Effects of flow variation on channel and floodplain biota and habitats of the Sacramento River, California, USA

TED R. SOMMER[a],*, WILLIAM C. HARRELL[a], ANKE MUELLER SOLGER[a], BRAD TOM[a] and WIM KIMMERER[b]

[a] *California Department of Water Resources, Sacramento, CA 95816, U.S.A.*
[b] *Romberg Tiburon Center, San Francisco State University, Tiburon CA 94920, U.S.A.*

ABSTRACT

1. Despite progress in the development of conceptual models of river processes, the validation and application of these models to conservation may be limited by a deficit of tools for intermediate-scale (1–100 km) reaches. A model was developed to examine the effect of variation in flow on the responses of two trophic levels in a large temperate river (Sacramento River) and its seasonal floodplain (Yolo Bypass). Field data and hydrologic simulations were evaluated for three hydrologically diverse years.

2. The simulations showed much more hydrologic variability in the floodplain than the river, with greater total surface and shallow area, longer hydraulic residence times, and lower water velocities for the floodplain.

3. Chlorophyll *a* levels were significantly higher in the floodplain than in the river, and were negatively associated with flow. These results were consistent with longer hydraulic residence times, increased surface area of shallow water, and warmer water temperatures.

4. Copepods and cladoceran densities were similar in the river and its floodplain, and were mostly negatively associated with flow.

5. There were significantly higher densities of Diptera and terrestrial invertebrates in the floodplain than the river. Diptera densities in the floodplain were positively associated with flow.

6. These results provide evidence of the incremental value of floodplain habitat to the conservation of large rivers. In particular, it appears that providing river–floodplain connectivity can enhance production of lower trophic levels at relatively rapid time scales, probably benefitting secondary consumers, including Chinook salmon (*Onchyrhynchus tshawytscha*). Copyright © 2004 John Wiley & Sons, Ltd.

KEY WORDS: floodplain; phytoplankton; invertebrates; hydrologic models; Yolo Bypass; Sacramento River; San Francisco estuary

*Correspondence to: Dr T. R. Sommer, California Department of Water Resources, 3251 S Street, Sacramento, CA 95816, USA. E-mail: tsommer@water.ca.gov.

INTRODUCTION

The river continuum concept remains the foundation for much of the current understanding about river and stream structure and function (Vannote et al., 1980; Tockner et al., 1999). This theoretical construct views rivers and streams as trophic gradients where processes are determined by longitudinal position along the channels. Several complementary models have been identified, including serial discontinuity (Ward and Stanford, 1995a), the flood pulse concept (Junk et al., 1989), the hyporheic corridor concept (Stanford and Ward, 1988), and the riverine productivity model (Thorp and Delong, 1994). Fausch et al. (2002) recently argued that the application of these models to river management and conservation has not yet been very successful because there has been insufficient work at spatial and temporal scales appropriate for major management decisions. They note that most field studies are conducted either at very small spatial scales ($<1\,km$ microhabitat units, channel units or reaches) or at catchment scales (100–1000 km drainage basins), whereas intermediate scales (1–100 km reaches) are frequently more relevant for resource management. Symptoms of the gap between research and conservation include worldwide declines in riverine fish over the past 50 years, and the listing of many freshwater crustaceans and molluscs under state or federal endangered species laws (Fausch et al., 2002; Richter et al., 2003).

   A major challenge is that relatively few tools have been developed to analyse rivers at intermediate scales. Instream Flow Incremental Methodology (IFIM), particularly the model PHABSIM, remains the most widely used approach to set flow criteria for streams and rivers (Reiser et al., 1989). Yet IFIM and PHABSIM continue to be criticized because of concerns about model accuracy, assumptions, and ecological relevance (Marthur et al., 1985; Castleberry et al., 1996; Williams, 1996). Significant innovation is under way in the area of landscape ecology, where methods such as patch dynamics and spatial ecology have been used successfully for a variety of resource management applications (Turner, 1989; Klopatek and Gardner, 1999; Wiens, 2002). Efforts are also under way to develop reach-scale hydrologic variables as a tool to define the attributes of natural hydrographs, and to develop flow regimes that will sustain ecosystem processes (Richter et al., 1997). However, river–floodplain systems are one of the most dynamic environments on Earth, creating special challenges in both variability and scale. For example, the hydrologic regime is thought to be the primary factor determining the structure and function of river–floodplain systems (Junk et al., 1989), yet detailed descriptions of basic characteristics such as surface area, depth, residence time, and velocity are often lacking at ecologically relevant temporal and spatial scales (Wiens, 2002). Two notable exceptions are Bowen et al. (2003), who used a hydraulic model to simulate habitat patch dynamics for two temperate rivers, and Baranyi et al. (2002) who evaluated the effects of simulated residence time on zooplankton biomass and community structure. Nonetheless, ecological studies measuring the concurrent responses of multiple trophic levels to flow in river and floodplain habitat are rare. In the absence of high-resolution data on both hydrologic and biological processes, modelling studies of large river–food-web dynamics (e.g. Power et al., 1995a, b) have relied instead upon generalized hydrologic patterns. Results from such modelling efforts are congruent with empirical data showing that flood pulses in large rivers enhance production of invertebrates and fish (Welcomme, 1979; Junk et al., 1989; Gutreuter et al., 2000).

   To help address gaps in knowledge about the functioning of rivers at intermediate scales, a landscape-scale hydrologic model was developed to examine how variation in hydrology affected several food-web organisms in a 60 km reach of a large temperate river–floodplain. The study focused on two components of the tidally influenced section of the Sacramento River and the adjacent Yolo Bypass, the river's largest floodplain (Figure 1). This river–floodplain system had several advantages for our evaluation. The Sacramento River channel is physically separated from its primary floodplain by a levee, allowing a well-defined comparison of each component's aquatic ecology. In addition, several years of concurrent ecological data on invertebrates and phytoplankton were available. Sufficient monitoring data on the

topography and hydrology of the river and floodplain had been collected to simulate physical descriptions on daily time-scales. Finally, the region is the focus of a major habitat restoration effort in response to declines in abundance of estuarine and riverine biota (CALFED, 2000; Jassby *et al.*, 2002). Populations of many consumers, such as zooplankton and macroinvertebrates, have declined substantially (Kimmerer and Orsi, 1996; Orsi and Mecum, 1996). Moreover, several native fish show marked population decreases (Bennett and Moyle, 1996), leading to the listing under the Federal Endangered Species Act of two races of Chinook salmon (*Onchyrhynchus tshawytscha*) and delta smelt (*Hypomesus transpacificus*). Many of these organisms are more abundant in high-flow years (Jassby *et al.*, 1995), when the floodplain is inundated. In an attempt to reverse these declines, the CALFED (2000) federal–state government partnership has been funding aquatic habitat restoration projects, including the breaching of leveed islands to create tidal wetlands, removing fish passage barriers, reconnecting rivers and seasonal habitat, and conducting studies to identify and design restoration projects. Thus, data on the responses of aquatic biota in river and floodplain habitat are relevant for conservation and resource management. The primary hypotheses were that: (1) phytoplankton and invertebrates will show strong responses to water surface area, residence time, and velocity; and (2) the responses will differ substantially between river and floodplain habitat. The basic approach was to use hydrologic modelling to help interpret biological data collected in each study area.
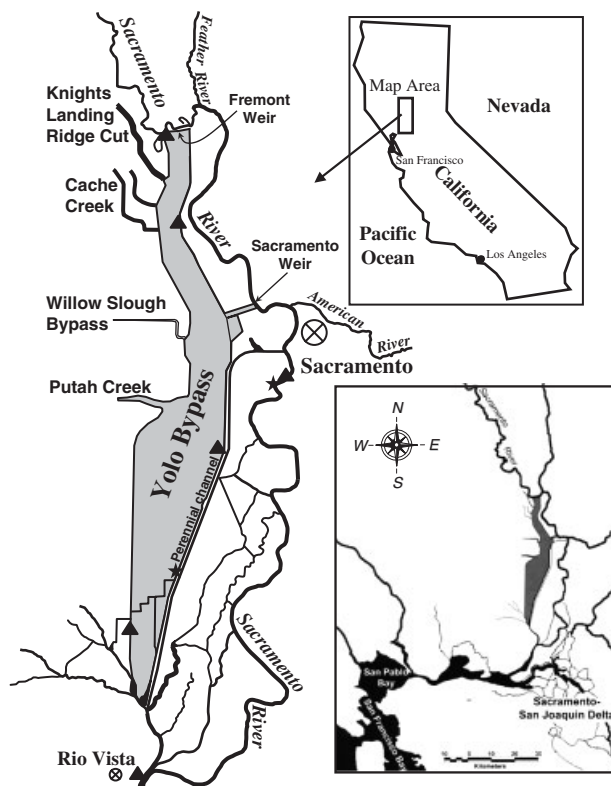

