Hydrobiologia **513:** 129–139, 2004.

Hydrologic variability, water chemistry, and phytoplankton biomass in a large floodplain of the Sacramento River, CA, U.S.A.

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Received 21 February 2003; in revised form 18 July 2003; accepted 21 July 2003

Key words: dissolved inorganic nutrients, floodplain hydrology, phytoplankton biomass, Sacramento River

Abstract

The Yolo Bypass, a large, managed floodplain that discharges to the headwaters of the San Francisco Estuary, was studied before, during, and after a single, month-long inundation by the Sacramento River in winter and spring 2000. The primary objective was to identify hydrologic conditions and other factors that enhance production of phytoplankton biomass in the floodplain waters. Recent reductions in phytoplankton have limited secondary production in the river and estuary, and increased phytoplankton biomass is a restoration objective for this system. Chlorophyll *a* was used as a measure of phytoplankton biomass in this study. Chlorophyll *a* concentrations were low (<4 μg l^{-1}) during inundation by the river when flow through the floodplain was high, but concentrations rapidly increased as river inflow decreased and the floodplain drained. Therefore, hydrologic conditions in the weeks following inundation by river inflow appeared most important for producing phytoplankton biomass in the floodplain. Discharges from local streams were important sources of water to the floodplain before and after inundation by the river, and they supplied dissolved inorganic nutrients while chlorophyll *a* was increasing. Discharge from the floodplain was enriched in chlorophyll *a* relative to downstream locations in the river and estuary during the initial draining and later when local stream inflows produced brief discharge pulses. Based on the observation that phytoplankton biomass peaks during drainage events, we suggest that phytoplankton production in the floodplain and biomass transport to downstream locations would be higher in years with multiple inundation and draining sequences.

Introduction

Many ecological benefits of floodplain inundation have been identified in large tropical and temperate river systems (Junk et al., 1989; Bayley, 1995; Tockner et al., 2000). A key attribute of floodplains is their potential for higher productivity compared to the river channel. Phytoplankton production enhanced by river-floodplain interactions can provide the base of food webs even in systems where phytoplankton account for a small fraction of the total primary production (Araujo-Lima et al., 1986; Bayley, 1989; Hamilton et al., 1992; Lewis et al., 2000, 2001). Even though benefits of inundation might be limited compared to tropical systems, restoration of floodplain function in large temperate rivers is likely to increase food resources for consumers in addition to providing ecologically valuable shallow-water habitat and other seasonal benefits (Bayley, 1991; Tockner et al., 2000).

In the lower Sacramento River and downstream in the San Francisco Estuary, declines in fishes and other aquatic species have been linked to reduced phytoplankton production and abundance and habitat alterations, including drastic reductions in floodplain and shallow water habitats (Bennett & Moyle, 1996; Kimmerer & Orsi, 1996; Jassby et al., 2002). In spite of this, fisheries and other biological resources are enhanced in high-flow years when the Sacramento River inundates its floodplains (Jassby et al., 1995; Bennett & Moyle, 1996). Restoration and improved management of floodplains and other shallow-water habitats have been proposed to increase phytoplankton abundance and restore fisheries and other beneficial attributes (Jassby & Cloern, 2000; CALFED, 2000). However, primary production is sensitive to many factors in this complex system (Jassby et al., 2002), and phytoplankton productivity and abundances can vary greatly among seemingly similar shallow-water habitats (Lucas et al., 2002).

We studied the Yolo Bypass, a large managed floodplain in the lower Sacramento River, which represents only a small portion of a once-extensive floodplain system throughout the central valley of northern California (Fig. 1). While recent research has indicated that food resources for fishes are produced in the Yolo Bypass (Sommer et al., 1997, 2001a,b), phytoplankton sources, abundances, and distributions have not been investigated. General conceptual models of river processes suggest that although river-floodplain interactions increase food supply for consumers, hydrologic variability in the Yolo Bypass and other temperate systems might limit the development of phytoplankton biomass (Junk et al., 1989; Tockner et al., 2000). Our objective was to evaluate variability in discharges, sources of water, and water chemistry in relation to phytoplankton biomass (chlorophyll *a* concentration) in the Yolo Bypass floodplain before, during, and after a major inundation by the Sacramento River. We intended to identify conditions that support production of phytoplankton biomass in the floodplain waters and periods when floodplain discharge supplies phytoplankton to the river.

