The Influence of Flood Cycle and Fish Predation on

Invertebrate Production on a Restored California Floodplain

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"This paper has not been submitted elsewhere in identical or similar form, nor will it be during the first three months after its submission to Hydrobiologia."

Abstract

Although floodplains are known to be tightly controlled by the flood cycle, we know comparatively little about how flooding influences predators and their consumption of secondary production, particularly in highly seasonal floodplains typical of Mediterranean climates. In this study, we investigate how the seasonal dynamics of a central California floodplain influence the timing and magnitude of fish predation and the abundance and composition of invertebrates. For three years (2000-2002), we compared changes in abundances and size distributions of invertebrates through the flood season (January-June) with seasonal changes in physical conditions and the abundance of larval and juvenile fishes. Using diet analysis of fishes and manipulative experiments with fishes in field enclosures, we link specific changes in invertebrate populations directly to feeding preferences of seasonally abundant fish. Prior to March, we found little influence of fish predation, consistent with the near absence of larval and juvenile fishes. Coinciding with increased abundance of larval and juvenile fishes in April, we found significant declines in zooplankton abundance as well as declines in the size of zooplankton consistent with fish feeding preferences. Our results were consistent with feeding enclosure experiments that showed that fish rapidly depressed zooplankton populations particularly populations of larger cladocerans. At the end of May and June, zooplankton abundances rapidly increased, consistent with gut contents data that showed juvenile fishes switched to aquatic insects and later high mortality. We that throughout the season, zooplankton biomass reached a maximum approximately 2-3 weeks after disconnection or the river from the floodplain. We suggest that floodplain restoration in this region should consider management strategies that ensure repeated flooding events on a 2-3 week cycle during periods that will best match peaks in the abundances native fishes.

Introduction

River floodplains provide numerous ecosystem services including habitat for native fishes and water fowl, recharging groundwater, extending riparian habitats and protecting downstream areas from flooding (Bayley 1995, Brunk & Gonser 1997, Ward et al. 1999). Floodplains are also sites of high primary and secondary production that may provide trophic support for river ecosystems and adjacent riparian habitats (Vegas-Vilarrubia & Herrera 1993, Bayley 1995, Sparks 1995, Ward 1998, Tockner & Bretschko 1996, Tockner et al. 1999a). The dynamics of this productivity are generally driven by patterns of flooding in which floodplain geomorphology interacts with the timing, magnitude, duration and frequency of flooding (Power et al. 1995). However, despite the acknowledged importance of floodplain hydraulics, we know little about the ways in which physical forcing influences biological interactions such as competition or predation that may strongly influence floodplain food webs. We have known for decades that predation by fishes can strongly influence the abundance, diversity and size distributions of zooplankton in lake systems (Brooks & Dodson 1965, Hall et al. 1976, Carpenter & Kitchell 1988, 1993, Hambright & Hall 1992, Wellborn et al. 1996, Shurin 2001, Cottenie & de Meester 2004). But few studies have examined how predation by fishes influences invertebrates populations in the highly seasonal flood cycle typical of floodplains in Mediterranean climates.

With some important exceptions (Fisher et al. 1982, Ellis et al. 1998, 1999, Valett et al. 2005), most of our understanding of floodplain food webs comes from other regions such as the Amazon River in Brazil (Junk et al. 1989, Furch & Junk 1993, Bayley 1995), the Orinoco River in Venezuela and Colombia (Lewis et al. 2000, Lewis et al. 2001), the Danube River in Austria (Tockner et al. 1999a, 1999b) and others around the world (Walker et al. 1995, Sheldon et al.

2002). From these studies have emerged important conceptual models of floodplain function

including the flood-pulse concept (Junk et al 1989, Bayley 1995) as well as extensive

documentation of the transition of floodplains from physically driven systems during the initial

flooding events to more biologically driven systems following disconnection. These studies

have also documented how nutrient dynamics and biological interactions play a role in dictating

the tempo of production (Heiler et al. 1995, Keckeis 2003, Hein et al. 2004). Only recently have

floodplains in the Mediterranean climate of central California been investigated in light of these

other studies (Sommer et al. 2001, 2004, Sobsczak et al. 2002, 2005, Schemel et al. 2004, Feyrer

et al. 2004).

  A central goal for this study is to determine the how the strongly seasonal hydrological

cycle of a Mediterranean-climate floodplain influences the predator-prey relationships between

invertebrate populations and floodplain fishes. Specifically, we address how the flood cycle

interacts with seasonal variation in the abundance of larval and juvenile fishes to shape the

abundance and size distribution of zooplankton and benthic invertebrates on a restored floodplain

of the lower Cosumnes River in the Central Valley of California, U.S.A. The Cosumnes River is

one of the few remaining rivers with head waters in California's Sierra Nevada range that

experiences a relatively "natural", flood cycle. We documented changes in the abundance and

size distribution of zooplankton and benthic invertebrates over a three-year period as well as the

variability in flood events and fish predation. We also quantified spatial variation by contrasting

different areas of the floodplain with the main stem river channel.

  Understanding how variation in the flood cycle influences food web dynamics in this

seasonal floodplain habitat will help guide current and future efforts to restore floodplain habitats

in California and throughout the western U.S. We know that the floodplains generally possess

higher levels of invertebrate food resources, higher water temperatures and additional refugia that can contribute to increased growth and survival of juvenile Sacramento splittail (*Pogonichthys macrolepidotus*) and Chinook salmon (*Oncorhynchus tshawytscha*) that are important conservation targets (Sommer et al. 2001, Ribeiro et al. 2004). Unfortunately, functioning river floodplains are rare in California, although efforts are underway in many areas to restore floodplain habitats. In order to restore floodplains that will effectively support higher trophic level consumers such as fishes, riparian birds and other targeted species, we need to understand how the flood cycle can be managed to produce high invertebrate abundances and to better match fish spawning with peaks in invertebrate populations. It has long been recognized that the degree of match or mismatch in the timing of zooplankton production and larval and juvenile fish abundance can have important consequences for fish population dynamics (Cushing 1972, 1990, Straile & Geller 1998, Chick & Van Den Avyle 1999). Therefore, effective floodplain restoration will need to incorporate management of the flood cycle that will lead to both high levels of invertebrate production and a good match with the spawning and abundance cycles of larval and juvenile fishes.

In this study, we examine how seasonal patterns of flooding and availability of larval and juvenile fish predators influences the dynamics of zooplankton and benthic insect populations. We measure the abundance, diversity and size distribution of zooplankton and benthic invertebrates in concert with phytoplankton abundance and physical and water quality variables at several sites in both the floodplain and the main stem river over a three year period. We also conduct manipulative experiments with fish predators and use gut contents analysis to determine the link between changing patterns of abundance and size distribution of invertebrates with fish

populations. We conclude by developing recommendations for future floodplain restoration based on our results.

METHODS

Study Site

The Cosumnes River watershed occupies an area of nearly 1600-km^2 on the west side of the central California Sierra Nevada (Figure 1). The watershed elevation ranges from the headwaters at an elevation of 2400 m in El Dorado National Forest to near sea level where it meets the larger Mokelumne River just above the Sacramento-San Joaquin Delta. Only 16% of the watershed lies above 1500 m, so most river flow is the result of rainfall, rather than snowmelt. Annual precipitation averages 45 cm year and falls almost entirely between November to May creating a five month dry season typical of Mediterranean climates. At the main gauging station at Michigan Bar, which is 40 km upstream for the floodplain, river flows range from no flow during dry years to a peak flow of 2,650 cubic meters/second (cms) during an exceptional event in 1997. Although there are many large and small diversions throughout the watershed, there are no large dams on the main stem or on the three major forks of the Cosumnes River. Therefore, this river has a hydrograph that is relatively natural compared to the managed flows found in nearly all the other major rivers in this region.