Figure 1. Location of Yolo Bypass in relation to the San Francisco estuary and its tributaries. The San Francisco estuary represents the region from San Francisco Bay upstream to Sacramento. The locations of gauging stations used for the hydrologic model are shown with dark triangles. Sampling areas for invertebrates and water temperature are shown with stars.

METHODS

Study area

The Sacramento River is the largest tributary to the San Francisco estuary and its two component regions, the Sacramento–San Joaquin Delta and downstream brackish bays (Figure 1). This highly regulated river has a mean annual discharge of about $800 \, \text{m}^3 \, \text{s}^{-1}$ from a catchment of $70\,000 \, \text{km}^2$. In about 60% of years, the total Sacramento Valley flow exceeds $2000 \, \text{m}^3 \, \text{s}^{-1}$ during winter or spring, when river flow spills into the Yolo Bypass via the Fremont and Sacramento weirs (Sommer *et al*., 2001a; Schemel *et al*., 2004). For most of the past two decades, agriculture was the major land use on this 61 km long, partially leveed 24 000 ha floodplain. As a result of recent restoration and land acquisition activities (e.g. CALFED, 2000), the majority of the floodplain is now managed for wildlife in 'natural' habitats, including riparian and upland areas, emergent marsh and permanent ponds. CALFED (2000) is at present examining ways in which this habitat could be managed for the benefit of aquatic species. Yolo Bypass also has a perennial channel along its eastern edge that is tidally influenced during low-flow periods, and drains the floodplain after high-flow events. Like many other large rivers in the Northern Hemisphere (Dynesius and Nilsson, 1994), the Sacramento River channel has been heavily altered by flood control and reclamation activities. In the study area, the river channel has steep, rock-covered banks with a narrow riparian corridor, and minimal emergent vegetation; the lower half of this reach is a tidal freshwater channel. Outflow from the Yolo Bypass and Sacramento River rejoin at Rio Vista, then the combined discharge enters the brackish regions of the estuary.

Physical modelling

Because of the difficulty in directly measuring variables such as water velocity, depth, and surface area in large river–floodplain systems, a hydrologic model was used to simulate daily trends in several physical variables at the landscape scale for three hydrologically diverse years: 1998, 2000, and 2001. Although data were available to simulate 1999 trends, this year was not modelled because the hydrology was very similar to 2000. The model treated the river and floodplain as two independent 'reservoirs' described by: (1) basin geometry; and (2) flow and stage time series. The floodplain bathymetry was developed from 200 cross-sections collected at 300 m intervals by the US Army Corps of Engineers. River bathymetry was taken from 75 cross-sections along the reach adjacent to Yolo Bypass (US Geological Survey, unpublished data). Mean daily stage and flow data were obtained from a series of gauging stations in Yolo Bypass and in the Sacramento River (Figure 1). For each date in the time series, the model used linear interpolation between the gauging stations to estimate the stage at each cross-section. Linear interpolation was considered a reasonable approach because the bottom surface slopes and cross-sections were fairly consistent for Yolo Bypass and Sacramento River, with relatively few constrictions. The estimated stage value was used to calculate each cross-section's conveyance characteristics: area, width, and wetted perimeter. The results for each cross-section were used to create a three-dimensional reservoir for each reach. Once the dimensions of the daily reservoir were defined, key hydrologic variables were calculated for each of the two reaches as follows: the total surface area is equal to the surface area of the reservoir; the hydraulic residence time is equal to the volume divided by the flow; and the mean velocity is equal to the reach length divided by the hydraulic residence time. The model also calculated an index of shallow water habitat, the surface area that had a mean depth of $<2 \, \text{m}$. Selection of the $<2 \, \text{m}$ depth index was somewhat arbitrary, as there are multiple definitions of 'shallow water'; however, the 2 m threshold has some biological relevance, as it is an accepted criterion defining wetland littoral zones (Cowardin *et al*., 1979). It is also important to note that the velocity and hydraulic residence time calculations represent idealized rather than actual values. The hydrologic model relied on a simple mass balance approach that did not account for daily tidal effects on velocity and residence time, a particularly important factor during low-flow conditions. To highlight this

limitation, these variables will be referred to as *idealized hydraulic residence time* and *idealized mean velocity*. Nonetheless, we believe that the model provided a useful index of relative differences between flows. Similar models have been used to gain insight into the effects of physical variables on floodplain biota (Baranyi *et al.*, 2002). Mean daily water temperature was measured from individual temperature recorders (Onset Corporation) placed in the Sacramento River and the perennial tidal channel of Yolo Bypass (Sommer *et al.*, 2001b).

The large scale of the study reach made it too difficult to validate all of the simulated variables. As a partial validation of the model, total inundated area for Yolo Bypass was estimated using 1:24 000 scale area on 3 days when a complete set of photographs was available: 2 March 1998; 28 April 1998; and 28 February 2001. Aerial photographs were taken of the entire floodplain, then scanned to create a georeferenced mosaic image. The inundated area for each set of images was delineated using the geographic information system (GIS) program ARCVIEW, then compared with model estimates for the same dates.

Biological data

The responses of two trophic levels were compared for the Sacramento River and the Yolo Bypass: primary producers (phytoplankton) and primary consumers (zooplankton and drift invertebrates). Floodplain samples were collected 48 km downstream of Fremont Weir, and river channel samples were collected 44 km downstream of Fremont Weir (Figure 1). These sites were not intended as a comprehensive evaluation of the spatial and temporal variation of each organism. Rather, data collection was designed to identify the major differences and trends in concentration between the two study areas.

