

*Primary Research Paper*

## The influence of flood cycle and fish predation on invertebrate production on a restored California floodplain

Edwin Grosholz\* & Erika Gallo

*Department of Environmental Science and Policy, University of California, Davis, CA 95616, USA*

*(\*Author for correspondence: E-mail: tedgrosholz@ucdavis.edu)*

Received 12 August 2005; in revised form 13 January 2006; accepted 29 January 2006; published online 21 June 2006

*Key words:* floodplain, predation, zooplankton, benthic invertebrates, fishes, top-down

### 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 3 years (2000–2002), we compared changes in abundances and size distributions of invertebrates through the flood season (January–June) with seasonal changes in the abundance of larval and juvenile fishes. Using diet analysis of fishes and manipulative feeding experiments with fishes in field enclosures, we link specific changes in invertebrate populations directly to feeding preferences of seasonally abundant fish. Early in the flood season prior to March, we found little influence of fish predation, consistent with the near absence of larval and juvenile fishes during this period. Coinciding with the midseason increase in the 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 results from feeding enclosure experiments that showed that fish rapidly depressed populations of larger cladocerans with much less effect on smaller cladocerans and calanoid copepods. At the end of the flood season, zooplankton abundances rapidly increased, consistent with a switch in the feeding of juvenile fish to aquatic insects and subsequent fish mortality. We also found that zooplankton biomass on the floodplain reached a maximum 2–3 weeks after disconnection with the river. We suggest that floodplain restoration in this region should consider management strategies that would ensure repeated flooding every 2–3 weeks during periods that would best match the peaks in abundance of 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; Brunke & 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; Tockner & Bretschko, 1996; Ward, 1998; 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; Benke et al., 2000). 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. In lake systems, we have known for decades that fish predators are an important force affecting zooplankton communities (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 zooplankton and benthic invertebrates 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 floodplains comes from studies in other regions, which have yielded general predictions about the relationship between flooding parameters, patterns of biological production and the potential roles of predators. Among these are studies of 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, 2001), the Danube River in Austria (Tockner et al., 1999a, b) and other river systems 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 physical 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 et al., 2003; Hein et al., 2004). Only recently floodplains in the Mediterranean climate of central California have been investigated in light of these other floodplain studies (Sommer et al., 2001, 2004; Sobczak et al., 2002, 2005; Feyrer et al., 2004; Schemel 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 relationship between invertebrate populations and larval and juvenile fishes. Specifically, we address how the flood cycle interacts with seasonal variation in the abundance of fishes to shape the abundance and size distribution of invertebrates on a restored floodplain of the lower

Cosumnes River in the Central Valley of California, USA. 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 floodplains in California and throughout the western US. 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 restoration efforts are underway in many areas. 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 abundances of invertebrates. But the match or mismatch in the timing of zooplankton production with larval and juvenile fish abundance has long been recognized to 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 high levels of invertebrate production and will match these peaks with the spawning and abundance cycles of larval and juvenile fishes.

In this study, we examine how seasonal patterns of flooding and the availability of larval and juvenile fish predators influence the dynamics of zooplankton and benthic insect populations. We measure the abundance, composition and size distribution of zooplankton and benthic invertebrates in concert with phytoplankton abundance and water quality variables at several floodplain

and main stem river sites 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.

## Methods

### *Study site*

The Cosumnes River watershed occupies an area of nearly 1600-km<sup>2</sup> on the west side of the central California Sierra Nevada (Fig. 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 and May creating a 5-month dry season typical of Mediterranean climates. At the main gauging station at Michigan Bar, which is 40 km upstream from 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 (Fig. 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 zoo-

plankton, aquatic insects and other benthic invertebrates. The sites include two on the main stem of the Cosumnes River (Fig. 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 and 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

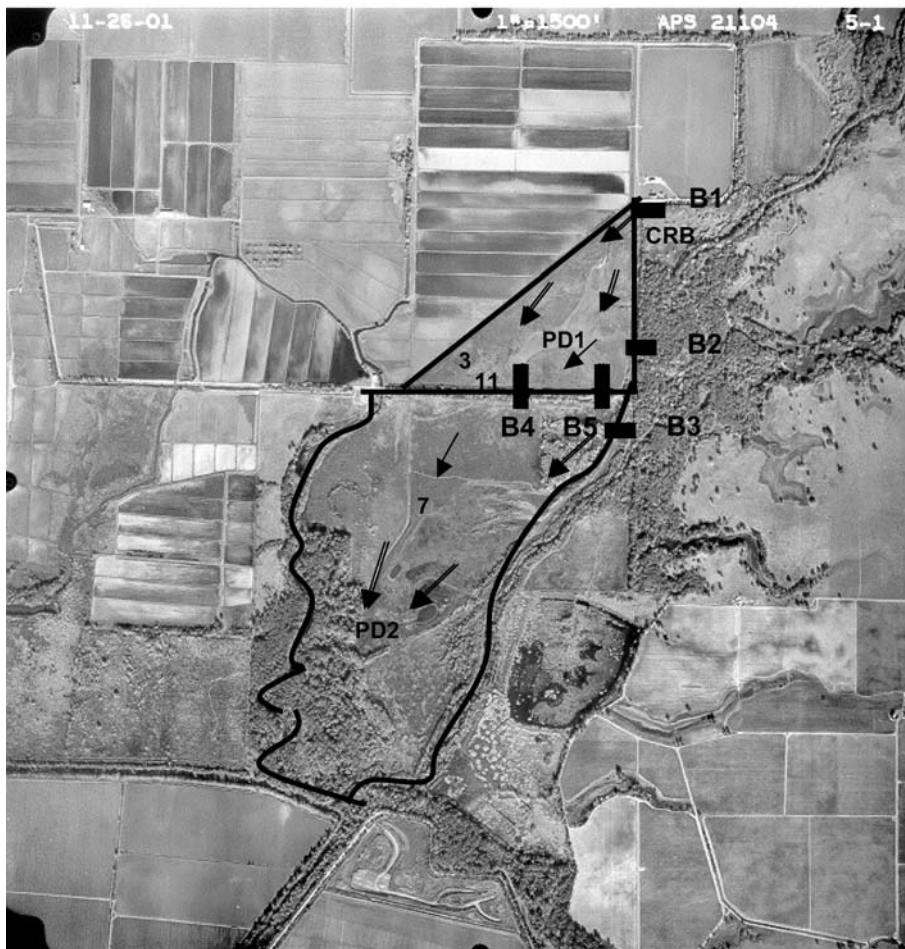
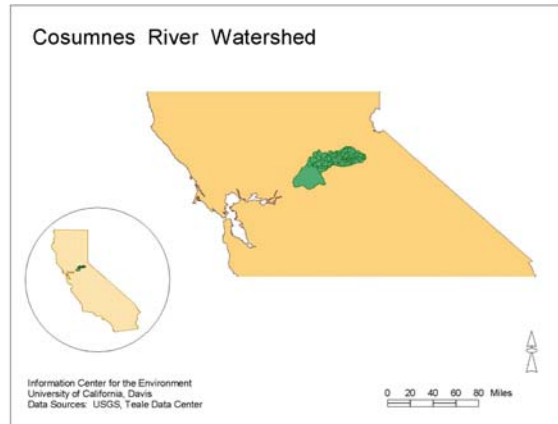
### *Water quality*