The Cosumnes River Floodplain (henceforth CRF) is an area consisting of upper (approximately 42 ha) and lower (approximately 100 ha) floodplains that were historically agricultural fields and were in row crop production as recently as 1997. The CRF is separated from the Cosumnes River by levees, which have been breached several times beginning in 1985 (Figure 1). These breaches now result in regular seasonal flooding of what is now the Cosumnes River Preserve, which is owned and managed by The Nature Conservancy.

We identified study sites in different habitats to compare patterns of abundance and distribution of lower trophic levels including crustacean zooplankton, aquatic insects and other benthic invertebrates. The sites include two on the main stem of the Cosumnes River (Figure 1, sites CRB and RRB), two floodplain ponds which in many years can retain water throughout the year, but are reduced in volume during the dry season from early summer through late fall (sites PD1 and PD2), and three floodplain grassland areas that are seasonally dry and in some cases hold water for only a few weeks a year (sites 3, 7, 11). We selected sites based on how well they represented the specific habitats and for their accessibility for collaborators studying fish populations and water quality

Water Quality

At each site, we measured several water column variables on site at least weekly during the flood season using a handheld YSI 85 multi-parameter meter. These variables included dissolved oxygen (DO- mg/L and %), temperature (ºC), electrical conductivity (EC - µs/cm), specific EC (corrected to 25 ºC - µs/cm) and salinity (ppt). We measured flow velocity at 40 – 50% water depth with a Marsh-McBirney Flow Mate 2000 and secchi depth with standard methods.

In 2001 and 2002, we also collected surface water grab samples on the same approximately weekly schedule as the zooplankton. Grab samples were collected in acid washed Nalgene bottles and were kept in a dark, iced cooler after collection and during transportation to the laboratory for analysis. Here we present the results for several summary variables including the ratio of total nitrogen to total phosphorous (TN:TP) and chlorophyll-*a* (Chl-*a*). We report a more complete analysis of water quality variables elsewhere (Gallo et al., *in review*.).

Unfiltered aliquots for total nitrogen (TN) and total phosphorous (TP) were digested as described by Stark and Hart (1986). TN was analyzed using the Carlson method described by Carlson (1986) and Yu et al. (1994). TP was analyzed using a spectrophotometer (Perkin Elmer Lambda 38) and the method described by Clescseri et al. (1998). Chorophyll-a (chl-a) measurements were made using the pigment extraction fluorometric method described by Clescseri et al. (1998).

Zooplankton

We used a hand-towed plankton net (150 um mesh, 0.3 m wide, 3:1 l/w ratio) outfitted with a propeller flow meter (Ocean Dynamics, Inc.) fastened in the middle of the net mouth. In sites with active flow, the net was tossed into the current and maintained just below the surface for a period long enough to allow a standard count of >1000 units on the flow meter (typically about 30 seconds in ~ 1 m/s flow). In sites with no or little flow, the net was towed by walking with the net extended to the side to minimize collecting benthos kicked up by walking. We took two replicate tows in adjacent areas per sampling site, transferred zooplankton from each tow into labeled 500 ml Nalgene bottles and placed them in a cooler until we returned to the laboratory. Zooplankton were fixed with Lugol's iodine solution with sucrose and enumerated under a dissecting scope at 25 x magnification on a Ward plankton counting wheel. During counting, zooplankton were identified to the lowest possible taxonomic level using identification keys by Thorp & Covich (2001) and with validation by systematic experts (S. Skelton, Cal. Dept. Fish and Game, W. Fields, Hydrozoology, Inc., and A. Kotov, A. N. Severtsov, Institute of Ecology and Evolution, Russian Academy of Sciences). Zooplankton biomass calculations were performed using the regression calculations described by Dermott & Paterson (1974) and Dumont et al. (1975).

To analyze the difference among sites using repeated samples taken over time, we used repeated measures ANOVA to test differences among habitats (river, pond and grassland sites defined above) that included main stem river sites (between subject) and time points (within subjects) and their interaction using 10 taxa counted in 2000 and 15 taxa distinguished in 2001 and 2002 (see Appendix for complete list of taxa). We had 10 time points in 2000, 15 in 2001 and 20 in 2002. In each year, the common covariance matrix failed to meet the assumptions of sphericity, therefore, we corrected F and p values using Huynh-Feldt Epsilon. To analyze temporal trends in zooplankton biomass, we used a Model I least squares regression to analyze the relationship between maximum zooplankton biomass and sampling date and curvilinear regression to analyze the relationship between invertebrate biomass and post-flood time interval.

Benthic Invertebrates

At each site, we collected invertebrates from two replicate sweeps, each involving a standard rectangular sweep net (0.46 m x 0.23 m x 0.25 m) pushed along the substratum through vegetation over a distance of 2 meters. Invertebrates from each sweep were rinsed into labeled plastic Ziploc bags, placed in a cooler and returned to the lab. In the lab, invertebrates were first separated alive from vegetation and debris, fixed in 70% ethanol and enumerated under a dissecting scope at 25 x magnification. Organisms were identified to the lowest possible level (generally genus) using standard identification keys (Usinger 1974, Pennak 1978, Merritt & Cummings 1996, Thorp & Covich 2001). Biomass estimates were calculated from either our own dry weight estimates or from published values.

Larval and Juvenile Fish Abundance

Abundances of juvenile and adult fish were estimated using beach seines and electrofishing as part of a collaborative effort and have been published elsewhere (Moyle &

Grosholz 2003, Crain et al. 2004, Ribeiro et al. 2004). Here we present summary data for this

work for purposes of explaining patterns of fish predation on the floodplain.

On several dates in 2000 and 2001 from late February through early July, larval fishes

and crustacean zooplankton were sampled by deploying light traps in the evening hours at

several sites including two floodplain sites. We were not able to deploy these at the shallower

floodplain sites because of inadequate depth of the water column. This method involves passive

sampling of both groups of organisms by attracting them with a light source and permitting

passage into a central collection area. At each site, three replicate collectors were deployed with

a waterproof flashlight as a light source. Collectors were deployed at each site in sequence, so

from deployment to collection, each collector was in place and actively "fishing" for one to two

hours. Samples were immediately fixed in 10% formalin after removal from the collector and

prior to return to the lab, because of the delicate condition of larval fish. Once in the lab,

zooplankton were separated from larval fish, transferred to Lugol's and enumerated with the

same methods as other zooplankton. Fish were counted separately from zooplankton (Crain et

al. 2004).

Juvenile Fish Diets

As part of a collaborative effort (Crain et al. 2004, Ribeiro et al. 2004), juvenile and adult

fishes were sampled with beach seines at least weekly during 2000-2002 to determine seasonal

and habitat specific patterns of abundance. We used some of these collections for diet analysis

and here we report data for one year (2001) for juvenile splittail (*Pogonichthys macrolepidotus*).

Previous work has shown that this species is the most abundant native juvenile fish in some years

(80-90% of native fishes) and one of the most abundant in this floodplain overall (often 50% of

all juvenile fishes) (Crain et al. 2004). The guts of individual juvenile splittail from the Pond 1

site on the floodplain were sampled for six days between April 26 and June 20, 2001 (mean

sample size per date=58, range 34-124). All taxa in the guts were identified to the nearest

practical level, typically order for insects and from order to genus for zooplankton, with a total of

17 taxa distinguished (Crain & Moyle, *unpubl. data*). Overall percent fullness of the gut and the

percentage of the guts contents represented by each taxon were recorded. Here we report the

percentage of all gut contents represented by each taxon focusing on the most common orders (or

suborders): Calanoida, Cladocera, Plecoptera, and Coleoptera.

Juvenile Fish Predation

In April 2002, we conducted an experiment to directly measure the impacts of juvenile

fishes on zooplankton density and community structure. We deployed eight square cages (1 m x

1 m x 1 m) made of 105 μm mesh supported by PVC pipe at floodplain site PD 1. The 105 μm

mesh is porous to most phytoplankton except large aggregations, but can exclude or retain most

macrozooplankton and fishes.