Chlorophyll *a* was measured as an indicator of phytoplankton biomass in discrete water samples collected weekly according to procedures described in Mueller-Solger *et al.* (2002). Drift samples were collected using nets at fixed stations on the Yolo Bypass and the Sacramento River (Sommer *et al.*, 2001b). The nets (0.46 m × 0.3 m mouth, 0.91 m length and 500 μm mesh) were sampled for approximately 30 min during mid-morning once or twice each week during flood events and every other week during lower flow periods. Sample volume was estimated from flow measurements with a flow meter (General Oceanics Model 2030R) and net dimensions. Drift samples were stored in ethanol or formaldehyde, then the invertebrates were identified to family or order using a dissecting microscope. Zooplankton samples were taken concurrently with the drift samples. However, zooplankton samples were collected using different methods in 1998 than in subsequent years. In 1998, zooplankton were collected in the Yolo Bypass at two fixed stations with battery-operated rotary vane pumps with a mean flow rate of 17 L min^{-1}. The samples were taken via pipes with outlets at multiple locations beneath the water surface. Discharge was directed into a 150 μm mesh net held in a basin on the bank. Flow rate was recorded at the beginning and end of the sample period, which varied from 1 to 6 h. Few samples were taken in the Sacramento River during the comparable period in 1998. For 2000 and 2001, zooplankton samples were taken with a Clarke–Bumpus net (0.13 m diameter, 0.76 m length, 160 μm mesh) placed into the surface flow in the Yolo Bypass and Sacramento River. Sample volume was recorded as for the drift net. The 1998 and 2000–01 sampling methods were not cross-calibrated, but this is not a major issue as the data analyses (see below) focused on comparisons between locations, not between years. For all years, samples were concentrated and stored in 5% formalin, after which the zooplankton were removed, and crustacean zooplankton were counted and identified to class or order.

Statistical analyses

Sign tests were used to compare the concentrations of phytoplankton and invertebrates in Yolo Bypass and the Sacramento River. In addition, the effect of flow on each biological variable was evaluated by calculating Pearson correlation coefficients for log-transformed data.

RESULTS

Physical habitat

As is typical for many temperate rivers, flow conditions varied substantially among years (Figure 2(a)). Total flow was higher in the Sacramento River than the Yolo Bypass throughout the study, except during a large flood in 1998. In 2000, the weather was moderately wet, resulting in a winter flow pulse. Flooding of the Yolo Bypass began when flow in the adjacent Sacramento River exceeded about $1500 \, m^3 \, s^{-1}$. In 2001, a dry year, peak Sacramento River flows were insufficient to inundate the floodplain; all of the observed flooding originated from small streams entering the Yolo Bypass from the west. Water temperature increased gradually throughout each of the study years (Figure 2(f)). The Sacramento River and Yolo Bypass temperatures closely tracked one another, although the floodplain was warmer in each year.

Peak inundation of Yolo Bypass occurred during February 1998, when the total simulated surface area of 23 500 ha was close to the 24 000 ha estimate of the basin surface area from the GIS analysis of aerial photographs (Figure 2(b)). The model and GIS estimates (21 000 ha) were equivalent for 2 March 1998. The model was somewhat less accurate for 28 April 1998, when the simulated area of 6750 ha was higher than the 5050 ha calculated from the GIS, and for 28 February 2001, when the simulated area of 10 200 ha was higher than the 7820 ha from the GIS. During 1998 and high-flow pulses in 2000 and 2001, the total inundated surface area of Yolo Bypass exceeded that of the Sacramento River. Surface area in the Yolo Bypass closely followed the flow peaks, with successively smaller amounts of inundated area for each of the study years. Floodplain surface area varied substantially on the order of days, with changes of 100% or more over 24 h. By contrast, the total surface area in the Sacramento River varied little among months and years. This was also true for the index of shallow water habitat (the estimated total surface area $<2 \, m$ depth), which remained at a level of less than 500 ha throughout the study (Figure 2(c)). The total surface area $<2 \, m$ was generally an order of magnitude higher in Yolo Bypass than in the Sacramento River during the flood events. Even modest flow events, such as February and March of 2001, resulted in peak inundation area of over 10 000 ha of $<2 \, m$ depth in Yolo Bypass. Unlike total surface area, the total surface area $<2 \, m$ depth showed a plateau at approximately 12 000 ha. This effect was most obvious during the extreme flood event in January and February 1998, when the total surface area of $<2 \, m$ depth was less than the following month due to high water levels during the peak flood period. The total area of $<2 \, m$ depth comprised 7–17% of the total surface area of the Sacramento River, whereas this shallow area comprised 50–100% of the total surface area in Yolo Bypass, except during the February 1998 flood peak (Figure 2(b) and (c)).

Simulations of idealized mean water velocity tracked flow trends at each location; however, the estimates were at least two to three times greater in the Sacramento River than in Yolo Bypass in all years except 2001 (Figure 2(d)). Idealized mean velocity in Yolo Bypass was actually highest in winter and spring of 2001, the driest water year, when all of the Yolo Bypass flow was confined to the perennial channel, except for a short February–March pulse. Water velocities were also much more variable in Yolo Bypass than in the Sacramento River, with daily changes of up to an order of magnitude in the floodplain, compared with maximum daily changes of less than 25% in the river.

Idealized hydraulic residence time remained less than 5 days in all years for the Sacramento River simulations (Figure 2(e)). In each year there were gradual seasonal increases: shortest residence times were found for 1998 (range: 1–2 days), the wettest year; and the longest residence times were during 2001 (range: 2–5 days), the driest study year. Idealized hydraulic residence times were much more variable for Yolo Bypass, and substantially longer than in the Sacramento River during all months except part of 2001. The high variability during late winter and spring of 2000 and 2001 corresponded to spring–neap tidal cycles.
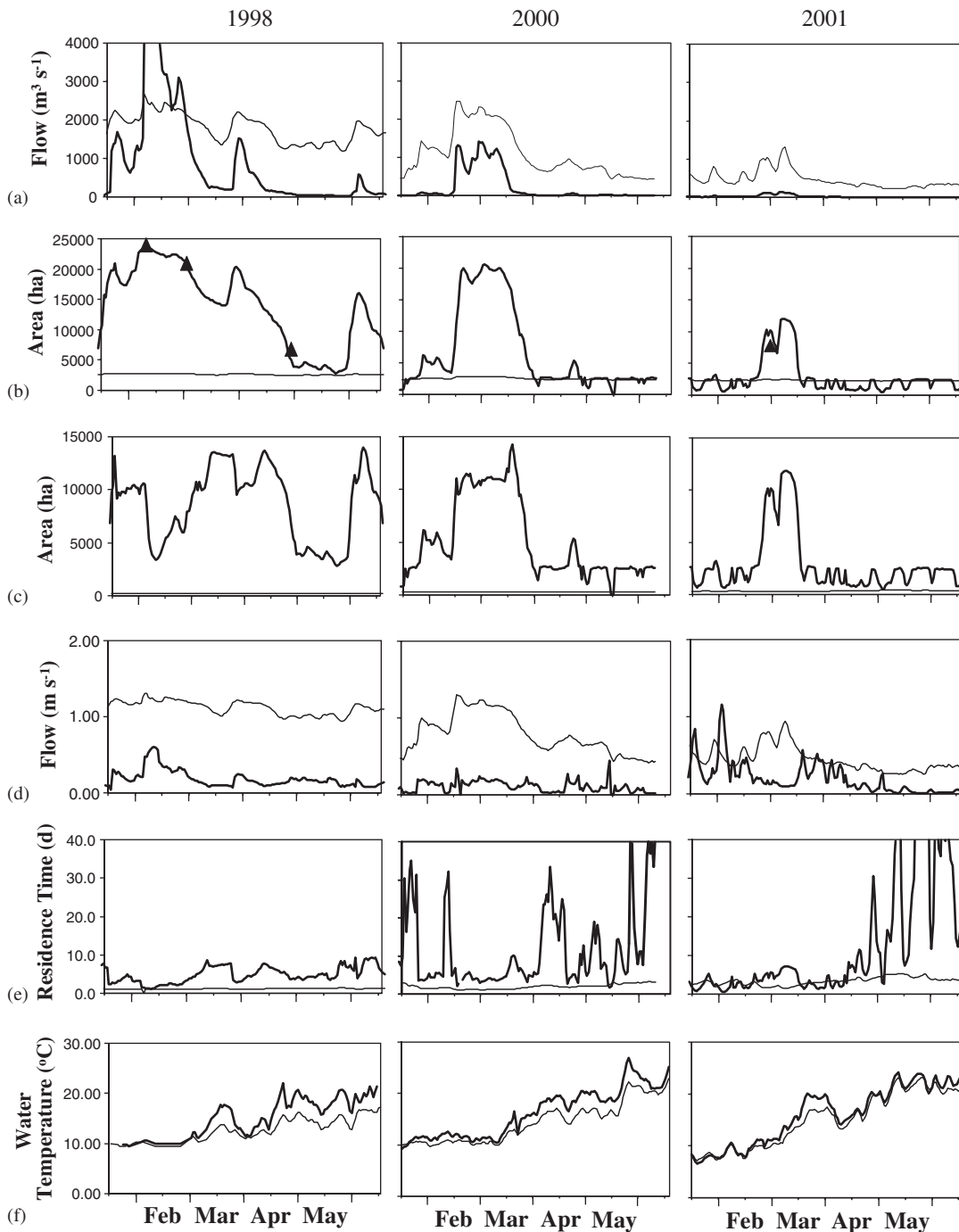
Figure 2. Results of hydrologic simulations and water temperature for the Yolo Bypass (thick line) and Sacramento River (thin line) during the winters and springs of 1998, 2000, and 2001. The variables from top to bottom are: (a) mean daily flow ($m^3 s^{-1}$); (b) simulated total surface area (ha); (c) simulated total surface area $<2 m$ depth (ha); (d) idealized mean water column velocity ($m s^{-1}$); (e) idealized mean hydraulic residence time (days); and (f) mean daily water temperature ($^\circ C$). Flooded area on the Yolo Bypass, estimated from GIS analysis of aerial photographs, is indicated with triangular symbols.

