (Moyle 2002).

The CCA for the mostly yearling fish caught in seines (Figure 7, Table 7) showed black crappie, western mosquitofish, bluegill, and inland silverside were associated with shallow ponds late in the season, although silversides were most abundant at stations where the bottom was predominately mud (i.e. little vegetation). Yearling pikeminnows and golden shiners, in contrast, appeared to be responding to early flooding, characterized by greater depth, lower conductivity, and lower water clarity.

DISCUSSION

What kinds of fish use floodplains?

Not all the fishes present in the permanent waters Cosumnes River and its sloughs used the floodplain, despite the abundance of invertebrate prey (T. Grosholz, UC Davis, unpublished data). Of the 33 species we collected over seven years, 15 were rare in our samples, although most of these rare species were common in the river or sloughs (Crain and Moyle, unpublished data). The 18 species captured on a regular basis were about equally divided among riverine, eurytopic, and limnetic species. Five species were floodplain spawners, and YOY of one native species, splittail, were among the most

abundant fish in most years. There were also five species of river spawners, whose

juveniles moved (or were carried) into the floodplain and reared there for several weeks.

Three slough-dwelling species (golden shiner, bluegill, and redear sunfish) apparently

moved onto the floodplain, mostly as yearlings, to forage; they were often found often

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, but two

pond species with short generation times, inland silverside and western mosquitofish,

typically dominated these ponds. A final component of the floodplain fish fauna was

species that either passed through the floodplain on their way downstream (e.g.,

transforming Pacific lamprey) or wandered out of sloughs and ditches, usually staying

close to their points of origin. The latter species were often stranded when flood waters

dropped rapidly.

What this diversity of floodplain users shows is that different species used

floodplains for different reasons, but relatively few species (e.g., splittail) depended 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 falling water. 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. 2004, Ribeiro et al. 2004).

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, 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 were a few foragers from ponds and ditches (e.g., golden shiner), some transient 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 left 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, western mosquitofish, inland silverside, and 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 a combination of individuals moving in through ditches or through spawning by stranded fish. In many years, the ponds dried up by August.   If the ponds persisted,

usually mainly western mosquitofish and inland silversides persisted in them

(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 can use the floodplain for

rearing of YOY which 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. Thus

native fishes mostly used the floodplain when temperatures were cool and flooding was

more or less continuous. Most of the natives are resident in the rivers or migrate onto the

floodplain from other areas. The sloughs and ditches were dominated 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 riverine species present that were rarely found on

the floodplain.

An interesting exception to these general patterns is the Sacramento blackfish, a

large cyprinid which 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 depended on floodplains for spawning and rearing (Woodley and Crain, unpubl. data).

Do large numbers of fish become stranded when the floodplain drains?

The shallow ponds that remained at the end of the flooding season contained large numbers of small fish, attracting flocks of fish-easting birds. The vast majority of these fish, however, were short-lived pond species (especially inland silverside and western mosquitofish), which achieved large populations through reproduction in the ponds. Remarkably few native fishes became stranded in these ponds, although in most years we did captur a few individuals in them, especially splittail and chinook salmon, usually shortly after the floodplain had drained. 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 and early disconnection stranded large numbers of splittail. Also in 2001, we noted large numbers of splittail trapped behind a dirt diversion dam that was present in Middle Slough; this dam maintained the slough at high water levels through the use of a flapper valve to capture tidal inflow. The fish in the slough presumably came from Pond 2, which has an artificial drainage ditch connecting it to the slough. When the dam was constructed, water backed up into the pond, allowing access of fish to the slough. When the slough was allowed to drain on June 4, to release the splittail, we observed that most individuals were small (30-40 mm SL) suggesting that growth conditions in the slough were relatively poor.

Alien fishes were more often stranded on the floodplain, especially after large flood events that spread water widely. Large carp frequently became trapped in floodplain ponds, albeit in small numbers compared to the numbers on the floodplain itself. Most were quickly captured by otters and other predators, as indicated by half-eaten carcasses along the shoreline. In some years (e.g., 1999) large numbers of YOY carp, apparently resulting from spawning of stranded adults, also were abundant. Likewise, the numbers of adults and yearlings of centrarchids and other fishes that were stranded were small compared to the numbers present in the sloughs. During electrofishing, most large alien fish from the sloughs 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 found small numbers of both slough and river fish stranded throughout the flooded area.

Is the pattern of fish use of floodplains similar to that of riverine fishes in other parts of the world?