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 (°C), electrical conductivity (EC –  $\mu$ s/cm), specific EC (corrected to 25 °C –  $\mu$ s/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 analyzed TN 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 Clesceri et al. (1998). Chlorophyll-*a* (chl-*a*) measurements were made using the pigment extraction fluorometric method described by Clesceri et al. (1998). We report a more complete analysis of water quality variables elsewhere (Gallo et al., in review).

### *Zooplankton*

We used a hand-towed plankton net (150  $\mu$ m mesh, 0.3 m wide, 3:1 l/w ratio) outfitted with a propeller



*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.

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 s 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× 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 (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 Supplementary material for complete list of taxa<sup>1</sup>). 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.

<sup>1</sup> Electronic supplementary material is available for this article at < <http://dx.doi.org/10.1007/s10750-006-0029-z> > and accessible for authorised users.

### *Benthic invertebrates*

At each site, we collected invertebrates from two replicate sweeps, each involving a standard rectangular sweep net (0.46 m×0.23 m×0.25 m) pushed along the substratum through vegetation over a distance of 2 m. 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× magnification. Organisms were identified to the lowest possible level (generally genus) using standard identification keys (Usinger, 1974; Pennak, 1978; Merritt & Cummins, 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 1–2 h. 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 1 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 6 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 × 1 × 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 (US 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<sup>2</sup>, 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 water samples to measure zooplankton abundance. At each time point, we collected three 1 l samples from 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 *post-hoc* 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 (Fig. 2). This resulted in diminished watershed and floodplain flushing and input of allochthonous material and nutrients from the river to the floodplain in 2001, which we compare

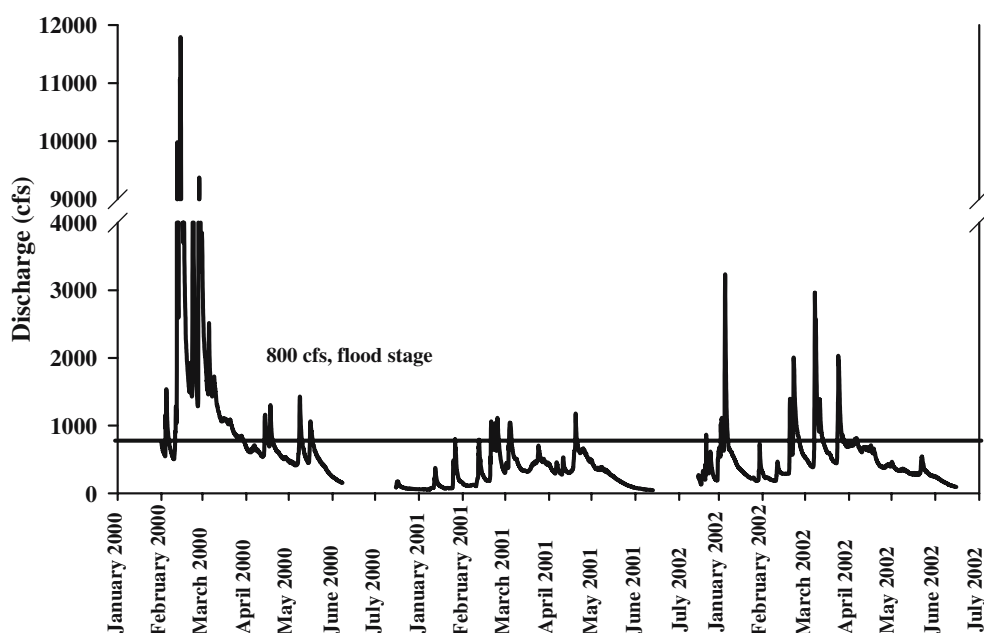


Figure 2. The discharge levels (cms) for Cosumnes River at the gauging station at Michigan Bar (38.5000°N, 121.0440°W, elevation 51 m) for 2000–2002. Dashed line denotes flood stage at the Cosumnes Floodplain Reserve.

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) (Fig. 3a and 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 (Fig. 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 (Fig. 3b). Temperatures on the floodplain by March were 5° 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 (Fig. 3a and 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 (Fig. 3a and 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 (Fig. 3a) where chl-*a* values were 5–10 times higher than values from the river site (Fig. 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 3 years (2000–2002), zooplankton biomass was 10–100 times greater at floodplain sites than at