Biological resources

Chlorophyll *a* levels were significantly higher in the Yolo Bypass than in the Sacramento River (Figure 3(b), Table 1). At each location the levels were lowest during mid-winter, when flow was highest. The sharpest increases in floodplain chlorophyll *a* occurred during falling limbs of the hydrographs (Figure 3(a) and (b)). There were statistically significant inverse relationships between flow and chlorophyll *a* for both the floodplain and the river (Table 2). The crustacean zooplankton community was dominated by *Bosmina* (22% of Cladocera counts for the study period), *Daphnia* (33% of Cladocera), and *Acanthocyclops* (4% of copepods). Substantial numbers of calanoid (26% of copepods) and harpactacoid copepods (1% of copepods) were also frequently present. There was no significant difference in the densities of cladocerans or copepods between the floodplain and river (Figure 3(c) and (d); Table 1). The trends in zooplankton densities were inversely related to flow; the relationships were all statistically significant, except for floodplain cladocerans (Table 2).

    The most abundant groups of organisms captured in drift samples were aquatic stages of dipterans, mainly chironomids (Figure 4(b)). Dipteran densities were significantly higher in the floodplain than in the
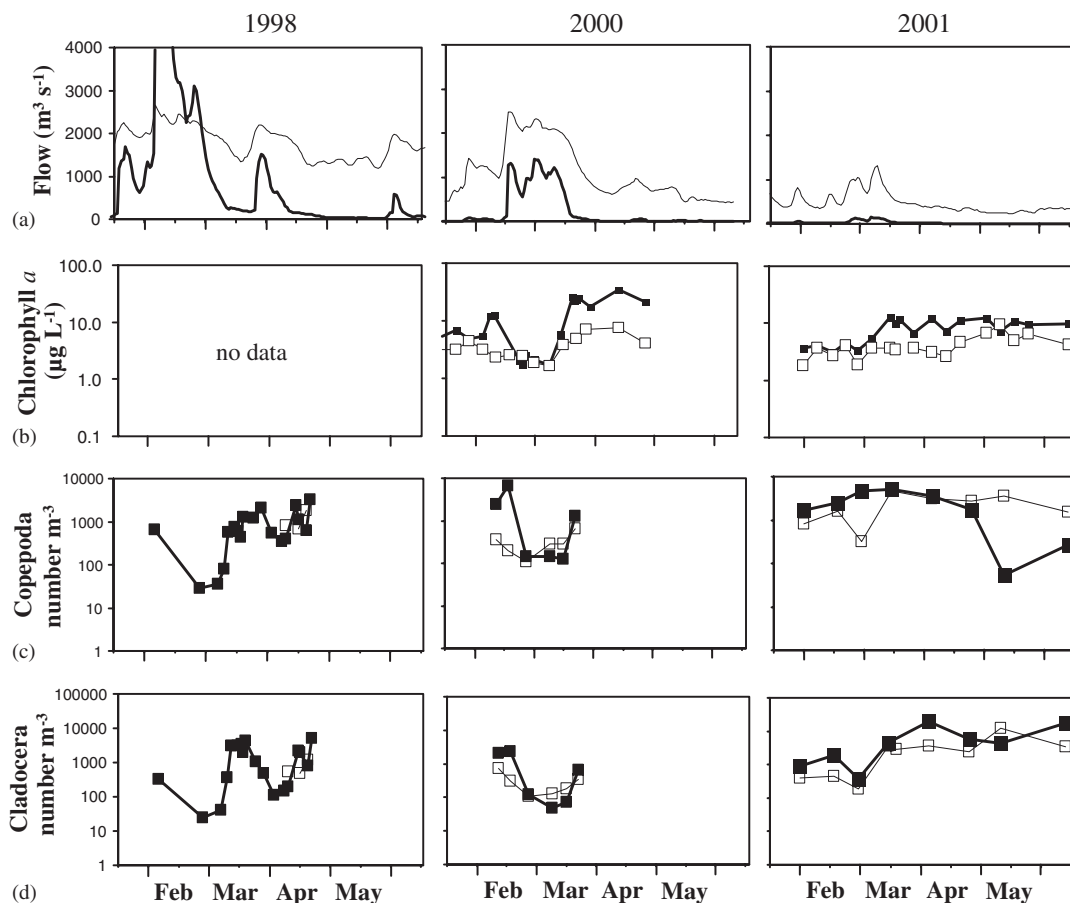

Figure 3. Trends in lower trophic levels in the Yolo Bypass (solid symbols) and Sacramento River (clear symbols) during the winters and springs of 1998, 2000, and 2001. The variables from top to bottom are: (a) Mean daily flow (m³ s⁻¹); (b) chlorophyll *a* (µg L⁻¹); (c) density of copepods (m⁻³); (d) density of cladocerans (m⁻³). Note that in 1998 the chlorophyll *a* data were not collected. A portion of the 2000 chlorophyll *a* data for Yolo Bypass are from Mueller-Solger *et al.* (2002) and Schemel *et al.* (2004).