King et al. (2003) present a conceptual model of the importance of floodplains to riverine fish faunas which 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

(Goulding 1980, Welcomme 1985, DeGraff 2003, Hogan et al. 2004). At the opposite

end of the floodplain use spectrum are the rivers of Australia (Puckridge et al. 1998). In

particular, flooding in the Murray-Darling system, the continent's largest river, 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 use 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. 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. There are few fishes that require newly flooded areas

for persistence, although many rheophilic species appear to 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 diverse

habitats, especially floodplain lakes.

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 predictable,

the extent and duration of flooding is not. Thus there appears to be a few floodplain

dependent species, such as Sacramento splittail, and others (e.g., Chinook salmon) for

whom survival and growth is enhanced when floodplains are available for rearing and

foraging (Sommer et al. 2001b, 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.

CONCLUSIONS

Restoring even small floodplain systems by breaching levees and allowing a natural regime of flooding and draining is demonstrably good for a variety of fishes in Central California, but especially for native fishes such as chinook salmon and splittail. The natives are clearly adapted for the seasonal pattern of flooding. They moved onto the floodplain as soon as it flooded and mostly left with the receding waters, avoiding being stranded. By and large, the alien fishes arrived on the flood plain later than the natives and often become stranded. This pattern resulted in a definite succession of fishes in floodplain habitats. Juvenile chinook salmon were the first major users entering the floodplain from upstream spawning areas in February and usually left by mid-April. The next arrivals (in March) were prickly sculpin (mainly as larvae), juvenile pikeminnows, and Sacramento suckers (adults and juveniles), although splittail also arrived at this time. Splittail spawned on the floodplain in March and April and their juveniles quickly became among the most abundant fish on the floodplain, although most left as the water receded in April and May.

Common carp, an alien, had a pattern very similar to that of splittail although their juveniles were more likely to be stranded as the water receded. Throughout the native fish period, small numbers of aliens were a constant presence. They typically did not become abundant, however, until the water receded and temperatures rose above 20°C. Once the ponds were isolated, the dominant fishes became golden shiners, Sacramento blackfish (a native), sunfish, inland silversides, and western mosquitofish. The latter two

species completely took over the fish fauna as the ponds became shallow, warm, and turbid. During years with extensive and late flooding, these fish persisted through the summer but during dry years they died when the ponds dried up.

In general, alien fishes found on the floodplains were the same limnophilic species that were resident in the adjacent sloughs all year around, although inland silverside and western mosquitofish were present in relatively low numbers and confined to edge habitats in the sloughs. Native fishes appeared in our slough samples mainly when juveniles were leaving the floodplain. The same pattern was true for the fishes in our river samples, although rheophilic fishes rarely found on the floodplain were also present.

RE-CREATION OF FISH-FRIENDLY FLOODPLAINS

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 tiny remnant patches (Tockner and Ward 2002). Restoration of active floodplains, at least on a limited basis, is now regarded an important conservation goal, with considerable economic benefits (Pinter 2005). However, restoration 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. The purpose of this section is to 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) and the nearby Yolo Bypass (Sommer et al. 2001, 2004,

Feyrer et al. 2004).

1. 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.

2. To avoid stranding of fish, create or maintain a topography that promotes rapid

draining. 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.

3. Permanent water on Central Valley floodplains, whether ponds or sloughs,

support mainly alien resident fishes, which maybe 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. 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 habitats that include large open

areas.

5. High year to year variability in the extent and duration of flooding is both natural and desirable but where flooding can be regulated, providing at least some flooded area every year is desirable, especially for the rearing of juvenile Chinook salmon.

6. 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) have 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.