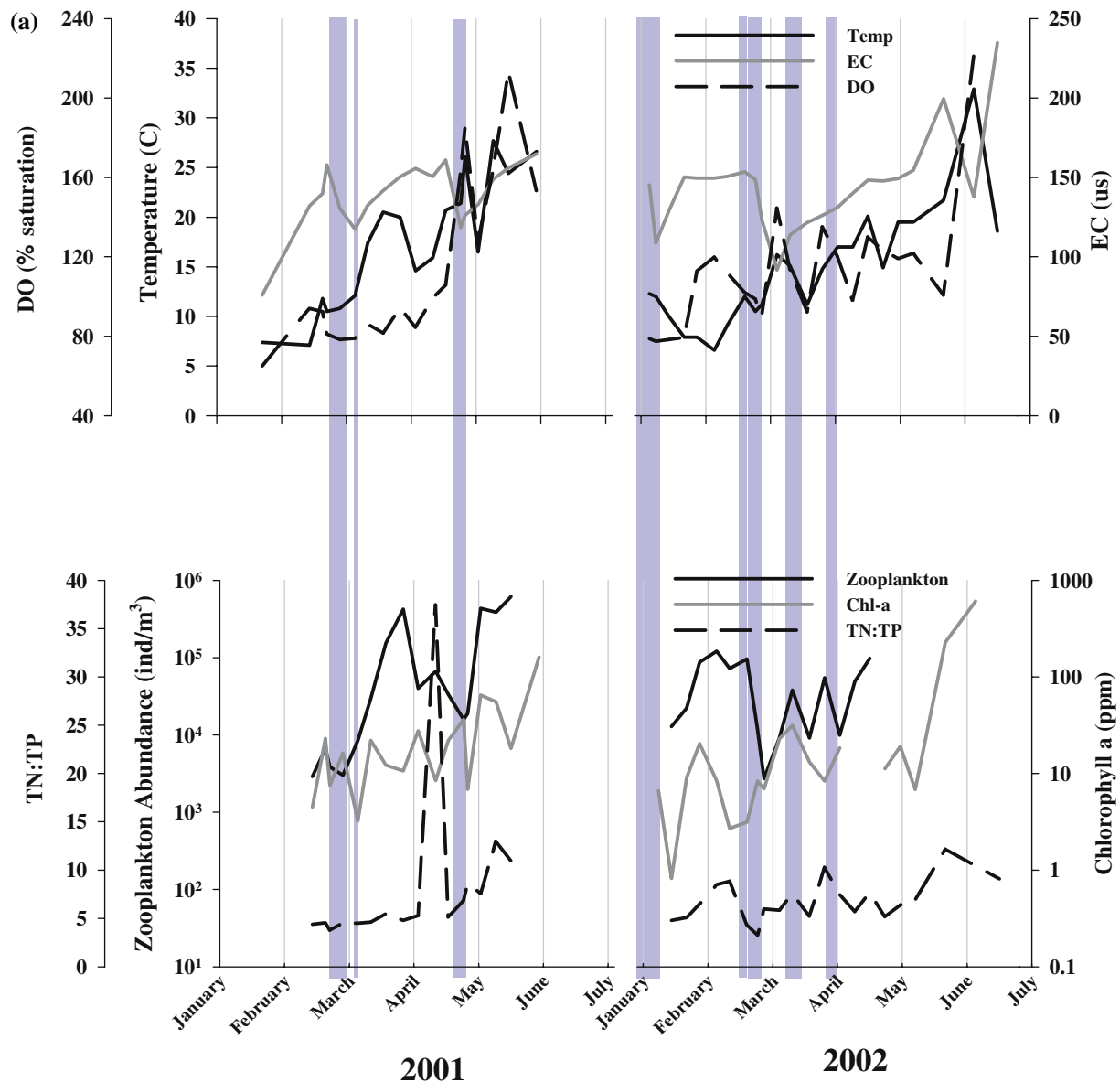


Figure 3. (a) Water temperature (TEMP), dissolved oxygen (DO), electrical conductivity (EC), ratio of total nitrogen to total phosphorous (TN:TP), zooplankton abundance and chlorophyll *a* (Chl-*a*) for one of the floodplain sites (PD1) for 2001 and 2002. Light gray bars denote flood events. (b) Water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

river sites (Fig. 3a and b). 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 signif-

icant time ( $F_{9,342} = 5.15$ ,  $p = 0.008$ ) and time $\times$ 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  $\times$  habitat