Table 1. Results of sign tests comparing levels of different organisms in the Yolo Bypass and Sacramento River for all years combined. There were no chlorophyll or zooplankton data for 1998, so the results for those organisms represent 2000 and 2001 only

Organism	Z	n	P
Chlorophyll a	3.35	20	0.007
Cladocera	0.8	14	0.42
Copepoda	1.9	14	0.06
Diptera	3.67	19	0.0002
Other aquatic invertebrates	1.57	20	0.12
Terrestrial invertebrates	2.46	20	0.013

Table 2. Correlations between flow and different organisms in the Yolo Bypass and Sacramento River for all years combined. The Pearson correlation coefficients are shown, together with the number of observations and P-values in parentheses. There were no chlorophyll or zooplankton data for 1998, so the results for those organisms represent 2000 and 2001 only

Organism	Sacramento River	Yolo Bypass
Chlorophyll a	-0.501 ($n = 31$, 0.004)	-0.637 ($n = 31$, $<< 0.001$)
Cladocera	-0.784 ($n = 17$, $<< 0.001$)	-0.214 ($n = 32$, 0.24)
Copepoda	-0.817 ($n = 17$, $<< 0.001$)	-0.682 ($n = 32$, $<< 0.001$)
Diptera	-0.328 ($n = 20$, 0.159)	0.448 ($n = 20$, 0.048)
Other aquatic invertebrates	-0.063 ($n = 20$, 0.792)	0.035 ($n = 20$, 0.884)
Terrestrial invertebrates	-0.219 ($n = 20$, 0.354)	-0.177 ($n = 20$, 0.454)

river (Table 1), and reached their highest levels during flood events in the two wet years (Figure 4(b)). Although there appeared to be a positive association between flow and dipteran density for the river, the relationship was statistically significant for the floodplain only (Table 2). There was also a variety of other aquatic taxa in the drift, with Naididae and Enchytraeidae (oligochaete worms), Physidae (snails), and Hydridae (cnidarians) as the most common families observed each year. As with Diptera, these aquatic invertebrates were generally more abundant in the floodplain than in the river (Figure 4(c)), although the differences were not statistically significant (Table 1). Densities of these aquatic invertebrates were generally highest during flow events (Figure 4(c)), but there was no significant relationship between density and flow for either location (Table 2). Six taxonomic orders (Homoptera, Araneida, Hymenoptera, Collembola, Hemiptera, Coleoptera) comprised more than 90% of the total catch of terrestrial invertebrates in drift samples. Terrestrial invertebrates were scarce in the river in each of the years, with significantly higher densities in the floodplain (Figure 4(d); Table 1). Trends of terrestrial invertebrates in the floodplain and the river suggested a positive response to flow during 1998 and 2000, but there was no statistically significant relationship with flow for all years combined (Table 2).

DISCUSSION

The general effect of seasonal inundation of terrestrial habitat on hydrologic variables has been qualitatively understood for years, with some basic, quantitative descriptions for large river-floodplains (e.g. Toth *et al*., 1995). The modelling described here provides quantitative data about how inundation of a floodplain from an adjacent river channel affects total wetted area, shallow habitat, mean water velocities, and hydraulic residence times over very short time periods (days). The dominant pattern in our study was that the floodplain showed much greater temporal variability than the river channel, reflecting the dynamic
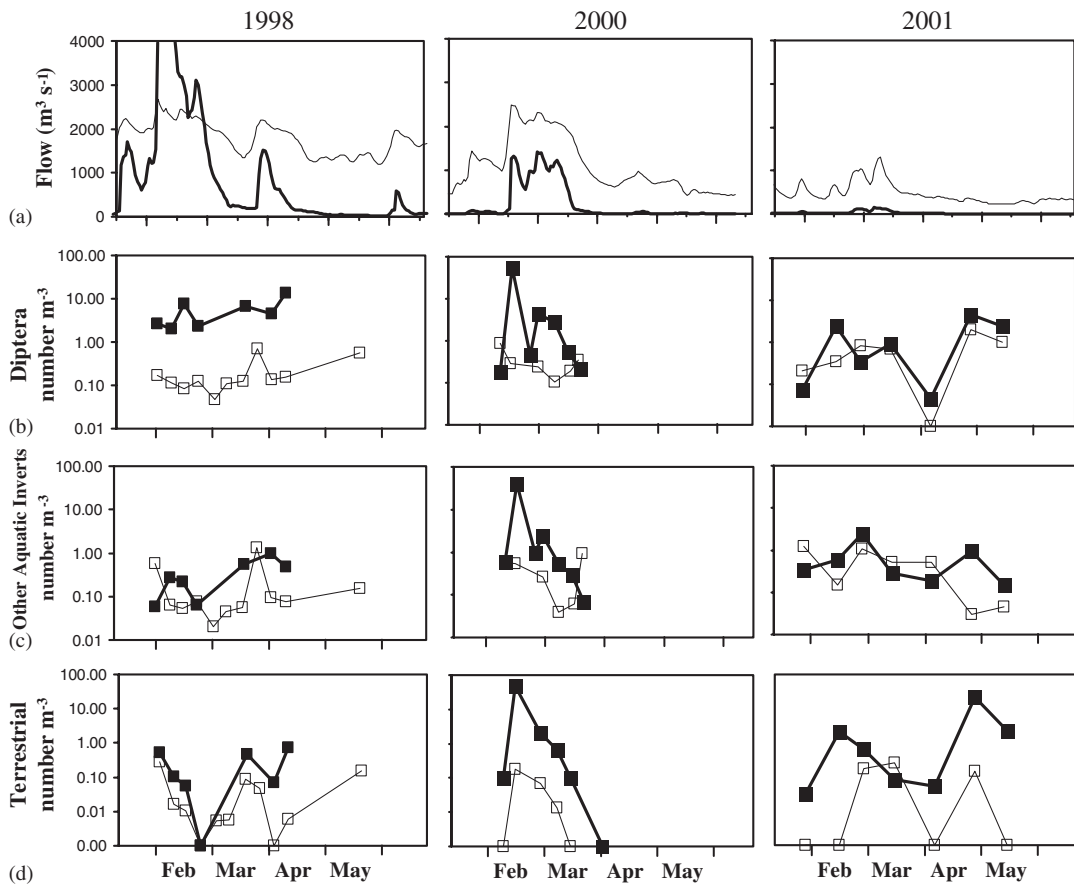
Figure 4. Trends in drift invertebrates in the Yolo Bypass (solid symbols) and Sacramento River (clear symbols) during the winters and springs of 1998, 2000, and 2001. The variables from top to bottom are: (a) mean daily flow ($m^3 s^{-1}$); (b) density of Diptera (m^{-3}); (c) density of aquatic invertebrates other than Diptera (m^{-3}); and (d) density of terrestrial invertebrates (m^{-3}).

nature of floodplain habitat (Bowen *et al.*, 2003). Several of the simulated hydrologic variables also provide reasonable mechanisms to explain temporal trends in phytoplankton and invertebrates, as well as differences in the responses of the biota in river and floodplain habitat. The relevance of these results to the ecology and conservation of river–floodplain habitat is discussed below.