ACKNOWLEDGMENTS

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Species	Floodplain user groupsl	Flood-Plain, years	River, Years	Slough, Years
Pacific lamprey, *Lampetra tridentata*	Inadvertent, R	5	5	5
American shad, *Alosa sapidissima**	Inadvertent, R	2	5	0
Threadfin shad, *Dorosoma petenense**	Inadvertent, L	4	5	5
Hitch, *Lavinia exilicauda*	FP spawner, E	4	4	3
Sacramento blackfish, *Orthodon microlepidotus*	FP spawner, L	5	5	5
Sacramento splittail, *Pogonichthys macrolepidotus*	FP spawner, E	5	5	5
Sacramento. Pikeminnow, *Ptychocheilus grandis*	River spawner,R	5	5	5
Golden shiner, *Notemigonus chrysoleucas**	Forager, L	5	5	5
Fathead minnow, *Pimephales promelas**	Inadvertent, L	1	0	0
Goldfish, *Carassius auratus**	FP spawner, L	3	3	3
Common carp, *Cyprinus carpio**	FP spawner, E	5	5	5
Sacramento sucker, *Catostomus occidentalis*	River spawner,R	5	5	5
Brown bullhead, *Ameieurus nebulosus**	, L	0	0	1
Black bullhead, *A. melas**	Inadvertent, L	3	5	5
White catfish, *A. catus**	Inadvertent, E	1	5	5
Channel catfish, *Ictalurus punctatus**	- E	0	5	5
Chinook salmon, *Oncorhynchus tshawytscha*	River spawner R	5	5	4
Rainbow trout, *O. mykiss*	Inadvertent R	1	3	0
Wakasagi , *Hypomesus nipponensis**	Inadvertent L	1	0	0
Inland silverside, *Menidia beryllina**	Pond L	5	5	5
Western mosquitofish, *Gambusia affinis**	Pond L	5	5	5
Prickly sculpin, *Cottus asper*	River spawner R	5	5	5
Tule perch, *Hysterocarpus traski*	- E	0	2	0
Bluegill, *Lepomis macrochirus**	Forager L	5	5	5
Redear sunfish, *L. microlophus**	Forager L	5	5	5
Green sunfish, *L. cyanellus**	- E	0	2	0
Warmouth, *L. gulosus**	- E	0	0	2
Black crappie, *Pomoxis nigromaculatus**	Forager L	5	5	5
Largemouth bass, *Micropterus salmoides**	Inadvertent E	5	5	5
Redeye bass, *M. coosae**	- R	0	5	0
Spotted bass, *M. punctulatus**	- E	0	5	5
Bigscale logperch, *Percina macrolepidota**	River spawner R	5	5	5

Table 1. Fishes collected as YOY and adults in the Cosumnes River floodplain, river, and sloughs, 1998-2002 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 a group were not collected on the floodplain but have the potential to be inadvertent users because of presence in adjacent sloughs.

Year	Week,/Month first flooding	Week/Month, last connection	No. days connected	No. of floods	% flooded	Pond #1 dry in late summer?
1998	2/12	4/6	158	3	100	No
1999	3/1	4/5	104	7	100	No
2000	4/1	3/5	63	7	20	Yes
2001	4/2	4/4	6	1	5	Yes
2002	5/12	2/4	22	5	10	Yes
2003	3/12	4/5	37	3	15	Yes
2004	1/1	1/3	15	3	10	Yes
2005	5/12	5/5	121	7	65	Yes

Table 2. Extent of flooding, Cosumnes River Preserve, 1998-2002. % flooding refers to approximate percentage of floodplain on the Cosumnes River Preserve covered with water at its maximum extent, compared to 1998, the wettest of the eight years.

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

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).

	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

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.

	2004			2005		
Period	**1**	**2**	**3**	**1**	**2**	**3**
N	**2**	**4099**	**-**	**5**	**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**	**-**	**20**	**8**	**35**
Common carp*	**0**	**16**	**-**	**0**	**41**	**2**
Sacramento sucker	**0**	**0**	**-**	**0**	**12**	**2**
Chinook salmon	**0**	**0**	**-**	**20**	**<1**	**0**
Inland silverside*	**0**	**0**	**-**	**0**	**0**	**0**
Western mosquitofish*	**0**	**2**	**-**	**20**	**4**	**0**
Black crappie*	**100**	**0**	**-**	**0**	**5**	**4**
Other species	**0**	**<1**	**-**	**40**	**7**	**4**

Table 5. Percent abundances of juveniles 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.

| Species	Year	Total #	%	Feb.	Mar.	Apr.
Sacramento splittail,	2000	12	2	8	3	1
	2001	30	4	13	14	3
	2002	19	3	3	11	5
Hitch,	2000	8	1	1	1	6
	2001	4	<1	0	2	2
	2002	8	1	0	7	1
Sacramento blackfish	2000	3	<1	2		1
	2001	10	1	2	6	2
	2002	5	<1	0	1	4
Golden shiner	2000	51	7	22	11	18
	2001	34	5	10	17	7
	2002	114	16	8	83	12
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
Chinook salmon	2001	1	<1	0	1	0
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
Black crappie	2000	13	2	5	2	6
	2001	8	1	0	2	6
	2002	19	3	4	13	2

Table 6. Numbers of adult and yearling fish captured by electrofishing on the Cosumnes River floodplain, February-April, 2000-2003.