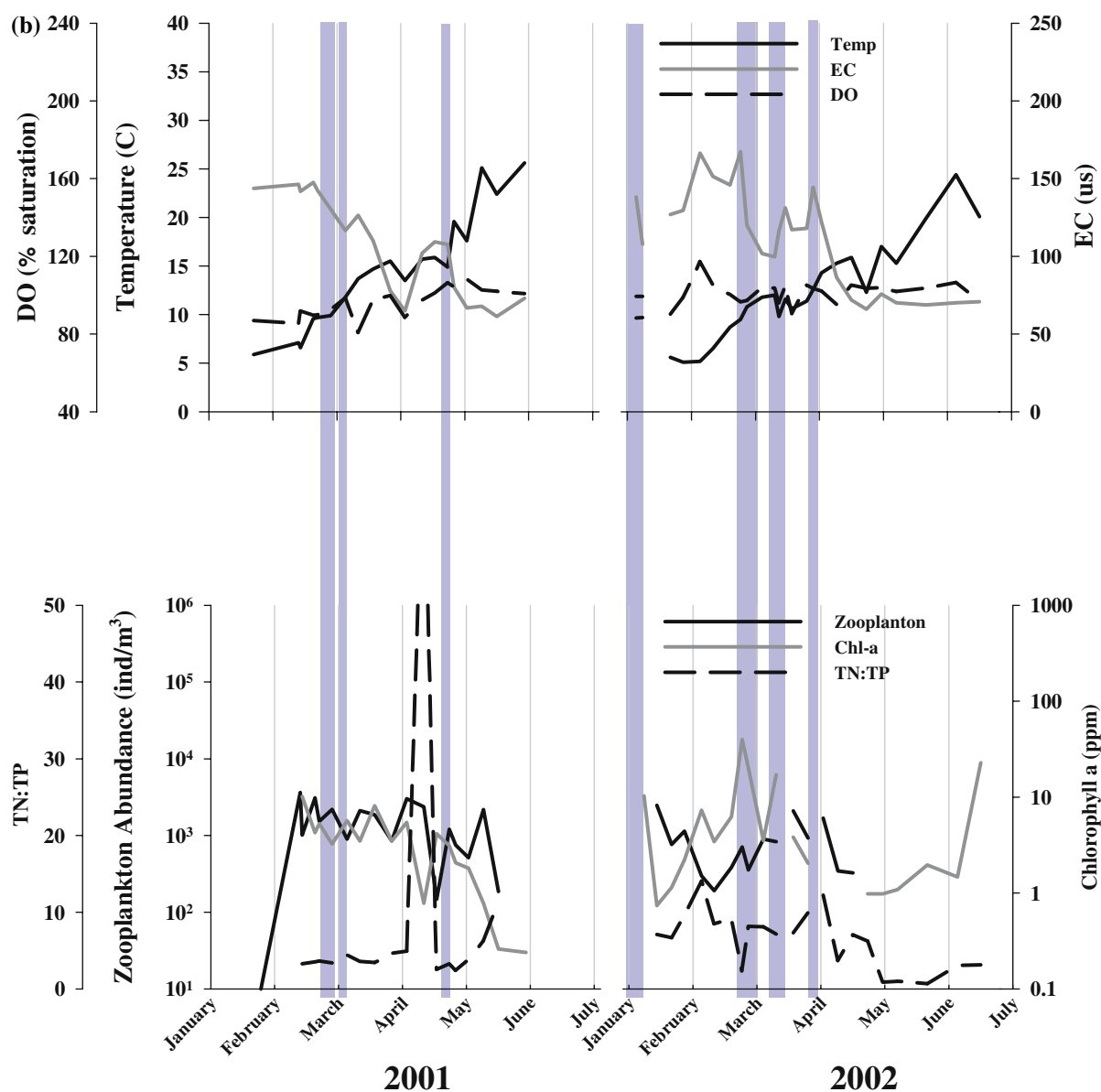


Figure 3. (Continued)

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  $\times$  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 association between zooplankton biomass at our floodplain sites and the frequency of flooding. There was a rapid 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 (Fig. 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 non-significant relationship ( $y = 2.9189x - 110819$ ,  $R^2 = 0.151$ , Fig. 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 c). 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 (Fig. 5a). This significant decline in zooplankton biomass did not parallel water temperature over this period (temperatures are generally increasing), but may be due to other factors (see Discussion). The

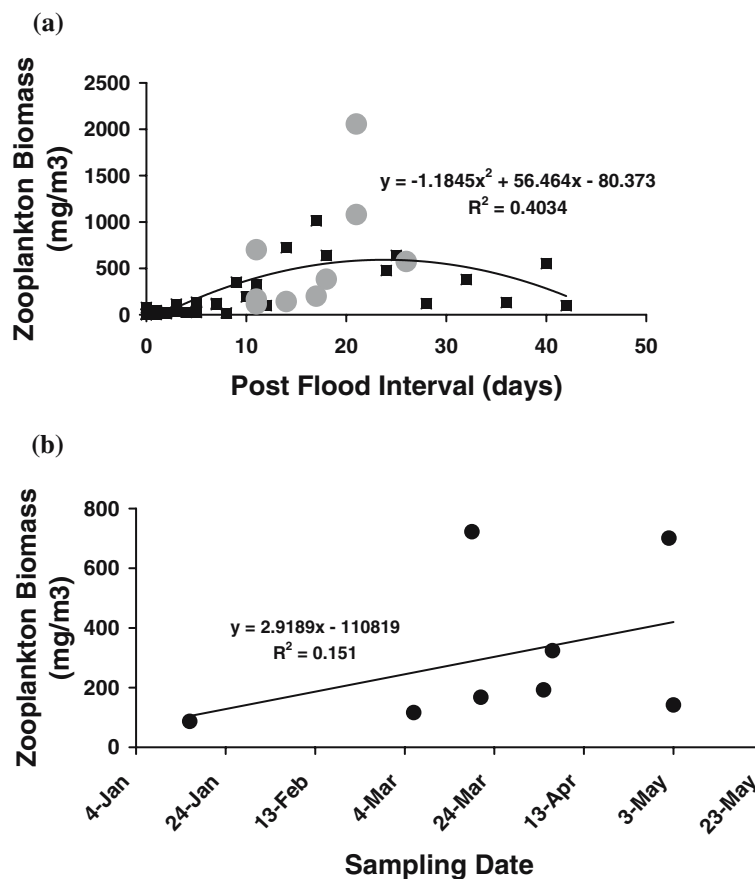


Figure 4. (a) Zooplankton biomass vs. the time since disconnection from the river channel (post-flood interval) for 2000–2002. Circles represent the maximum biomass for each flood event ( $n=8$ ) during that period. (b) Maximum zooplankton biomass vs. date of occurrence for eight flood events between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