Applications to aquatic ecology

Higher levels of phytoplankton biomass, as indicated by chlorophyll *a* in the floodplain compared with the river, are consistent with a statistical modelling study by Jassby and Cloern (2000). Of the physical variables that were measured or modelled, surface area (<2 m depth), hydraulic residence time, and temperature could provide explanations for the observed trends. Based on simulations of the amount of total area <2 m depth, phytoplankton in the floodplain experienced substantially shallower mean depths than in the river, which may have increased light availability due to more spatially constrained, and thus more intense, vertical mixing (Reynolds, 1994). Shallower depths and longer residence times are probably the primary reason for significantly warmer water temperatures on the floodplain, and they also aid phytoplankton

production (Montagnes and Franklin, 2001). The observation that chlorophyll *a* is inversely related to flow (i.e. positively related to hydraulic residence time) confirms the results of a number of other studies (Lewis, 1988; Heiler *et al*., 1995; Garcia de Emiliani, 1997; Hein *et al*., 1999). Nutrient levels and phytoplankton grazing by invertebrates were not measured but may have affected chlorophyll *a* levels. However, nutrient limitation is unlikely in this region because of the overriding effect of nutrient enrichment from irrigation tailwaters and sewage treatment plants, and light limitation resulting from high suspended sediment concentrations (Jassby *et al*., 2002). Phytoplankton may have been grazed by either zooplankton or macroinvertebrates. The zooplankton data suggest that there was relatively little difference between the densities in the river and its floodplain, so it is unlikely that zooplankton grazing was an important factor determining differences in levels of chlorophyll *a* between the river and the floodplain. The potential effect of greater benthic grazing by the clam *Corbicula* in the river channel cannot be ruled out, as it is an abundant organism that may have played a role in the long-term decline in primary production in the delta (Jassby *et al*., 2002). This clam is uncommon in the Yolo Bypass, because most of the habitat seasonally dewaters.

In contrast to chlorophyll *a*, no major differences were observed in zooplankton densities between the river and its floodplain. This is similar to the findings of Speas (2000). The results for chlorophyll *a* and temperature suggest greater food availability and slightly higher water temperatures in the floodplain than in the river channel, which should have been bioenergetically favourable to zooplankton. This was not reflected by zooplankton density; however, it is possible that zooplankton may have benefited from increased phytoplankton levels in ways not measured in this study. For example, laboratory studies by Mueller-Solger *et al*. (2002) showed that increased chlorophyll *a* concentrations in the Yolo Bypass result in faster potential growth rates for the cladoceran *Daphnia magna* than in the adjacent river. Another potentially important biological factor is grazing by zooplanktivores, but this group of organisms was not assessed in the study. It is unlikely, however, that grazing by fish was a major factor controlling zooplankton densities, as fish densities are typically lower in the floodplain than in the river, especially during high-flow periods (Sommer, unpublished data).

Given the apparent inverse relationships between zooplankton density and flow, it seems likely that physical processes had a greater effect on zooplankton than 'bottom up' (i.e. phytoplankton availability) or 'top down' (i.e. grazing pressure) trophic interactions. First, storm run-off is likely to have diluted the concentration of zooplankton. Second, although greater than in the river, hydraulic residence time in the floodplain was not long enough to allow for complete zooplankton development and resulting population growth. Third, flow velocities in both study areas may have been too high for successful zooplankton reproduction throughout most of the study period. Support for the first hypothesis comes from the decrease in the densities of copepods and cladocera by close to an order of magnitude following the Feburary 1998 increase in peak Yolo Bypass discharge of a similar magnitude. Similarly, in February 2000, a Yolo Bypass flow increase of two to three orders of magnitude was associated with a two orders of magnitude drop in zooplankton densities. Prey dilution effects during flood events have also been predicted based on floodplain food-web simulation models (Power *et al*., 1995b). The second hypothesis is supported by the fairly low idealized hydraulic residence times (< 10 days) in both study areas throughout much of the study period (Figure 2). These residence-time estimates should be interpreted with caution because they do not take into account tidal effects, but they are useful approximations of actual values, particularly during the high-flow events that were the focus of this study. Hydraulic residence time is an important factor in determining seasonal variation in zooplankton abundance and differences in abundance among a wide range of habitats (Pace *et al*., 1992). Baranyi *et al*. (2002) found that, for a floodplain–river system of the Danube River, 'water age', a measure closely related to hydraulic residence time, controlled zooplankton biomass for water ages up to about 14 days. In support of the third hypothesis, idealized mean water-column velocities in both the Yolo Bypass and Sacramento River often approached or exceeded $0.4 \, \mathrm{m \, s}^{-1}$, a critical flow velocity above which successful zooplankton reproduction becomes rare (Rzoska, 1978).

Zooplankton feeding is inhibited by high suspended sediment concentrations, a possible mechanism by which zooplankton production is suppressed at high water velocities (Kirk and Gilbert, 1990; Baranyi *et al*., 2002).

Higher densities of Diptera and terrestrial invertebrates in the floodplain are consistent with the results of Gladden and Smock (1990), who found exceptional production of these organisms in floodplain habitats. The most likely factors responsible for the higher densities of these drift invertebrates include biotic (food availability and predation rates) and abiotic (habitat availability and water temperature) factors. The chlorophyll *a* data indicate that the floodplain had higher phytoplankton levels, increased surface area during high flow (particularly for shallow water habitat), and warmer water than the river. Predation rates of consumers were not examined; however, fish are well known to structure invertebrate communities in some habitats (Batzer and Resh, 1992), and predation rates are often lower in frequently disturbed habitats such as floodplains (Corti *et al*., 1997). Nonetheless, the fact that Diptera showed a positive flow response in both locations suggests that abiotic factors had a stronger effect than predation on this drift invertebrate. Of the various physical factors, the positive association between dipteran density and flow was probably due either to increased substrate area or to higher velocities, which made the invertebrates more vulnerable to capture. Of the two hypotheses, the former is the most reasonable. The most abundant group of Diptera was chironomids, which show a strong association with substrate, particularly at later life stages (Smith, 2001). In other words, the floodplain probably had a higher abundance of these drift invertebrates during flood events because the floodplain had much more inundated terrestrial habitat than the Sacramento River. Increased surface area could also explain why there were significantly higher densities of terrestrial invertebrates in the floodplain than in the river, although we were unable to find statistically significant relationships between flow and density of the organisms to support this hypothesis.

Applications to conservation biology

These results are consistent with the conclusions of Richter *et al*. (2003), that hydologic modelling can provide important insight into the flow requirements and conservation of rivers. In the case of the present study, the reach-scale hydrologic model helped to identify mechanisms that control temporal variation in several lower trophic levels. As noted by Richter *et al*. (2003), such models can also be essential tools to help establish minimum flow requirements and design ecologically sustainable water management.

From a conservation perspective, perhaps one of the most valuable products of the study is that the incremental value of floodplain relative to channel habitat could be identified. Floodplain is often difficult to evaluate because of uncertain boundaries between floodplain and channel habitat, and because of the biotic exchange between them. Because Yolo Bypass and the Sacramento River were partially separated by levees, measurements in each habitat were clearly defined. The results suggest that the floodplain habitat provided food-web organisms, including phytoplankton, and several types of invertebrate at levels up to an order of magnitude higher than its channel habitat. In turn, it may be expected that enhancement of lower trophic levels through floodplain restoration would support the conservation of fish that reside in the floodplain or migrate through seasonally. As has been reported in other large floodplain-rivers (Fisher *et al*., 2001), chironomids are likely to be a key link to these higher trophic levels. In the San Francisco estuary, fish that would benefit from higher densities of these invertebrates include the federally listed Chinook salmon. Sacramento River and its tributaries are responsible for the majority of salmon production in California (Yoshiyama *et al*., 2000). Sommer *et al*. (2001b) found that floodplains represent one of the most important rearing habitats for young Chinook salmon during their downstream migration from the Sacramento River basin; high levels of chironomids were a major reason for enhanced salmon growth, and perhaps survival. Similarly, the native minnow splittail (*Poginichthys macrolepidotus*) mainly consumes

chironomids and cladocerans during its early life stages (Moyle *et al.*, in press). Our observation that chironomids were at higher densities in the Yolo Bypass may, therefore, help to explain, in part, why year class strength of splittail is directly related to the frequency and duration of inundation of floodplain (Sommer *et al.*, 1997).