Juvenile fish			Canonical coefficients		Interset correlations	
Axes	Axis 1	Axis 2	Axis 1	Axis 2	Axis 1	Axis 2
Eigenvalues:	.235	.032				
Species-environment correlations:	.735	.407				
Cumulative percentage variance						
of species data:	21.0	23.9				
of species-environment relation:	75.2	85.5				
Maximum depth			-.291	-.559	-.221	-.241
Annual vegetation			.233	-.407	.400	-.161
Floating vegetation			.471	.342	.487	.050
Temperature			-.438	.452	-.500	.151
Secchi depth			.396	.676	.551	.144
Julian date			-.149	-.224	.123	-.110

Adult fish						
Axes	Axis 1	Axis 2	Axis 1	Axis 2	Axis 1	Axis 2
Eigenvalues:	.262	.199				
Species-environment correlations:	.679	.620				
Cumulative percentage variance						
of species data:	11.3	19.9				
of species-environment relation:	48.5	85.4				
Maximum depth			.361	.025	.155	.124
Floodplain pond			-.350	.009	-.415	-.222
Slough margin			.260	-.020	.166	.113
Mineral mud			-.730	.425	-.449	.310
Conductivity			.222	-.504	-.033	-.454
Secchi depth			-.265	-.356	-.103	-.289
Julian date			-.251	-.400	-.350	-.393

Table 7. Results of canonical correspondence analysis of environmental variables and juvenile and adult fish abundance (number of each fish species captured) for the Cosumnes River floodplain 1999 through 2002. Shown is the CCA summary table for the first two ordination axes, canonical regression coefficients, and interest correlations for the standardized environmental variables.
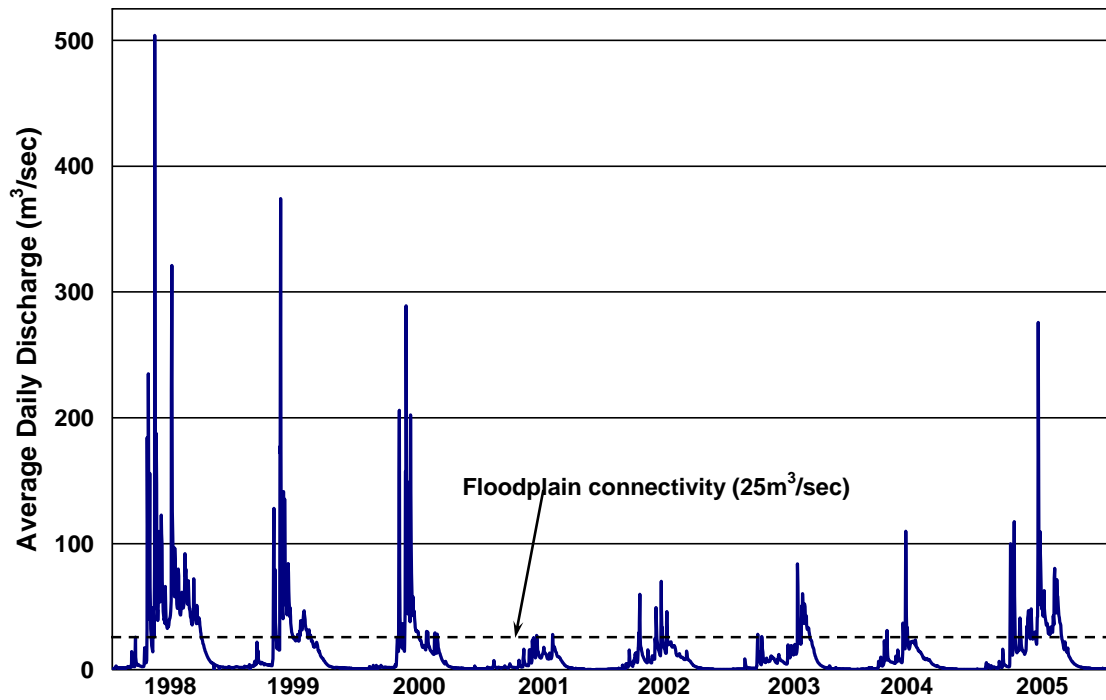
Figures