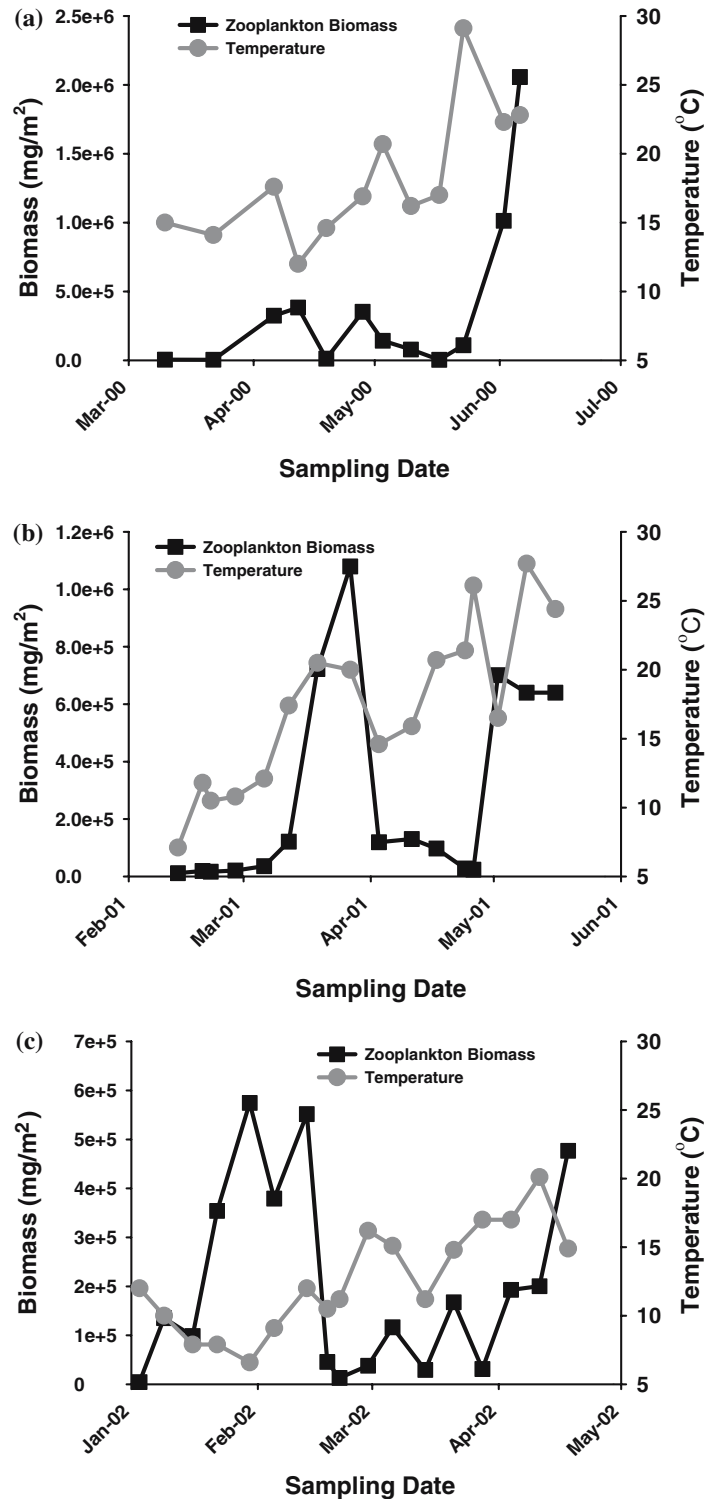


Figure 5. Zooplankton biomass as a function of water temperature at one of the floodplain sites (PD 1) for: (a) Flood season 2000, (b) Flood season 2001, and (c) Flood season 2002.

rapid increase at the end of the season (late May–June) coincided with water temperatures of 20–25 °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 (Fig. 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 (Fig. 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 (Fig. 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

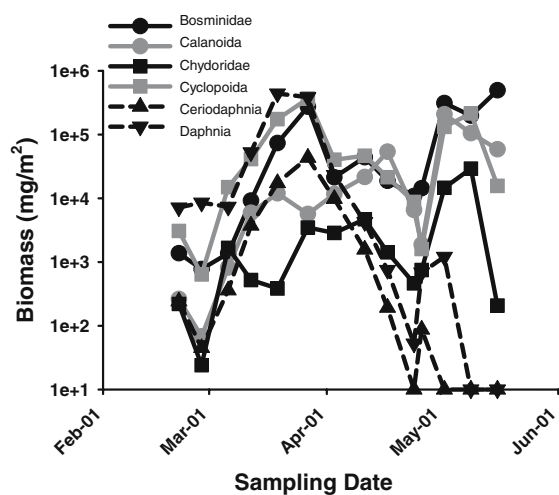


Figure 6. Changes in zooplankton biomass by date in 2001 showing the relative declines of cladocera (*Ceriodaphnia* and *Daphnia*) beginning in April.

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 3 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 invaded the floodplain and

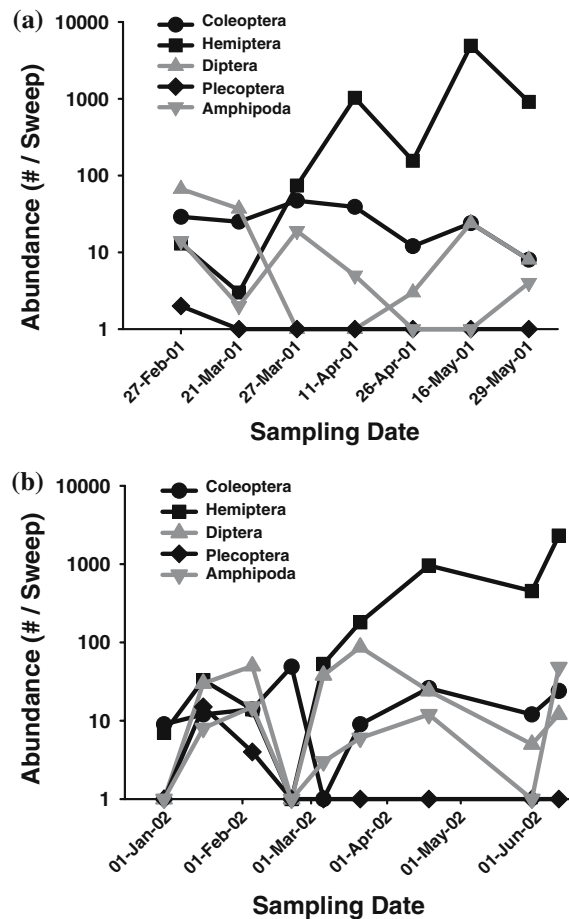


Figure 7. Abundance of benthic invertebrates as a function of sampling date showing relative changes among major taxa for (a) Flood season 2001, and (b) Flood season 2002.

began spawning after the first flood events. Adults were then present throughout much of the season, but then migrated off the floodplain. Data from the light traps showed that larval fish were virtually absent until early to mid-March. However, by April, juvenile fish had become more abundant, larger (15–20 mm) and are efficient predators of zooplankton. These data also showed that an 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 showed 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 (Fig. 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, 18 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 (Fig. 8).

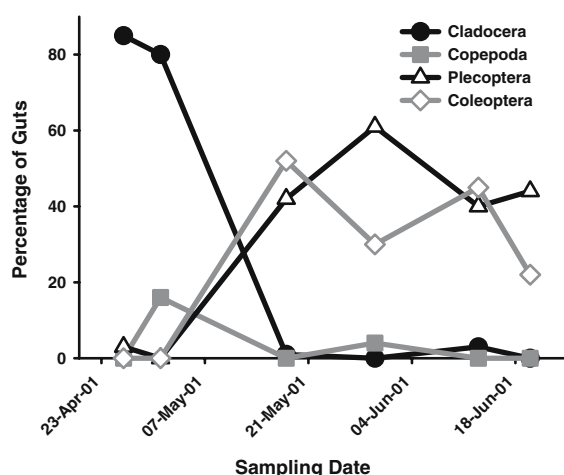


Figure 8. Diet analysis of juvenile splittail captured on the floodplain by sampling date in 2001. Data for each taxon are expressed as the percentage of fishes that contained that taxon on that date.