This study also supports the growing body of evidence that river–floodplain connectivity is critical to the conservation of large rivers (Ward and Stanford, 1995b; Wiens, 2002). Although improvements were noted in the density of several aquatic organisms in years with extensive floodplain inundation, in dry years there is poor river–floodplain connectivity. A good example is 2001, when 10 000 ha of flooded habitat was created by water inputs from small streams. Because there was no inundation from the Sacramento River, salmon and native fish from the river and its tributaries had no access to the floodplain and, therefore, could not take advantage of the higher levels of prey. The lack of Sacramento River flow also may have reduced downstream transport of primary or secondary production that could have subsidized the downstream reaches of the estuary. This finding is congruent with a review of different habitat rehabilitation alternatives by Jassby and Cloern (2000); they concluded that increased inundation of floodplain habitat probably offers the greatest potential for enhancement of high-quality organic matter to the food web of the San Francisco estuary.

Another observation with conservation applications was that several types of food-web species responded to floodplain inundation at relatively rapid time scales (i.e. days), and could ostensibly provide crucial food resources for higher trophic levels. These results suggest that even very short periods of inundation may be sufficient to provide ecosystem-level benefits. The biological responses are likely to be linked to rapid changes in physical habitat that occur during floodplain inundation. A major effect of floodplains on physical habitat is consistent with the findings of Bowen *et al.* (2003), who used hydraulic modelling to demonstrate that the availability of low-velocity habitat changed very quickly with flow in two large rivers. Moreover, the responses of the food-web organisms are reasonable given their life history traits. As an example, during 1999–2000, the phytoplankton community in 12 samples taken at various Yolo Bypass locations was dominated by picoplankton (*Synechococcus* sp.) and to a lesser degree by nanoflagellates, small diatoms, and filamentous cyanobacteria (Mueller-Solger, unpublished data). These small, fast-growing (often more than one doubling per day), ubiquitous algae are recognized for their adaptations to turbid and turbulent environments (Reyholds, 1994). These and similar types of algae are thus likely to be 'first-responders' to floodplain inundation. Primary consumers benefiting from short floodplain inundation periods include small organisms with short development times such as rotifers (Baranyi *et al.*, 2002), highly vagile organisms, such as drift insects (Collier and Quinn, 2003), and organisms like chironomids that are associated with wetted substrate (Smith, 2001). Thus, although longer inundation periods would be desirable for maximum food-web benefits, even shorter inundation periods can provide ecosystem functions that might prove crucial for the continued survival of many species, including several of the threatened and endangered fish species in the Sacramento River system. Greater recognition of the ecological benefits of floodplain inundation and potential floodplain restoration are, therefore, important goals for conservation.

REFERENCES

Baranyi C, Hein T, Holarek C, Keckeis S, Schiemer F. 2002. Zooplankton biomass and community structure in a Danube River floodplain system: effects of hydrology. *Freshwater Biology* **47**: 473–482.

Batzer DP, Resh VH. 1992. Macroinvertebrates of a California seasonal wetland and responses to experimental habitat manipulation. *Wetlands* **12**: 1–7.

Bennett WA, Moyle PB. 1996. Where have all the fishes gone? Interactive factors producing fish declines in the Sacramento–San Joaquin Estuary. In *San Francisco Bay: The Ecosystem*, Hollibaugh JT (ed.). American Association for the Advancement of Science: San Francisco; 519–542.

Bowen ZH, Bovee KD, Waddle TJ. 2003. Effects of flow regulation on shallow-water habitat dynamics and floodplain connectivity. *Transactions of the American Fisheries Society* **132**: 809–823.

CALFED. 2000. Programmatic record of decision August 28, 2000. CALFED, Sacramento. Available at http://wwwcalfed.water.ca.gov/current/ROD.html.

Castleberry DT, Cech JJ, Erman DC, Hankin D, Healey M, Kondolf GM, Mangel M, Mohr M, Moyle PB, Nielsen J, Speed TP, Williams JG. 1996. Uncertainty and instream flow standards: *Fisheries* **21**: 20–21.

Collier KJ, Quinn JM. 2003. Land-use influences macroinvertebrate community response following a pulse disturbance. *Freshwater Biology* **48**: 1462–1481.

Corti D, Kohler SL, Sparks RE. 1997. Effects of hydroperiod and predation on a Mississippi River floodplain invertebrate community. *Oecologia* **109**: 154–165.

Cowardin LM, Carter V, Golet FC, LaRoe ET. 1979. Classification of wetlands and deepwater habitats of the United States. US Fish and Wildlife Service Publication FWS/OBS-79/31, Washington, DC.

Dynesius M, Nilsson C. 1994. Fragmentation and flow regulation of river systems in the northern third of the world. *Science* **166**: 753–762.

Fausch K, Torgersen C, Baxter C, Li H. 2002. Landscapes to riverscapes: bridging the gap between research and conservation of stream fishes. *Bioscience* **52**: 483–498.

Fisher SJ, Brown ML, Willis DW. 2001. Temporal food web variability in an upper Missouri River backwater: energy origination points and transfer mechanisms. *Ecology of Freshwater Fish* **10**: 154–167.

Garcia de Emiliani MO. 1997. Effects of water level fluctuations on phytoplankton in a river–floodplain lake system (Parana River, Argentina). *Hydrobiologia* **357**: 1–15.

Gladden JE, Smock LA. 1990. Macroinvertebrate distribution and production on the floodplains of two lowland headwater streams. *Freshwater Biology* **24**: 533–545.

Gutreuter S, Bartels AD, Irons D, Sandheinrich MD. 2000. Evaluations of the flood-pulse concept based on statistical models of growth of selected fishes of the Upper Mississippi River system. *Canadian Journal of Fisheries and Aquatic Sciences* **56**: 2282–2291.

Heiler G, Hein T, Schiemer F, Bornette G. 1995. Hydrological connectivity and flood pulses as the central aspects for the integrity of a river–floodplain system. *Regulated Rivers: Research and Management* **11**: 351–361.

Hein T, Heiler G, Pennetzdorfer D, Riedler P, Schagerl M, Schiemer F. 1999. The Danube restoration project: functional aspects and planktonic productivity in the floodplain system. *Regulated Rivers: Research and Management* **15**: 259–270.

Jassby AD, Cloern JE. 2000. Organic matter sources and rehabilitation of the Sacramento–San Joaquin Delta (California, USA). *Aquatic Conservation: Marine and Freshwater Ecosystems* **10**: 323–352.

Jassby AD, Kimmerer WJ, Monismith SG, Armor C, Cloern JE, Powell TM, Schubel JR, Vendlinski TJ. 1995. Isohaline position as a habitat indicator for estuarine populations. *Ecological Applications* **5**: 272–289.