Figure 1   Map of study area
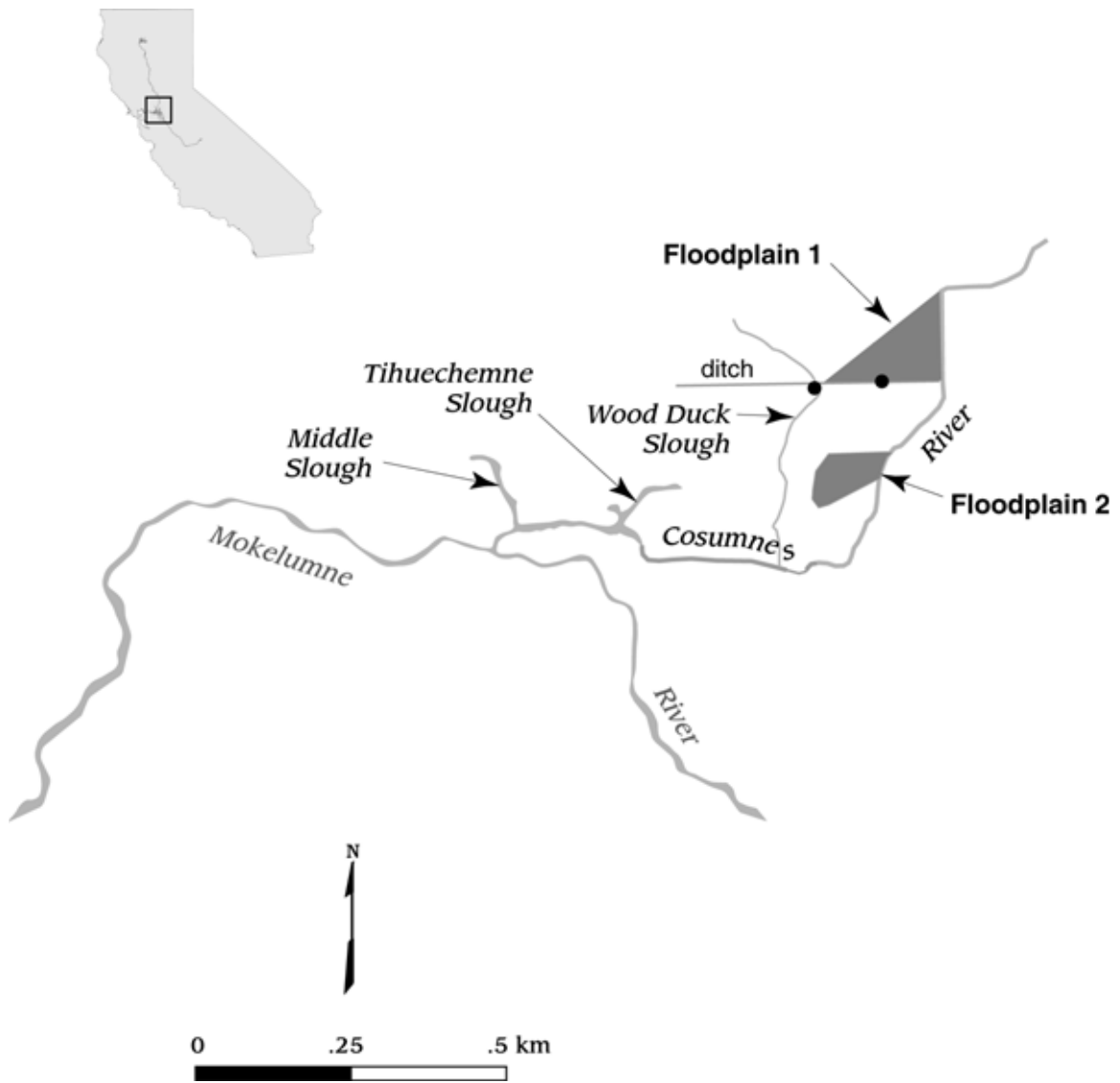
Figure 2. Hydrograph of the Cosumnes River at the USGS gauging station at Michigan