#### Juvenile fish predation

Fish predation had a significant impact on zooplankton density 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 ( $F=9.94$ ,  $df=2.8$ ,  $p=0.007$ ) (Fig. 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 also 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 ( $F=6.92$ ,  $df=2.8$ ,  $p=0.018$ ) (Fig. 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

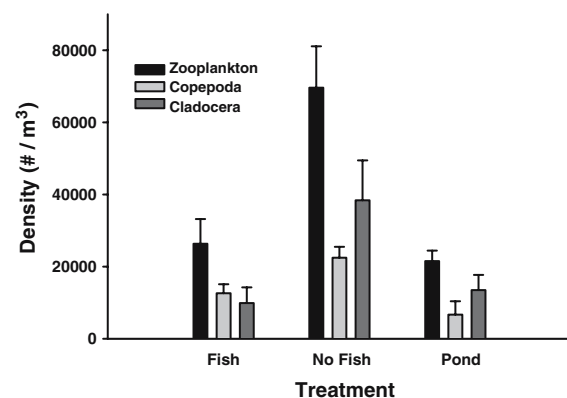


Figure 9. Results of manipulative field experiment showing the density of all zooplankton and cladocerans and copepods separately in samples from cages with fish (fish), cages without fish (no fish) and outside the cages in the open pond (pond) at the end of the experiment (day 12).

*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 (Fig. 9).

### Discussion

The Cosumnes River floodplain ecosystem is typical of many other floodplain ecosystems and is under the strong physical control of the annual flood cycle (Bayley, 1995; Ward & Stanford, 1995; Ward, 1998; Ward et al., 1998; Tockner et al., 2000; Sommer et al., 2001, 2004; Baranyi et al., 2002; 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 floodplain (during both rising and falling limbs of the flood), the flooding river waters rapidly reduced both planktonic and benthic invertebrate densities, presumably through dilution. During flood events occurring later in the season, this dilution likely 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 enclosure experiments inevitably include cage effects that often cannot be adequately controlled. The height of our cages relative to the area ( $1\text{ m}^2$ ) 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 benthic 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, some 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 patterns that have long been recorded 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 constancy of the period of the zooplankton cycle throughout the flood season was remarkable given the strongly seasonal effects of fish predation.

Traditional predator–prey theory (Murdoch & 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 during the season and likely decreasing carrying capacity ( $K$ ) as the 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 regardless of the time of year, despite fish predation that was dramatically higher during the middle 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 factor limiting zooplankton production on the floodplain. We found the peak in 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 factor or set of factors must also 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, similar to that seen in other systems (Robertson et al., 2001). 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. 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 pattern 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 particu-

lar, the shallow floodplain ponds generated large standing abundances of zooplankton exceeding several hundred thousand per m<sup>3</sup>. Also chl-*a* values are typically 10–50 ppm or 5–10 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 inter-flood intervals on the order of 2–3 weeks. This would result in high levels of zooplankton biomass that can provide trophic support for floodplain fishes such as Sacramento splittail (Crain et al., 2004).

Active management of the flood cycle could 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 is the match in the timing of fish spawning relative to the peak in zooplankton abundance (Cushing, 1972, 1990; Straile & Geller, 1998; Chick & Van Den Avyle, 1999). The likelihood of a mismatch would be most likely in dry years where 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 (Sommer et al., 2001, 2004; Crain et al., 2004; Feyrer et al., 2004; Ribeiro 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 floodplain restoration that must 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.

## Acknowledgements

We would like to thank P. Crain, R. Dahlgren, K. Keller, J. Mount, P. Moyle, J. Quinn, J. Vanderzanden for project data, discussion of ideas, or comments on earlier drafts. We thank T. Ashcroft, K. Forshay, S. Hongola, C. Jannusch, D. Kimbro, S. Norton, and A. Welch for countless hours in the field and lab collecting, enumerating and identifying invertebrates. Finally, we wish to thank the CALFED Bay-Delta Program contracts #NFW-9946 and #NFW-2001 for generous support of this project.

## References

- Bayley, P. B., 1995. Understanding large river-floodplain ecosystems. *BioScience* 45: 153–158.
- Baranyi, B., T. Hein, C. Holarek, S. Keckeis & F. Schiemer, 2002. Zooplankton biomass and community structure in a Danube River floodplain system: effects of hydrology. *Freshwater Biology* 47: 473–482.
- Benke, A. C., I. Chaubey, G. M. Ward & E. L. Dunn, 2000. Flood pulse dynamics of an unregulated river floodplain in the Southeastern US coastal plain. *Ecology* 81: 2730–2741.
- Brooks, J. L. & S. I. Dodson, 1965. Predation, body size and the composition of the plankton. *Science* 150: 28–35.
- Brunke, M. & T. Gonser, 1997. The ecological significance of exchange processes between rivers and groundwater. *Freshwater Biology* 37: 1–33.
- Carlson, R. M., 1986. Continuous-flow reduction of nitrate to ammonia with antigranulocytes zinc. *Analytical Chemistry* 58: 1590–1591.
- Carpenter, S. R. & J. T. Kitchell, 1988. Consumer control of lake productivity. *Bioscience* 38: 764–769.
- Carpenter, S. R. & J. F. Kitchell, 1993. *The Trophic Cascades in Lakes*. Cambridge University Press, Cambridge, UK.
- Chick, J. H. & M. J. Van Den Avyle, 1999. Zooplankton variability and larval striped bass foraging: evaluating potential match/mismatch regulation. *Ecological Applications* 9: 320–334.
- Clarkson, R. W., P. C. Marsh, S. E. Stefferud & J. A. Stefferud, 2005. Conflicts between native fish and non-native sport fish management in the southwest United States. *Fisheries* 30: 20–27.
- Clesceri, L. S., A. E. Greenberg & A. D. Eaton, 1998. *Standard Methods for the Examination of Water and Wastewater*. APHA, AWWA, WEF, Baltimore, MD.
- Cottenie, K. & L. de Meester, 2004. Metacommunity structure: synergy of biotic interactions as selective agents and dispersal as fuel. *Ecology* 85: 114–119.
- Crain, P. K., K. Whitener & P. B. Moyle, 2004. Use of a restored central California floodplain by larvae of native