Jassby AD, Cloern JE, Cole BE. 2002. Annual primary production: patterns and mechanisms of change in a nutrient-rich tidal ecosystem. *Limnology and Oceanography* **47**: 698–712.

Junk WJ, Bayley PB, Sparks RE. 1989. The flood pulse concept in river–floodplain systems. In *Proceedings of the International Large River Symposium*, Dodge DP (ed.). Canadian Special Publication of Fisheries and Aquatic Sciences 106, NRC Research Press: Ottawa; 110–127.

Kimmerer WJ, Orsi JJ. 1996. Changes in the zooplankton of the San Francisco Bay estuary since the introduction of the clam *Potamocorbula amurensis*. In *San Francisco Bay: The Ecosystem*, Hollibaugh JT (ed.). American Association for the Advancement of Science: San Francisco; 403–425.

Kirk KL, Gilbert JJ. 1990. Suspended clay and the population dynamics of planktonic rotifers and cladocerans. *Ecology* **71**: 1741–1755.

Klopatek JM, Gardner RH (eds.) 1999. *Landscape Ecological Analysis: Issues and Applications*. Springer: New York.

Lewis WM. 1988. Primary production in the Orinoco River. *Ecology* **69**: 679–692.

Marthur D, BassonWH, Purdy Jr EJ, Silver CA. 1985. A critique of the instream flow incremental methodology: *Canadian Journal of Fisheries and Aquatic Sciences* **42**: 825–831.

Montagnes DJS, Franklin DJ. 2001. Effect of temperature on diatom volume, growth rate, and carbon and nitrogen content: reconsidering some paradigms. *Limnology and Oceanography* **46**: 2008–2018.

Moyle PB, Baxter KD, Sommer TK, Foin TC, Matern SA. In press. Biology and population dynamics of Sacramento splittail (*Pogonichthys macrolepidotus*) in the San Francisco Estuary: a review. *San Francisco Estuary and Watershed Science*.

Mueller-Solger AB, Jassby AD, Mueller-Navarra DC. 2002. Nutritional quality for zooplankton (*Daphnia*) in a tidal freshwater system (Sacramento–San Joaquin River Delta, USA). *Limnology and Oceanography* **47**: 1468–1476.

Orsi JJ, Mecum WL. 1996. Food limitation as the probable cause of a long-term decline in the abundance of *Neomysis mercedis* the Oppossum Shrimp in the Sacramento–San Joaquin estuary. In *San Francisco Bay: The Ecosystem*, Hollibaugh JT (ed.). American Association for the Advancement of Science: San Francisco; 375–402.

Pace ML, Findlay SEG, Lints D. 1992. Zooplankton in advective environments: the Hudson River community and a comparative analysis. *Canadian Journal of Fisheries and Aquatic Sciences* **49**: 1060–1069.

Power ME, Sun A, Parker G, Dietrich WE, Wootton JT. 1995a. Hydraulic food-chain models. An approach to the study of food-web dynamics in larger rivers. *Bioscience* **45**: 159–167.

Power ME, Parker G, Dietrich WE, Sun A. 1995b. How does floodplain width affect floodplain river ecology? A preliminary exploration using simulations. *Geomorphology* **13**: 310–317.

Reiser DW, Wesche TA, Estes C. 1989. Status of instream flow legislation and practices in North America. *Fisheries* **14**: 22–29.

Reynolds CS. 1994. The long, the short, and the stalled: on the attributes of phytoplankton selected by physical mixing in lakes and rivers. *Hydrobiologia* **289**: 9–21.

Richter BD, Baumgartner VJ, Wigington R, Braun DP. 1997. How much water does a river need? *Freshwater Biology* **37**: 231–249.

Richter BD, Mathews R, Harrison DL, Wigington R. 2003. Ecologically sustainable water management: managing river flows for ecological integrity. *Ecological Applications* **13**: 206–224.

Rzoska J. 1978. *On the Nature of Rivers*. Junk: The Hague.

Schemel LE, Sommer TR, Mueller-Solger, Harrell WC. 2004. Hydrologic variability, water chemistry and phytoplankton biomass in a large floodplain of the Sacramento River, CA, USA. *Hydrobiologia* **513**: 129–139.

Smith DG. 2001. *Pennak's Freshwater Invertebrates of the United States: Porifera to Crustacea*, 4th edition. John Wiley: New York.

Sommer TR, Baxter R, Herbold B. 1997. The resilience of splittail in the Sacramento–San Joaquin Estuary. *Transactions of the American Fisheries Society* **126**: 961–976.

Sommer TR, Harrell WC, Nobriga ML, Brown R, Moyle PB, Kimmerer WJ, Schemel L. 2001a. California's Yolo Bypass: evidence that flood control can be compatible with fisheries, wetlands, wildlife, and agriculture. *Fisheries* **26**: 6–16.

Sommer TR, Nobriga ML, Harrell WC, Batham W, Kimmerer WJ. 2001b. Floodplain rearing of juvenile Chinook salmon: evidence of enhanced growth and survival. *Canadian Journal of Fisheries and Aquatic Sciences* **58**: 325–333.

Speas DW. 2000. Zooplankton density and community composition following an experimental flood in the Colorado River, Grand Canyon, Arizona. *Regulated Rivers: Research and Management* **16**: 73–81.

Stanford JA, Ward JV. 1988. The hyporheic habitat of river ecosystems. *Nature* **335**: 64–66.

Thorp JH, Delong MD. 1994. The riverine productivity model: an heuristic view of carbon sources and organic processing in large river ecosystems. *Oikos* **70**: 305–308.

Tockner K, Pennetzdorfer D, Reiner N, Schiemer F, Ward JV. 1999. Hydrological connectivity and the exchange of organic matter and nutrients in a dynamic river–floodplain system (Danube, Austria). *Freshwater Biology* **41**: 521–535.

Toth LA, Arrington DA, Brady MA, Muszick. 1995. Conceptual evaluation of factors potentially affecting restoration of habitat structure within the channelized Kissimmee River ecosystem. *Restoration Ecology* **3**: 160–180.

Turner MG. 1989. Landscape ecology: the effect of pattern on process. *Annual Review of Ecology and Systematics* **20**: 171–198.

Vannote RL, Minshall GW, Cummins KW, Sedell FR, Cushing CE. 1980. The river continuum concept. *Canadian Journal of Fisheries and Aquatic Sciences* **37**: 130–137.

Ward JV, Stanford JA. 1995a. The serial discontinuity concept: extending the model to floodplain rivers. *Regulated Rivers: Research and Management* **10**: 159–168.

Ward JV, Stanford JA. 1995b. Ecological connectivity in alluvial river ecosystems and its disruption by flow regulation. *Regulated Rivers: Research and Management* **11**: 105–119.

Welcomme RL. 1979. *Fisheries Ecology of Floodplain Rivers*. Longman: London.

Wiens J. 2002. Riverine landscapes: taking landscape ecology into the water. *Freshwater Biology* **47**: 501–515.

Williams JG. 1996. Lost in space: minimum confidence intervals for idealized PHABSIM studies. *Transactions of the American Fisheries Society*: **125**: 458–465.

Yoshiyama RM, Gerstung ER, Fisher FW, Moyle PB. 2000. Chinook salmon in the California Central Valley: an assessment. *Fisheries* **25**: 6–20.