To stock enclosures with macrozooplankton at natural densities and relative species

abundances, we collected zooplankton with plankton tows taken adjacent to the enclosures cages,

calculated the volume sampled, and distributed equal zooplankton samples to all eight cages.

We used one of the most common juvenile fishes, splittail, as the predator in the enclosure cages.

These feed in similar ways to as several other common species at this site including golden

shiners (*Notemigonus crysoleucas*), Sacramento blackfish (*Orthodon microlepidotus*), and

common carp (*Cyprinus carpio*). We collected small juvenile splittail approximately 20-25 mm

SL (U.S. Fish and Wildlife collection permits issued to P. Moyle) with beach seines and quickly

distributed them to four of the eight cages at a density of approximately nine per m^2, which is

within the normal range of juvenile fish densities (Crain et al. 2004). Henceforth, we refer to the four cages stocked with fish as "fish cages" and the four cages without fish as "control cages".

At the start of the experiment, and at 3, 6, 9 and 12 day intervals, we collected 1 L water samples to measure zooplankton abundance. At each time point, we collected three 1 L samples from within each of the four control and four fish cages and as well as three samples from outside the cages to represent natural background abundances. All samples were kept cool, returned to the lab, and fixed with Lugol's solution and all taxa were counted as above.

For the fish predation experiments, we analyzed the results of the experiments using univariate ANOVA comparing fish cages vs. control cages vs. pond treatments with total zooplankton, total number of copepods and total number of cladocerans as dependent variables. To avoid analysis of repeated observations, we present analyses of the beginning and ending date of the experiment (day 12). Count data were square-root transformed as necessary to meet parametric assumptions and Tukey's LSD test was used for posthoc comparison of treatment means.

RESULTS

Water Quality

Flood pulse magnitude and duration was smaller and shorter during 2001 than 2002, although both were much smaller than the flood cycle evident in 2000 (Figure 2). This resulted in leading to diminished watershed and floodplain flushing and input of allochthonous material and nutrients from the river to the floodplain in 2001, which we compare with 2002. Very limited water quality data were collected for 2000 and are not presented.

Several important physical parameters varied significantly among habitats and through time. Temperature, electrical conductivity (EC) and dissolved oxygen (DO) (Figs. 3A, B)

showed significant variation with the flood cycle. Temperature, EC and DO generally declined after the first spillover associated with flooding, especially later in the season when temperature differences between floodplain and river were greatest. Differences between habitats in temperature, EC and DO were also observed. On the floodplain (Figure 3A), all three parameters showed a general increasing trend during the flood season, whereas in the river channel only temperature showed an increasing seasonal trend (Figure 3B). Temperatures on the floodplain by March were 5 degrees higher than in the river. EC on the floodplain was also significantly higher than in the river. DO was also dramatically higher in some cases on the floodplain relative to the river channel, when we measured supersaturation that was likely the result of high rates of photosynthesis by benthic and planktonic algae.

We also observed TN:TP increases as hydrologic residence time increased and at the end of the flooding season beginning in May (Figs. 3A, B), suggesting a shift from slight nitrogen limitation as well as nitrogen and phosphorous co-limitation to phosphorous limitation. There were important spatial differences in the TN:TP ratios that mirrored other habitat differences.

We found temporal patterns of chl-*a* (a proxy for phytoplankton biomass) were similar across the two years 2001 and 2002 in both habitats (Figs. 3A, B). There were significant increases throughout the season, rapid declines due to dilution following flood events, and generally very high values at the end of the flood season (June). We also found strong and significant differences among sites in phytoplankton biomass with the highest values seen in the floodplain ponds (Figure 3A) where chl-*a* values were 5 to 10 times higher than values from the river site (Figure 3B). Extremely high chl-*a* levels occurred at the end of the season generally coinciding with high zooplankton abundance.

Zooplankton Abundance

Spatial patterns. In all three years (2000-2002) we measured zooplankton biomass 10-100 times greater at floodplain sites than at river sites (Figure 3A, 3B). For all zooplankton taxa combined, repeated measures ANOVA showed that these differences were significant for all years. For 2000, there was a significant effect of habitat ($F_{1,38}$= 8.63, p=0.006) as well as a significant time ($F_{9,342}$=5.15, p=0.008) and time x habitat interaction ($F_{9,342}$=6.41, p=0.003). The same was true for 2001 with a significant effect of habitat ($F_{1,58}$= 13.32, p=0.001), time ($F_{13,754}$=3.81, p=0.008) and time x habitat interaction ($F_{13,754}$=3.71, p=0.010). This also held for 2002 with a significant effect of habitat ($F_{1,58}$= 12.30, p=0.009), marginally significant effect of time ($F_{14,812}$=2.29, p=0.058) and a significant time x habitat interaction ($F_{14,812}$=3.18, p=0.013). For all years, an examination of the means showed that the significant time by habitat interaction was the straightforward result of higher biomass at floodplain sites relative to river sites during periods of overall higher biomass coincident with lower flows.

Temporal Patterns. We found a strong relationship between zooplankton biomass at our floodplain sites and the frequency of flooding. There was a strong increase in zooplankton biomass in the floodplain following each flood event with a peak in biomass generally between 10 and 25 days after flooding ceases with the highest values observed at approximately 21 days (Figure 4A). Zooplankton biomass declined after this period and never regained the highest biomass even after more than 40 days post disconnection. Similar data for phytoplankton show patterns of increase that match those of zooplankton. Interestingly, we found that seasonal timing of flooding did not significantly influence the peak of zooplankton biomass. This biomass maximum occurred approximately 21 days after both winter and spring floods alike. When we compared the biomass maximum per flood cycle across dates throughout the flood season, we found a weakly positive, but nonsignificant relationship (y = 2.9189x – 110819, R^2 =

0.151, Figure 4B). An additional test comparing the time to reach maximum zooplankton biomass after flooding showed no significant difference between early season (prior to March 30) and late season (after April 1).

In addition to the short-term dynamics of zooplankton abundance driven by the flood cycle, there was a broader mid-season decline in overall biomass between late March and April for 2001 and 2002 (Fig 5B and 5C). This was not seen in 2000 likely due to low overall zooplankton biomass earlier as the result of an extended flooding period and low water residence time from February through early April (Figure 5A). This significant decline in zooplankton biomass did not parallel water temperature over this period (temperatures are generally increasing), but may be to due to other factors (see Discussion).   The rapid increase at the end of the season (late May to June) coincided with water temperatures of 20-25 ^{o}C, which may have negatively affected fish predators (see Discussion).

Temporal changes in the taxonomic composition of zooplankton were also evident. Larger cladocera such as *Daphnia* spp. and *Ceriodaphnia* sp. showed greater proportional abundance during floods in the early part of the year and much lower densities during later parts of the year (Figure 6). In contrast, small cladocera such as *Bosmina* sp. and calanoid copepods showed generally the opposite trend with greater proportional abundance later in the season (Figure 6).

Benthic Invertebrates

Benthic invertebrate abundance developed more slowly during the flood season than crustacean zooplankton, but increased steadily after the peak of the flood cycle in 2001 and 2002 (Figure 7A and B). Because of data limitations, we cannot analyze the timing of peak biomass as we did with zooplankton. The majority of taxa initially increased very early in the season

(Jan. 2002) and slowly declined or maintained their abundances through the early spring while Hemiptera (mostly Corixidae) rapidly increased beginning in March in both years. At the end of the season in June 2002, many taxa once again declined. By the end of the season, a large proportion of invertebrates in the majority of samples consisted of corixids. Also at the end of the season, there were fewer chironomids and other diptera and large numbers of other predators particularly odonates, belostonomids, and particularly corixids, which represent the majority of taxa in most sweeps. Interestingly, there were never any corixids found in fish guts (see below).