Bar, 1998-2005. The dotted line indicates flows at which water enters the floodplain from
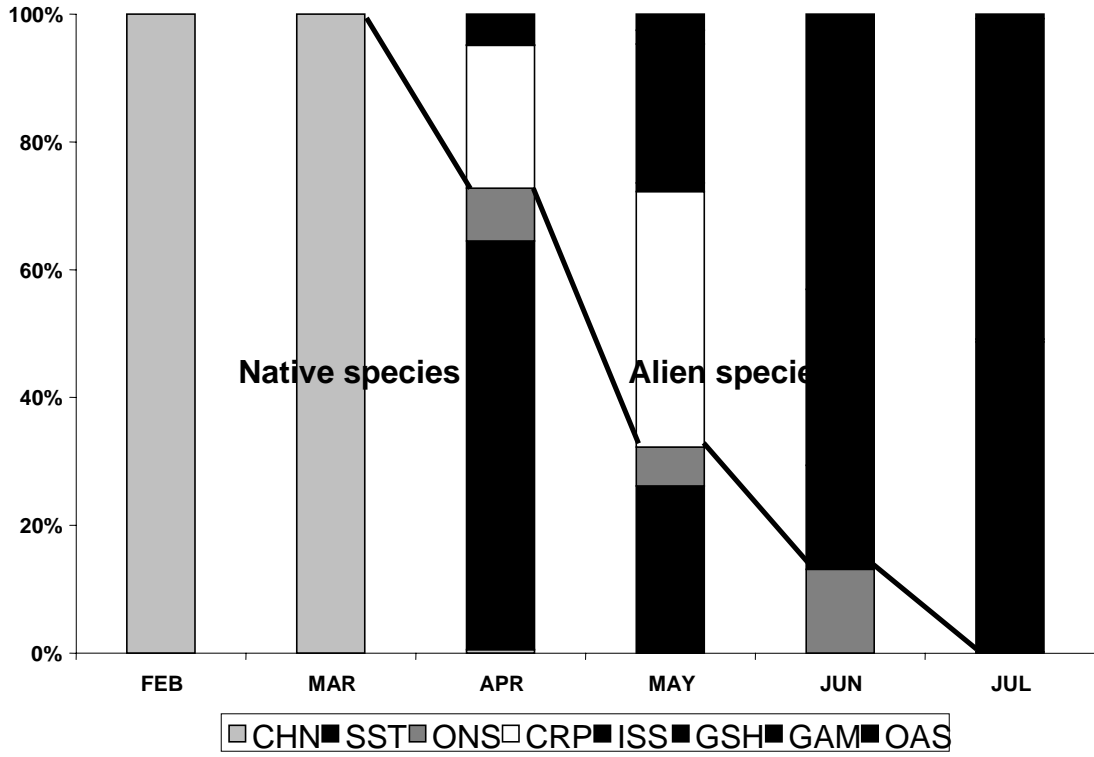
the river.

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 conditions. 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, GAM = western mosquitofish, and OAS = other aliens.
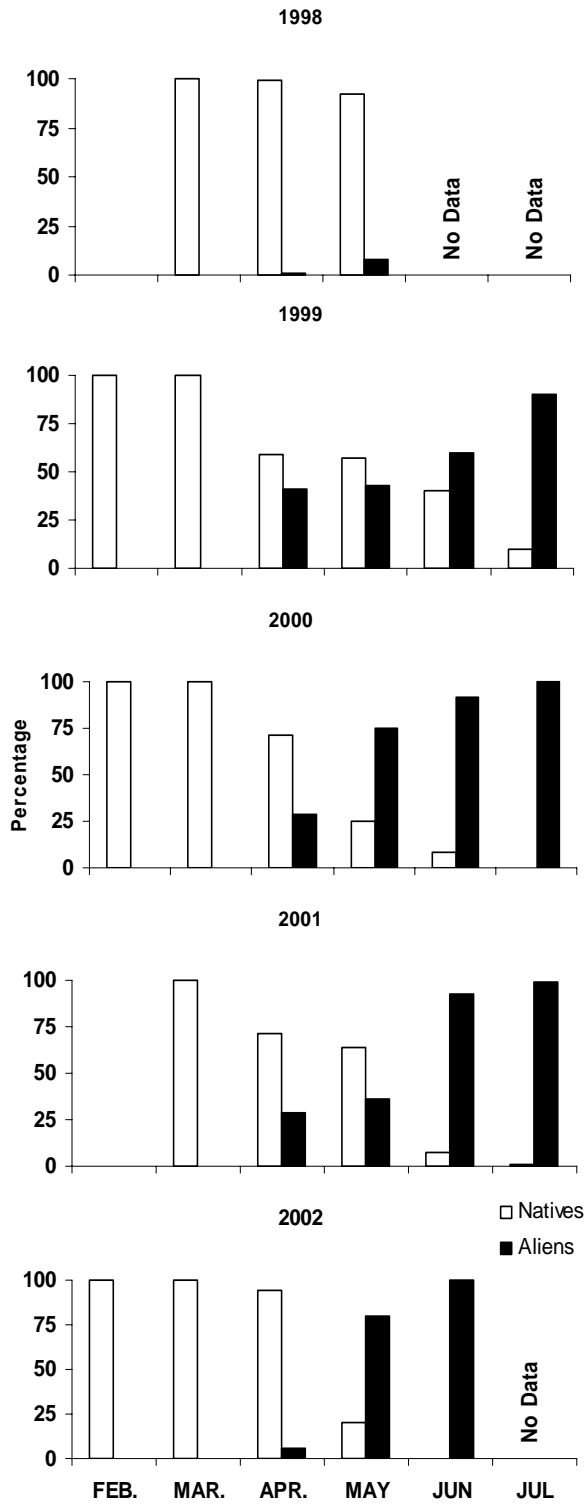
Figure 4. Percentages of juvenile native and alien fishes in seine hauls, by month,