- and alien fishes. American Fisheries Society Symposium 39: 125–140.
- Cushing, D. H., 1972. The production cycle and the numbers of marine fish. Symposium of the Zoological Society of London 29: 213–232.
- Cushing, D. H., 1990. Plankton production and year-class strength in fish populations: an update of the match/mismatch hypothesis. *Advances in Marine Biology* 26: 250–293.
- Dermott, R. M. & C. G. Paterson, 1974. Determining dry weight and percentage dry matter of chironomid larvae. *Canadian Journal of Zoology* 52: 1243–1250.
- Dumont, H. J., I. Van de Velde & S. Dumont, 1975. Dry weight estimate of biomass in a selection of cladocera, copepoda, and rotifera from plankton, periphyton and benthos of continental waters. *Oecologia* 19: 75–97.
- Ellis, L. M., M. C. Molles Jr. & C. S. Crawford, 1999. Influence of experimental flooding on litter dynamics in a Rio Grande riparian forest, New Mexico. *Restoration Ecology* 7: 193–204.
- Feyrer, F., T. R. Sommer, S. C. Zeug, G. O'Leary & W. Harrell, 2004. Fish assemblages of perennial floodplain ponds of the Sacramento River, California (USA), with implications for the conservation of native fishes. *Fisheries Management and Ecology* 11: 335–344.
- Fisher, S. G., L. G. Gray, N. B. Grimm & D. E. Busch, 1982. Temporal succession in a desert stream ecosystem following flash flooding. *Ecological Monographs* 43: 421–439.
- Furch, K. & W. J. Junk, 1993. Seasonal nutrient dynamics in an Amazonian floodplain lake. *Archiv Fur Hydrobiologie* 128: 277–285.
- Gallo, E. L., R. A. Dahlgren & E. D. Grosholz, 2005. Floodplain hydrobiogeochemistry as revealed by high resolution spatiotemporal sampling. *Freshwater Biology* (in review).
- Hall, D. J., S. T. Threlkeld, C. W. Burns & P. H. Crowley, 1976. The size efficiency hypothesis and the size structure of zooplankton communities. *Annual Review of Ecology and Systematics* 1: 177–208.
- Hambright, K. D. & R. O. Hall, 1992. Differential zooplankton feeding behaviors, selectivities, and community impacts of 2 planktivorous fishes. *Environmental Biology of Fishes* 35: 401–411.
- Harvey, C. J. & J. F. Kitchell, 2000. A stable isotope evaluation of the structure and spatial heterogeneity of a Lake Superior food web. *Canadian Journal of Fisheries & Aquatic Sciences* 57: 1395–1403.
- Heiler, H., T. Hein, F. Schiemer & G. Bornette, 1995. Hydrological connectivity and food pulses as the central aspects for the integrity of a River floodplain system. *Regulated Rivers* 11: 351–361.
- Hein, T., C. Baranyi, W. Reckendorfer & F. Schiemer, 2004. The impact of surface water exchange on the nutrient and particle dynamics in side-arms along the River Danube. *Science of the Total Environment* 328: 207–218.
- Junk, W. J., P. B. Bayley & R. E. Sparks, 1989. The flood pulse concept in river-floodplain systems. In Dodge, D. P. (ed.), *Proceedings of the International Large River Symposium*. Canadian Special Publications in Fisheries and Aquatic Sciences 106: 110–127.
- Keckeis, S., C. Barnayi, T. Hein, C. Holarek, P. Reidler & F. Schiemer, 2003. The significance of zooplankton grazing in a floodplain system of the River Danube. *Journal of Plankton Research* 25: 243–253.
- Lewis, W. M., S. K. Hamilton, M. A. Lasi, M. A. Rodriguez & J. F. Saunders, 2000. Ecological determinism on the Orinoco floodplain. *Bioscience* 50: 681–692.
- Lewis, W. M., S. K. Hamilton, M. A. Rodriguez, J. F. Saunders & M. A. Lasi, 2001. Foodweb analysis of the Orinoco floodplain based on production estimates and stable isotope data. *Journal of the North American Benthological Society* 20: 241–254.
- Merritt, R. W. & K. W. Cummins, 1996. *An Introduction to the Aquatic Insects of North America* (3rd edn). Kendall/Hunt Publ. Co, Dubuque, Iowa.
- Mittelbach, G. G., 1981. Foraging efficiency and body size – a study of optimal diet and habitat use by bluegills. *Ecology* 62: 1370–1386.
- Mittelbach, G. G. & L. Persson, 1998. The ontogeny of piscivory and its ecological consequences. *Canadian Journal of Fisheries & Aquatic Sciences* 55: 1454–1465.
- Moyle, P. & E. Grosholz, 2003. *Cosumnes-Mokelumne Paired Basin Project-linked Hydrogeomorphic-ecosystem Models to Support Adaptive Management: Part IV Aquatic Resources*. Report to the California Bay-Delta Program (Project #99-N06). Center for Integrative Watershed Science and Management.
- Müller-Solger, A. B., A. D. Jassby & D. C. Müller-Navarra, 2002. Nutritional quality of food resources for zooplankton (*Daphnia*) in a tidal freshwater system (Sacramento-San Joaquin River Delta). *Limnology and Oceanography* 47: 1468–1476.
- Muller, G. A., 2005. Predatory fish removal and native fish recovery in the Colorado River mainstream: what have we learned? *Fisheries* 30: 10–19.
- Murdoch, W. W. & A. Oaten, 1975. Predation and population stability. *Advances in Ecological Research* 9: 1–132.
- Pennak, R. W., 1978. *Freshwater Invertebrates of the United States*. John Wiley and Sons, New York.
- Power, M. E., A. Sun, G. Parker & W. E. Dietrich, 1995. Hydraulic food chain models. *Bioscience* 45: 159–167.
- Ribeiro, F., P. K. Crain & P. B. Moyle, 2004. Variation and condition factor and growth in young-of-year fishes in floodplain and riverine habitats of the Cosumnes River, CA. *Hydrobiologia* 527: 77–84.
- Robertson, A. I., P. Bacon & G. Heagney, 2001. The responses of floodplain primary production to flood frequency and timing. *Journal of Applied Ecology* 38: 126–136.
- Schemel, L. E., T. R. Sommer, A. B. Müller-Solger & W. C. Harrell, 2004. Hydrologic variability, water chemistry, and phytoplankton biomass in a large floodplain of the Sacramento River, CA, USA. *Hydrobiologia* 513: 129–139.
- Schiemer, F., C. Baumgartner & K. Tockner, 1999. Restoration of floodplain rivers: the Danube Restoration Project. *Regulated Rivers: Research and Management* 15: 231–244.
- Sheldon, F., A. J. Boulton & J. T. Puckridge, 2002. Conservation value of variable connectivity: aquatic invertebrate assemblages of channel and floodplain habitats of a central Australian arid-zone river, Cooper Creek. *Biological Conservation* 103: 13–31.