Larval and Juvenile Fish Abundance

There was a consistent temporal pattern of abundance of juvenile fishes on the floodplain in all three years for which data were collected (1999-2001 for larval fish, 1999-2002 for juvenile fishes, Crain et al. 2004, Ribeiro et al. 2004). Native adult fishes including splittail invade the floodplain and begin spawning after the first flood events, although they may do so somewhat later. Adults are then present throughout much of the season but then migrate off the floodplain. Data from the light traps show that larval fish are virtually absent until early to mid-March. However, by April, juvenile fish have become more abundant, larger (15-20 mm) and are efficient predators of zooplankton. These data also showed that increase in the number of larval fish on the floodplain was followed by a rapid decline of zooplankton from March to April.

Juvenile Fish Diets

Analysis of juvenile splittail gut contents show a rapid shift in diet over periods of a few weeks. Data from April 26, 2001 showed that 85% of the fish with identifiable items in their guts contained cladocerans (mostly *Daphnia* and *Bosmina*), while few if any fishes contained identifiable copepods or insects (Figure 8). One week later 16% of fishes contained copepods in

their guts and the percentage of fish with cladocerans began to decline (80%). Insects were

identified in less than 5% of fishes in these first two sample dates. However, eighteen days later,

presumably following intensive grazing, Cladocera (1%) and Copepoda (0%) were rare in

sampled fish guts. Instead, fishes had switched to insects with 42% containing Plecoptera and

52% containing Coleoptera (Figure 8).

Juvenile Fish Predation

Fish had a significant impact on both the density and composition of zooplankton in the

fish cages in comparison with the control cages. With respect to total zooplankton density,

although there were no significant differences either at the start of the experiment (day 0), or day

3, we found significantly higher zooplankton densities in no fish cages by day 6, which

continued until the end of the experiment on day 12 ($F=9.94$, $df=2,8$, $p=0.007$) (Figure 9).

Interestingly, zooplankton densities in the unmanipulated pond samples taken outside the cages

(natural abundance) declined in parallel and were not statistically different from zooplankton

densities inside the fish cages.

Fish predation in experimental enclosures strongly influenced zooplankton species

composition. We saw no difference in copepod densities (pooling calanoids and cyclopoids)

among any of the treatments at the start of the experiment and no difference between fish and no

fish cages at the end of the experiment. However, copepod densities in the pond were

significantly lower by day 12 ($F=6.92$, $df=2,8$, $p=0.018$) (Figure 9). Densities of copepods in the

both the fish and control cages actually increased during the experiment (mean for controls: day

3=14/ml, day 12= 45/ml, means for fish cages: day 3=7/ml, day 12= 25/ml). In contrast,

cladocerans showed significant treatment differences due to declines in density (particularly

Daphnia and *Ceriodaphnia*). Like copepods, there were no treatment differences at the start of

the experiment, but there were significant differences between fish cages and control cages at day 12 ($F=6.26$, $df=2,8$, $p=0.023$). Interestingly, the cladoceran abundances in fish cages did not differ significantly from the pond samples outside cages (natural abundance) at the end of the experiment (Figure 9).

DISCUSSION

The Cosumnes River floodplain ecosystem is typical of many other floodplain ecosystems and is strongly controlled by the annual flood cycle (Bayley 1995, Ward & Stanford 1995, Ward 1998, Ward et al. 1998, Tockner et al. 2000, Sommer et al. 2001, Baranyi et al. 2002, Sommer et al. 2004, Schemel et al. 2004). It progressed rapidly from a physically driven system to a biologically driven system in a matter of weeks. During the flooding or connection stage where the river was actively filling the flood plain (during both rising and falling limbs of the flood), the flooding river waters rapidly reduced both planktonic and benthic invertebrate densities, presumably through simple dilution. During flood events occurring later in the season, this dilution likely also reduced fish abundance and predator-prey interactions. After the river inflow ceased, the floodplain made the transition from a simple extension of the river to a more pond-like system, with rapidly increasing water temperatures and primary and secondary productivity.

The mechanisms responsible for rapid changes in invertebrate abundance are only partially understood in this system. Our work suggests that fish predation may have influenced zooplankton population dynamics during the later part of the season. Work by Crain et al. (2004) demonstrated that beginning in March, high abundances of larval and then juvenile fishes became common on the floodplain, whereas they were virtually absent prior to this period.

Several lines of evidence support the idea that this increased presence of juvenile fishes in the spring significantly influenced abundance patterns of zooplankton.

First, the results from the feeding experiment conducted with enclosure/exclosure cages supported the role of fishes in producing the observed patterns of zooplankton abundance late in the season. These data also showed that natural densities of juvenile fishes could limit production of zooplankton over short time scales. We recognize that enclosures experiments inevitably include cage effects that often cannot be adequately controlled. The height of our cages relative to the area (1 m^2) would not be sufficient to result in significant shading and the flow of water through the mesh was adequate to minimize any temperature artifacts. There is the possibility that caging juvenile fishes could have resulted in higher than normal rates of predation, however, the declines in our control samples taken concurrently from the open floodplain were statistically similar to the declines inside the fish cages. This suggests that the rates of fish predation inside our experimental cages reasonably approximated natural rates of predation on the adjacent floodplain. Therefore, we feel that cage artifacts, although inevitably present, have not significantly influenced our general conclusions resulting from this experiment.

Just as inside the cages, the declines in the larger cladocerans from areas outside the cages were also much more rapid than other zooplankton. The results from this experiment clearly indicate that juvenile fish rapidly consumed larger (and slower) cladocerans such as *Daphnia* relative to *Bosmina* and calanoid and cyclopoid copepods. This suggests that fishes were responsible for the observed changes in the distribution of zooplankton (from larger, slower taxa to smaller, faster taxa) as well as sharp declines in overall zooplankton abundance from late April through May.

These results were consistent with similar trends that have long been observed in zooplankton communities in lake systems (Brooks & Dodson 1965, Hall et al. 1976, Carpenter & Kitchell 1988, 1993, Hambright & Hall 1992, Wellborn et al. 1996, Shurin 2001, Cottenie & de Meester 2004). These studies have documented selective predation of larger and more easily captured zooplankton by consumers and a shift towards dominance of smaller and less easily captured taxa. The parallels between these studies and our results highlight the rapid transition of the Cosumnes floodplain from a lotic to a lentic system in a matter of a few weeks.

The declines in zooplankton abundance were also supported by our diet analysis of juvenile splittail. We found that small juveniles initially consumed largely zooplankton, but showed a dramatic shift in diet from zooplankton to aquatic insects over the course of a few weeks. This switch in diet coincided with the sharp increase in zooplankton seen in mid-May in 2001 presumably as growing fishes made the transition away from zooplankton. The changing physical regime of the floodplain also contributed to this result as the temperatures at the end of the season reached levels that were lethal for many juvenile fishes. Also, many fishes such as Sacramento splittail migrate off the floodplain during this late season period. These diet data are also consistent with changing abundances of benthic invertebrates. Declines in some taxa such as Coleoptera and Diptera coincided with the timing of fish shifting diets away from zooplankton and towards insects. Others such as Plecoptera, which were at low abundance through 2001 and 2002, were a significant part of fish diets (in 2001) suggesting a strong preference of fish for this taxon.

These shifts in diet with increasing fish size mirror similar patterns that have long been witnessed in a range of lake systems. Ontogenetic shifts in diet and habitat use, typically as a function of fish size, have been documented for many fish species (Mittlebach 1981, Werner &

Hall 1988, Werner & Anholt 1993, Mittlebach & Persson 1998, Harvey & Kitchell 2000). These shifts in fish diets have also been shown to frequently have significant impacts on prey populations as well.

The timing and intensity of fish predation varied seasonally and was influenced by characteristics of the flood cycle. Although our data suggest that fish predation likely influenced zooplankton populations from April to June, when floods occurred during this period, the rapid growth of zooplankton following each flood suggests that dilution of floodwaters reduced the impacts of fish predation for a week or two after disconnection. This idea was supported by the fact that the peak in standing biomass of zooplankton occurred predictably during the 2-3 week period post-flood.