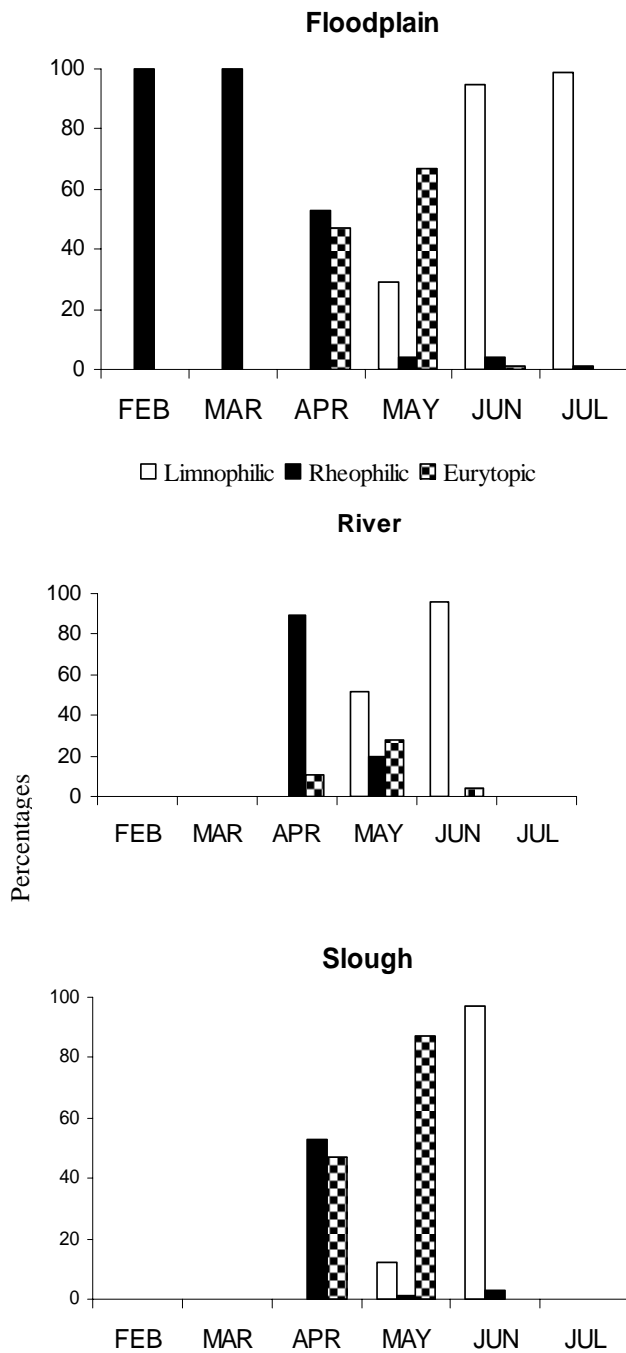Cosumnes River floodplain, 1998-2002.

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
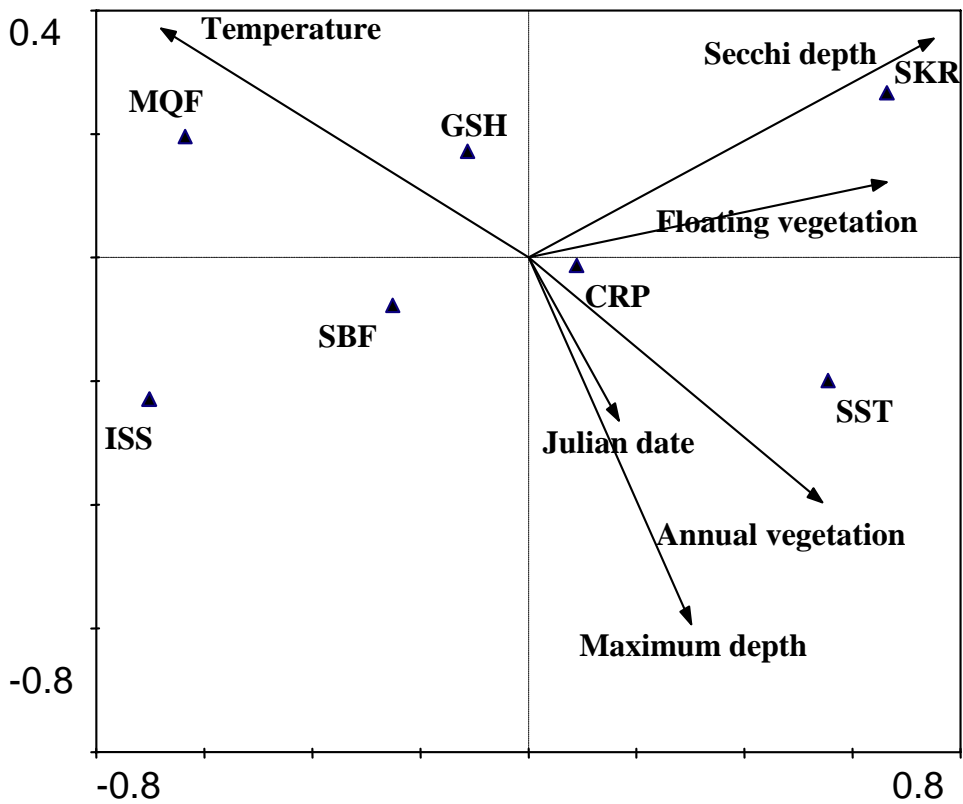
hauls, 1860 fish) habitats, year 2000.