- Shurin, J. B., 2001. Interactive effects of predation and dispersal on zooplankton communities. *Ecology* 82: 3404–3416.
- Sobczak, W. V., J. E. Cloern, A. D. Jassby, B. E. Cole, T. S. Schraga & A. Arnsberg, 2005. Detritus fuels ecosystem metabolism but not metazoan food webs in San Francisco estuary's freshwater Delta. *Estuaries* 28: 124–137.
- Sobczak, W. V., J. E. Cloern, A. D. Jassby & A. B. Müller-Solger, 2002. Bioavailability of organic matter in a highly disturbed estuary: the role of detrital and algal resources. *Proceedings of the National Academy of Sciences USA* 99: 8101–8105.
- Sommer, T. R., W. C. Harrell, A. M. Solger, B. Tom & W. Kimmerer, 2004. Effects of flow variation on channel and floodplain biota and habitats of the Sacramento River, California, USA. *Aquatic Conservation-Marine and Freshwater Ecosystems* 14: 247–261.
- Sommer, T. R., M. L. Nobriga, W. C. Harrell, W. Batham & W. J. Kimmerer, 2001. Floodplain rearing of juvenile chinook salmon: evidence of enhanced growth and survival. *Canadian Journal of Fisheries and Aquatic Sciences* 58: 325–333.
- Sparks, R. E., 1995. Need for ecosystem management of large rivers and their floodplains. *Bioscience* 45: 168–182.
- Stanley, E. H. & M. W. Doyle, 2003. Trading off: the ecological removal effects of dam. *Frontiers in Ecology and the Environment* 1: 15–22.
- Straile, D. & W. Geller, 1998. The response of *Daphnia* to changes in trophic status and weather patterns: a case study from Lake Constance. *ICES Journal of Marine Science* 55: 775–782.
- Thorp, J. H. & A. P. Covich, 2001. Ecology and classification of North American freshwater invertebrates. Academic Press San Diego, CA.
- Tockner, K. & G. Bretschko, 1996. Spatial distribution of particulate organic matter (POM) and benthic invertebrates in a river-floodplain transect (Danube, Austria): importance of hydrological connectivity. *Archiv fuer Hydrobiologie* 115: 11–27.
- Tockner, K., D. Pennetzdorfer, N. Reiner, F. Schiemer & J. V. Ward, 1999a. Hydrological connectivity and the exchange of organic matter and nutrients in a dynamic river-floodplain system (Danube, Austria). *Freshwater Biology* 41: 521–535.
- Tockner, K., F. Schiemer, C. Baumgartner, G. Kum, E. Weigand, I. Zweimüller & J. V. Ward, 1999b. The Danube restoration project: species diversity patterns across connectivity gradients in the floodplain system. *Regulated Rivers: Research and Management* 15: 245–258.
- Tockner, K., F. Malard & J. V. Ward, 2000. An extension of the flood pulse concept. *Hydrological Processes* 14: 2861–2883.
- Usinger, R. L., 1974. *Aquatic Insects of California: With Keys to North American Genera and California Species*. University of California, Press, Berkeley, CA.
- Valett, H. M., M. A. Baker, J. A. Morrice, C. S. Crawford, M. C. Molles, C. N. Dahm, D. L. Moyer, J. R. Thibault & L. M. Ellis, 2005. Biogeochemical and metabolic responses to the flood pulse in a semiarid floodplain. *Ecology* 86: 220–234.
- Vegas-Vilarrubia, T. & R. Herrera, 1993. Seasonal alternation of lentic/lotic conditions in the Mapiro system, a tropical floodplain lake in Venezuela. *Hydrobiologia* 262: 43–55.
- Walker, K. F., F. Sheldon & J. T. Puckridge, 1995. A perspective on dryland river ecosystems. *Regulated Rivers* 11: 85–104.
- Wahlstrom, E., L. Persson, S. Diehl & P. Bystrom, 2000. Size-dependent foraging efficiency, cannibalism and zooplankton community structure. *Oecologia* 123: 138–148.
- Ward, J. V., 1998. Riverine landscapes: biodiversity patterns, disturbance regimes, and aquatic conservation. *Biological Conservation* 83: 269–278.
- Ward, J. V. & J. A. Stanford, 1995. The serial discontinuity concept: extending the model to floodplain rivers. *Regulated Rivers: Research and Management* 10: 159–168.
- Ward, J. V., K. Tockner & F. Schiemer, 1999. Biodiversity of floodplain river ecosystems: ecotones and connectivity. *Regulated Rivers: Research and Management* 15: 125–139.
- Wellborn, G. A., D. K. Skelly & E. E. Werner, 1996. Mechanisms creating community structure across a freshwater habitat gradient. *Annual Reviews in Ecology and Systematics* 27: 337–363.
- Werner, E. E. & D. J. Hall, 1988. Ontogenetic habitat shifts in bluegill – the foraging rate predation risk trade-off. *Ecology* 69: 1352–1366.
- Werner, E. E. & B. R. Anholt, 1993. Ecological consequences of the trade-off between growth 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 conductimetric quantification of nitrate-nitrogen. *Communications in Soil Science and Plant Analysis* 25: 3161–3169.

Copyright of *Hydrobiologia* is the property of Springer Science & Business Media B.V. and its content may not be copied or emailed to multiple sites or posted to a listserv without the copyright holder's express written permission. However, users may print, download, or email articles for individual use.

Copyright of *Hydrobiologia* is the property of Springer Science & Business Media B.V. and its content may not be copied or emailed to multiple sites or posted to a listserv without the copyright holder's express written permission. However, users may print, download, or email articles for individual use.