The strong, but seasonal, effects of fish predation were remarkable with respect to constancy of the period of the zooplankton cycle. Traditional predator-prey theory (Murdoch and Oaten 1975) can explain a relatively constant period for zooplankton predator-phytoplankton prey cycle, despite increasing amplitude of the cycle as population growth rates (r) increase with temperature and likely decreasing carrying capacity "K" as floodplain size and depth decreases. Although zooplankton abundance decreased dramatically in response to flood events as the result of dilution, we found that the peak standing biomass of zooplankton was reached approximately 2-3 weeks after flooding ceased, despite the fact that fish predation was dramatically higher during the middle part of the flood period (early April-late May). This is consistent with the idea that fish predation may not limit zooplankton growth for approximately the first week post-flood.

We also must conclude that fish predation is not the only or perhaps the primary factor limiting zooplankton production on the floodplain. We found the peak is zooplankton abundance was independent of the time of year and the presence of fish predation. So although water

temperatures on the floodplain were 15 C warmer in April than in January, and fish predation was high in April and nearly non-existent in January, the peak of the zooplankton biomass cycle remained fairly constant. Therefore some of factor or set of factors must also be contribute to limiting zooplankton biomass.

Other factors limiting zooplankton biomass may include phytoplankton availability, which can limit zooplankton population growth throughout the season (Schemel et al. 2004, Sobczak et al. 2005). Although phytoplankton may limit zooplankton growth under some circumstances, our data do not suggest a tight coupling between zooplankton and phytoplankton biomass, although there were indications of increases in phytoplankton following declines in zooplankton abundances. Standing abundance of phytoplankton as measured by chl-*a* first declined after floods due to dilution and then rapidly increased. Later in the season as phytoplankton density increased, the system seemed to shift towards nitrogen-fixing primary producers, which may be more grazer resistant, and which may alleviate nitrogen limitations and shift the system toward phosphorous shortages. This is roughly supported by our TN:TP data suggest that there may be some early season periods of nitrogen limitation and a shift to late season phosphorous limitation. The role of nutrient limitation and the specific roles of nitrate, ammonium, orthophosphate and other water quality variables that may have influence primary production in this system are examined more completely elsewhere (Gallo et al., *in review*).

The dynamics of zooplankton are also likely influenced by the microbial food web for which we have little or no information. Unfortunately little is known about the microbial food web in this system. Preliminary work (Müller-Solger et al, unpublished) suggests that zooplankton may often prey heavily on microbial organisms in this system. However, recent work comparing the nutritional value of phytoplankton from the Cosumnes River Floodplain

with other similar habitats in this region and the utilization of detrital carbon in the near-by Sacramento-San Joaquin River Delta suggest that nutritional factors associated with phytoplankton regulate zooplankton growth despite substantial inputs of detrital carbon (Sobzack et al 2002, 2004, Müller-Solger et al. 2002).

Overlaying this temporal patterns of variation in primary and secondary production is spatial variation in these patterns. Temperature was significantly higher on the floodplain than in the adjacent river channel, which implied a higher water residence time, although this is only estimated and actual residence time was not measured. EC was also generally higher on the floodplain, especially towards the end of the season implying higher evapotranspiration rates than in the river habitats. We also found that the floodplain experienced greater N limitation in the early spring, but apparently less so in the late spring as the result of recycling, a shift from primary producers to N-fixing cyanobacteria or other processes including mineralization of dissolved organic N (Gallo et al., *in review*).

Paralleling these differences in the physical and chemical properties of the water column were strong differences between the river channel and the floodplain ponds and grassland areas with respect to the magnitude of primary and secondary production. The floodplain areas had benthic invertebrate biomass and zooplankton biomass that were one to two orders of magnitude greater than in the river channel, which supports similar results from other floodplain systems. In particular, the shallow floodplain ponds generated large standing abundances of zooplankton exceeding several hundred thousand per m^3. Also chl-*a* values are typically 10-50 ppm or five to ten times the levels in the river.

In summary, the results presented here and those from recent studies of nearby floodplains in central California demonstrate the important linkage between the timing of the

flood cycle, production of lower trophic levels and the seasonal role of fish predators. We found

strong and predictable cycles of invertebrate abundance both across the flood season and within

seasons closely linked with the flood cycle. The timing of these patterns suggest ways in which

floodplains in this habitat could be managed to encourage high levels of zooplankton and insect

production to support fish and other higher trophic level consumers.

We found distinct peaks in zooplankton biomass on the floodplain that occurred

predictably 2-3 weeks after disconnection from the river. Therefore, our work suggests that

management of the Cosumnes floodplain should aim to produce repeated flooding through the

season with interflood intervals on the order of 2-3 weeks. This would result in high levels of

zooplankton biomass thereby providing trophic support for floodplain fishes such as Sacramento

splittail (Crain et al. 2004).

Active floodplain management that could produce periodic flooding with a period of 2-3

weeks may be particularly effective in dry years where there may be only one or a small number

of flood events. One of the challenges for larval and juvenile fish populations, first formalized as

the match-mismatch hypothesis (Cushing 1972, 1990, Straile & Geller 1998, Chick & Van Den

Avyle 1999) is a possible mismatch in the timing of fish spawning relative to the peak in

zooplankton abundance. The likelihood of a mismatch would be most likely in dry years where

only flooding events might be very limited or only occur early in the season before larval fish

become abundant. By managing floodplains to create multiple flooding events in a dry year, this

would produce multiple peaks in the abundance of zooplankton, which presumably would result

in a better match between the abundance of zooplankton and larval and juvenile fishes. River

management that would increase the match between the timing of larval and juvenile fishes and

zooplankton peaks have been suggested in other systems as well (Chick & Van Den Avyle 1999).

We caution that simple management techniques such as creating multiple flooding events at regular intervals may not be a panacea for floodplain management. Increased temperature and food availability on floodplains has been shown to positively affect some but not all fish species in this habitat. Comparisons of Sacramento splittail between floodplain habitats and adjacent riverine areas showed higher condition and growth increment on the floodplain, but not for Sacramento suckers (*Catostomus occidentalis*), which may do better in the cooler edge habitats of streams rather than the warmer floodplain, despite higher food levels (Ribeiro et al. 2004). Even for fishes like splittail that do better in floodplain habitats, it remains to be determined whether increased food resources will translate into increased recruitment into adult populations. There are other important management considerations, such as the presence of non-native fish predators that can present enormous challenges for native fish recruitment and fisheries management (Muller 2005, Clarkson et al. 2005). There are many invasive non-native fishes on the Cosumnes floodplain, and managing the timing and frequency of flooding events, other than shifting them earlier in the season, will have little effect on the abundance of alien predators and their impacts on native fish recruitment (Crain et al. 2004).

Given the potential importance of floodplains as spawning and rearing grounds for native fishes such as juvenile Chinook salmon and Sacramento splittail (Moyle & Grosholz 2003, Sommer et al. 2001, 2004, Crain et al. 2004, Ribeiro et al. 2004, Feyrer et al. 2004) managing floodplain habitats in order to maximize the productivity of lower trophic levels and hopefully benefit populations of targeted fish species is an important restoration goal for rivers in California and elsewhere (Schiemer et al 1999, Stanley & Doyle 2003). There are many other

obstacles to successful restoration that must also be integrated into restoration planning for rivers in this region. Further work is needed to better understand the sources of spatial and temporal variation in invertebrate productivity and the other important ecosystem services floodplains provide, as these habitats increasing become high priority targets for restoration efforts.