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 MQF = western mosquitofish
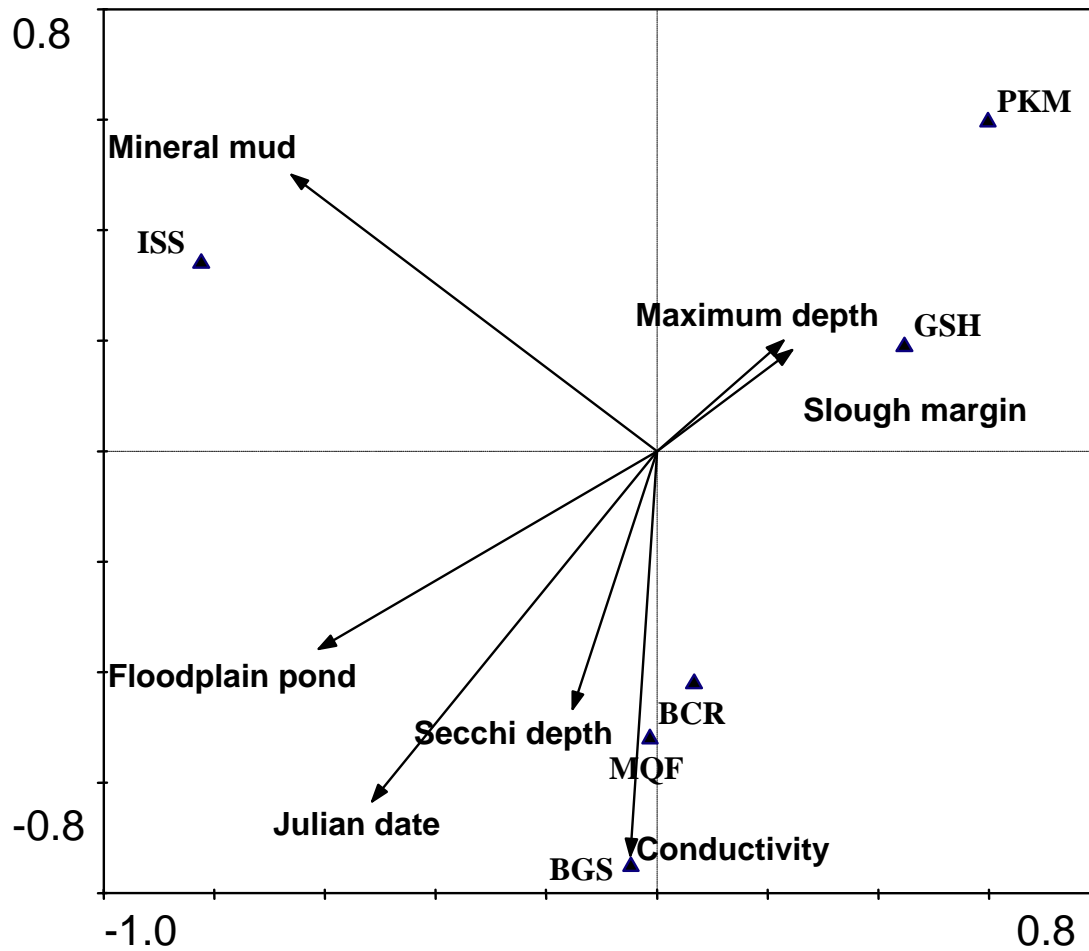
 Figure 7. Canonical correspondence ordination diagram showing the relationships of

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 BCR = black crappie.