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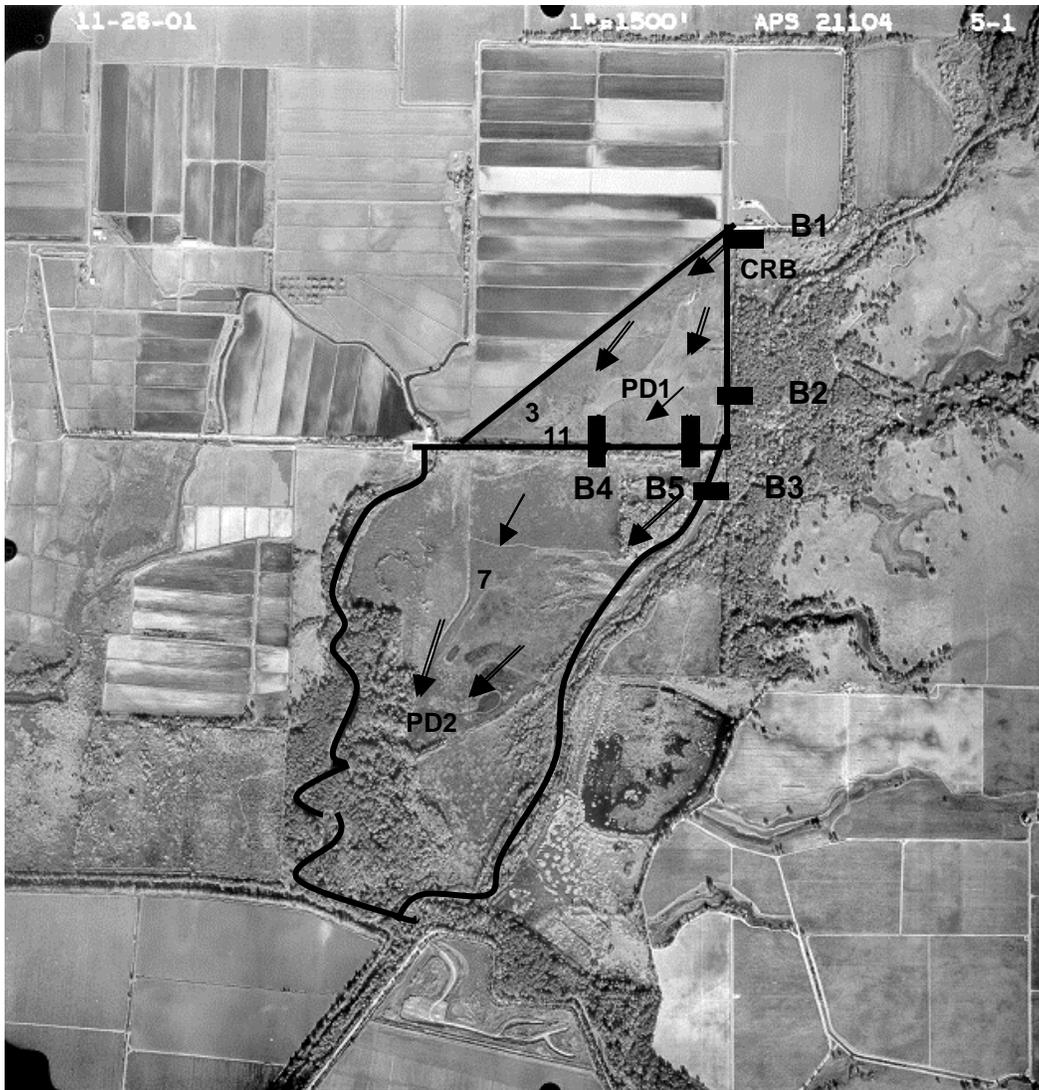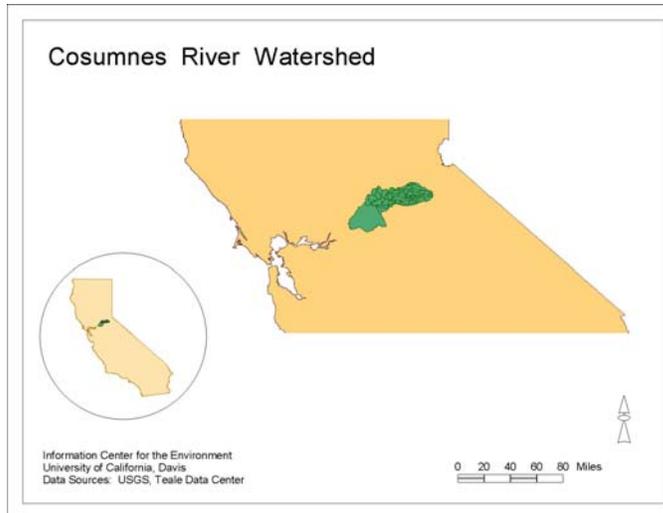
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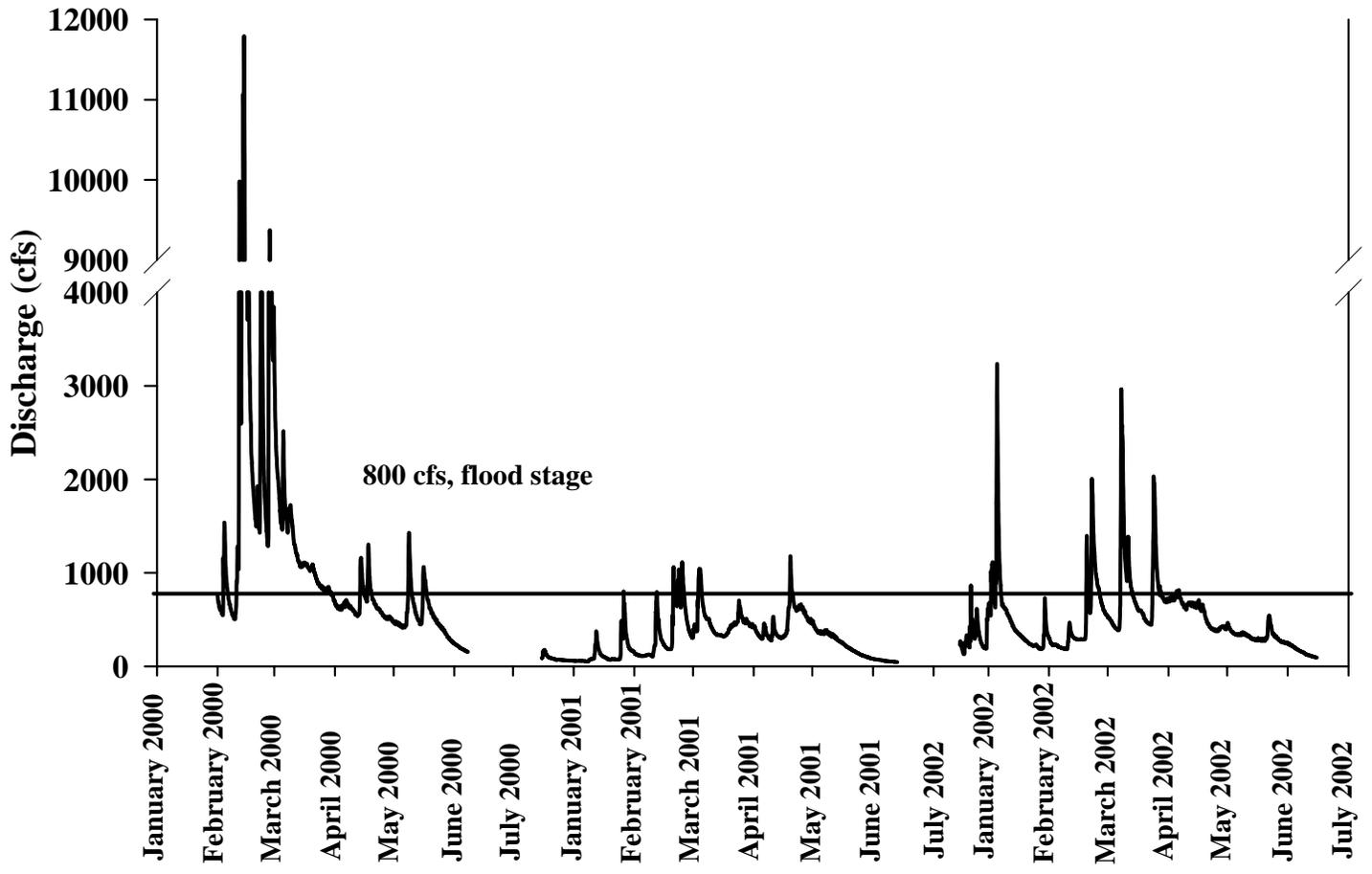and mortality-rates mediated by foraging activity. American Naturalist 142: 242-272.

Yu, Z. S., R. R. Northup & R. A. Dahlgren, 1994. Determination of dissolved organic nitrogen
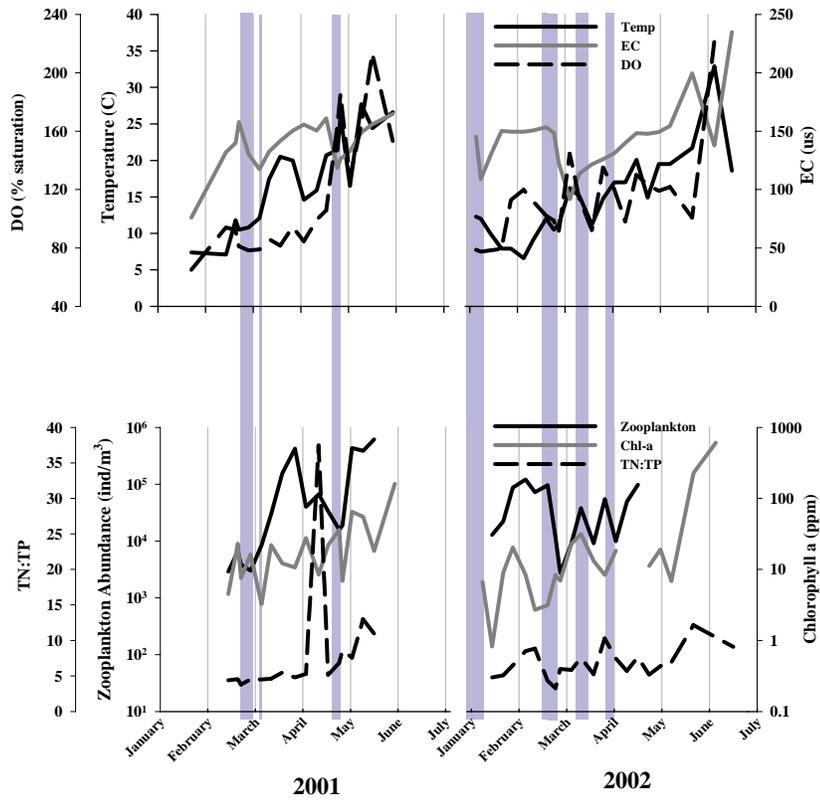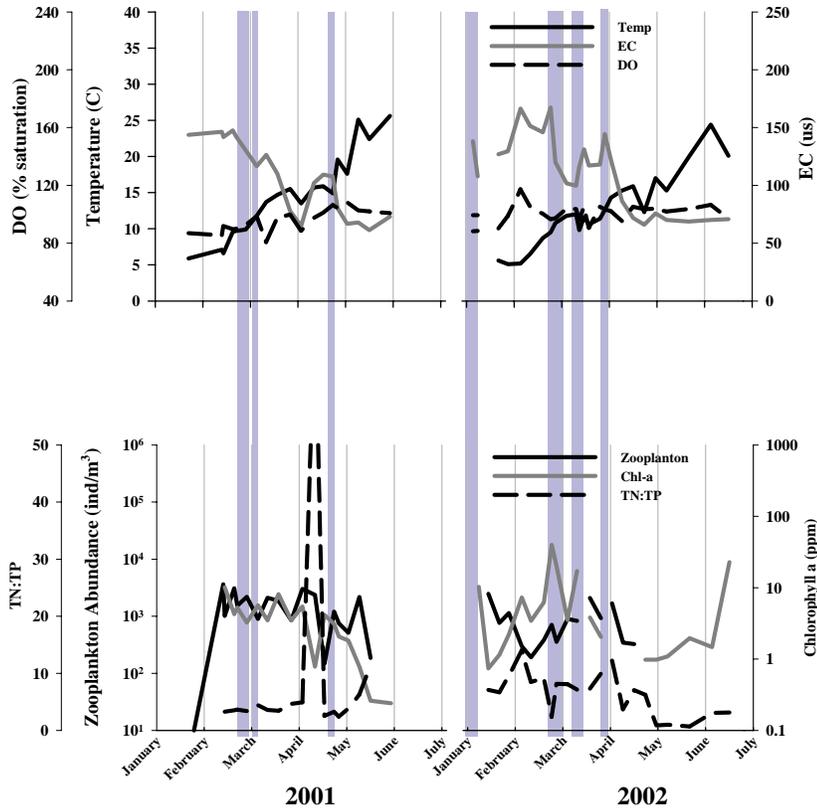using persulfate oxidation and coductimeterc quatification of nitrate-nitrogen.
Communications in Soil Science and Plant Analysis 25: 3161-3169.

FIGURE LEGENDS

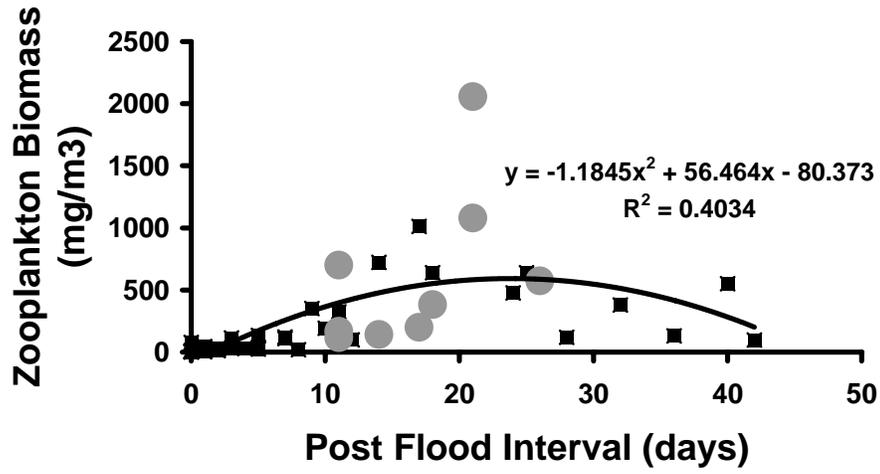**Figure 1.** Diagram of Cosumnes River watershed relative to state of California and aerial photo of the Cosumnes Floodplain Reserve. Lettered symbols show the location of the main levee breaches shown as black rectangles where the river flows into the floodplain as well as two levee breaches that connect the upper and lower floodplains. Sampling sites are labeled and arrows indicate generalized hydrologic flow path.

Figure 2. The discharge levels (cms) for Cosumnes River at the gauging station at Michigan Bar (38.5000°N, 121.0440°W, elevation 51 m.) for 2000-2002. Dashed line denotes flood stage at the Cosumnes Floodplain Reserve.

Figure 3. A. Water temperature (TEMP), dissolved oxygen (DO), electrical conductivity (EC), ratio of total nitrogen to total phosphorous (TN:TP), zooplankton abundance and chlorophyl *a* (Chl-*a*) for one of the floodplain sites (PD1) for 2001-2002. Light gray bars denote flood events. **B.** Water temperature (TEMP), dissolved oxygen (DO), electrical conductivity (EC), ratio of total nitrogen to total phosphorous (TN:TP), zooplankton abundance and chlorophyl *a* (Chl-*a*) for one of the river sites (CRB) for 2001-2002. Light gray vertical bars denote flood events.

Figure 4. A. Zooplankton biomass vs. the time since disconnection from the river channel (post-flood interval) for 2000-2002. Circles represent the maximum biomass for each flood event (n=8) during that period. **B.** Maximum zooplankton biomass vs. date of occurrence for eight flood events between 2000-2002.

Figure 5. Zooplankton biomass as a function of water temperature at one of the floodplain sites (Pond 1) for: **A.** Flood season 2000, **B.** Flood season 2001, and **C.** flood season 2002.

Figure 6. Changes in zooplankton biomass by date in 2001 showing the relative declines of cladocera (*Ceriodaphnia* and *Daphnia*) beginning in April.

Figure 7. Abundance of benthic invertebrates as a function of sampling date showing relative changes among major taxa for **A.** Flood season 2001, and **B.** Flood season 2002.

Figure 8. Diet analysis of juvenile splittail captured on the floodplain by sampling date in 2001. Data for each taxon are expressed as the percentage of fishes that contained that taxon on that date.

Figure 9. Results of manipulative field experiment showing the density of all zooplankton and cladocera and copepoda separately in samples from cages with fish (fish), cages without fish (no fish) and outside the cages in the open pond (pond) at the end of the experiment (day 12).
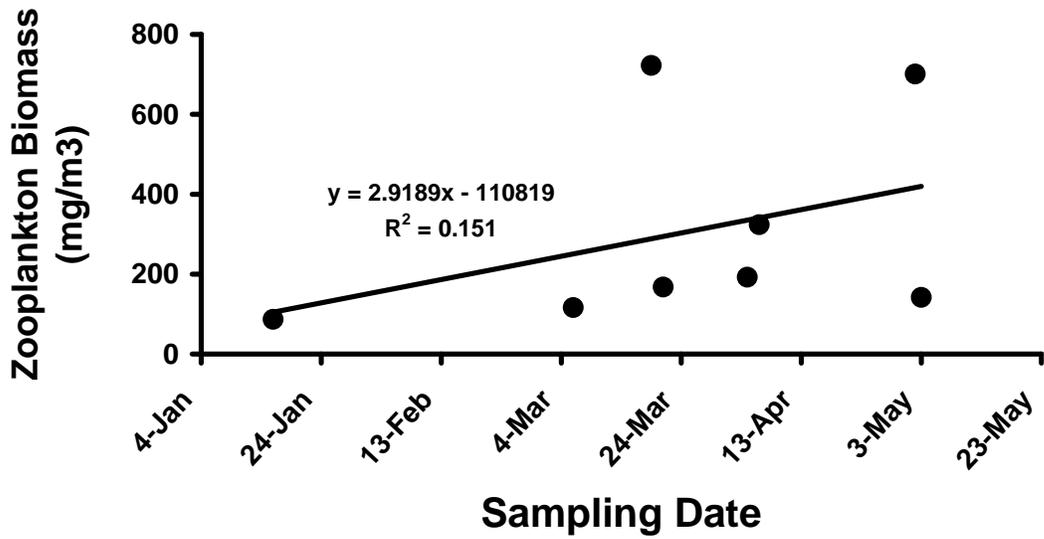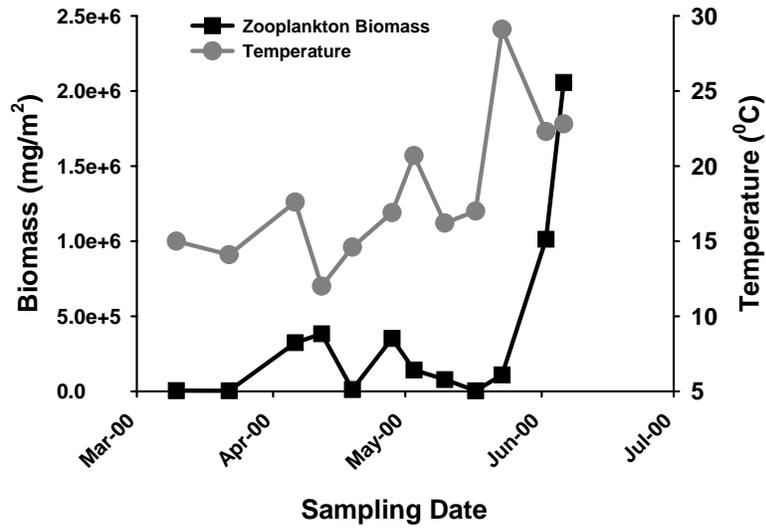
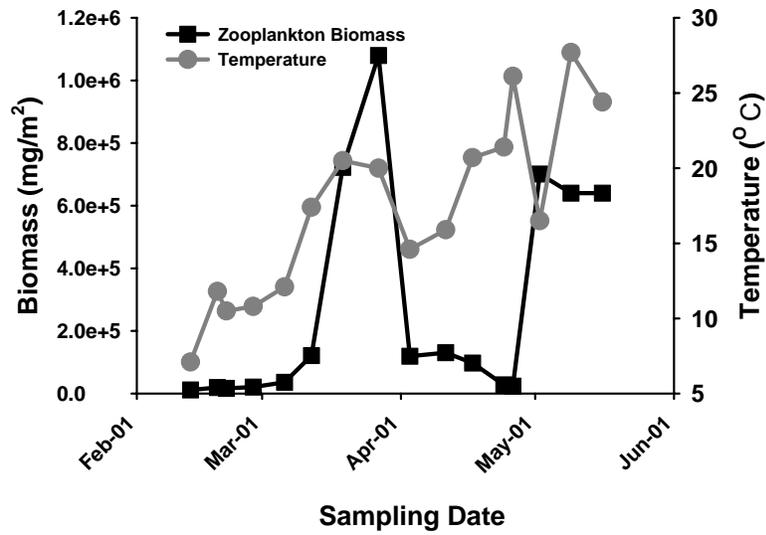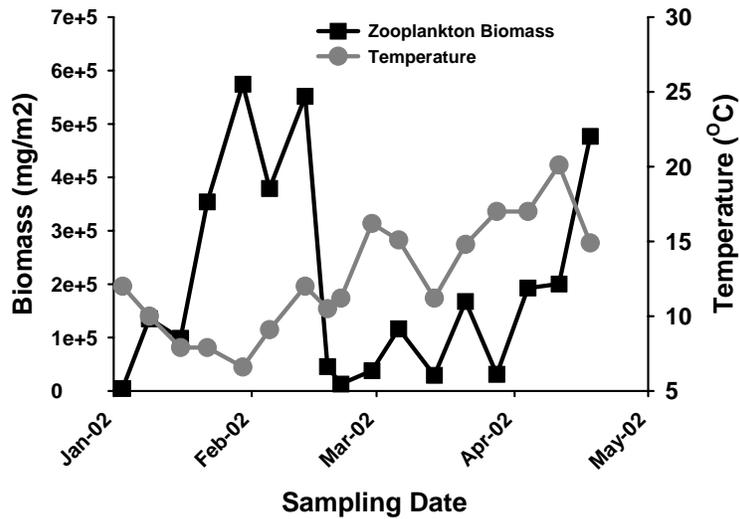Cosumnes River Watershed

Information Center for the Environment
University of California, Davis
Data Sources: USGS, Teale Data Center

0 20 40 60 80 Miles

11-26-01   1"=1500'   APS 21104   5-1

B1
CRB
PD1
B2
3
11
B4   B5   B3
7
PD2

A

DO (% saturation) / Temperature (C) / EC (us)

TN:TP / Zooplankton Abundance (ind/m³) / Chlorophyll a (ppm)

Temp
EC
DO

Zooplankton
Chl-a
TN:TP

2001 2002

B

DO (% saturation) / Temperature (C) / EC (us)

TN:TP / Zooplankton Abundance (ind/m³) / Chlorophyll a (ppm)

Temp
EC
DO

Zooplanton
Chl-a
TN:TP

2001 2002

A

Zooplankton Biomass (mg/m3)

$y = -1.1845x^2 + 56.464x - 80.373$
$R^2 = 0.4034$

Post Flood Interval (days)

B

Zooplankton Biomass (mg/m3)

$y = 2.9189x - 110819$
$R^2 = 0.151$

Sampling Date

A

B

C

A

B