Study area

The Sacramento River is the major freshwater source for the San Francisco Estuary, and, consequently, it is a key element in the large-scale plan for the CALFED Ecosystem Restoration Program (Conomos et al., 1985; CALFED, 2000). This large river has been highly modified primarily to provide water for agriculture and cities throughout California and flood protection for the Sacramento Valley (Nichols et al., 1986). Modifications include major reservoirs that control discharge during most of the year as well as a system of flood-control weirs, levees, and managed floodplains. The Yolo Bypass, the largest floodplain in the system (approx. 61 km long, 24 000 ha), discharges directly to the tidal headwaters of San Francisco Estuary, the inland delta of the Sacramento and

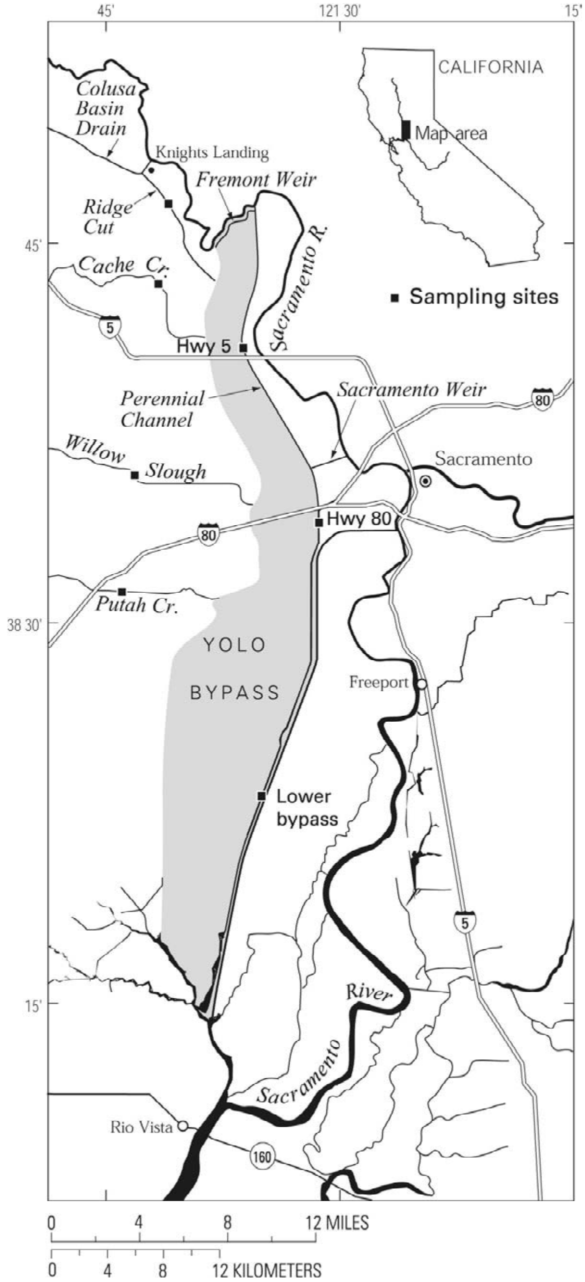

Figure 1. Map of the Yolo Bypass and the lower Sacramento River showing sampling sites along the eastern margin of the floodplain (HWY80, HWY5, Lower Bypass) and in the local streams (Ridge Cut, Putah Creek, and Cache Creek). Smaller rivers join the Sacramento River downstream of Rio Vista in the headwater region of the San Francisco Estuary known as the Delta.

San Joaquin river systems (referred to here as the Delta; Fig. 1). The greatest discharge to the Yolo Bypass floodplain is from the Sacramento River at Fremont Weir, but floodwaters can spill over the downstream Sacramento Weir during extremely high river flows. The floodplain is not connected to the Sacramento River other than at the two inflow weirs and the southern outlet. This configuration simplifies the hydrology of the floodplain compared to most natural river-floodplain systems where a greater degree of connectivity is maintained with the river during inundation.

Floodwaters are confined to the perennial channel along the eastern levee of the floodplain when flows through the Yolo Bypass are less than about 100 m^3 s^{-1}. Higher flows cause flooding toward levees along the western margin, creating a broad, shallow (typically $<$2 m average depth) floodplain. Although local streams that enter the west side can flood limited areas, extensive inundation of the Yolo Bypass occurs only when the Sacramento River discharges over Fremont Weir. The Sacramento River inundated the floodplain in nearly two-thirds of the years from 1956 to 2000; however, the extent, timing, and duration of flooding varied greatly among years. Most flooding by the Sacramento River occurred between January and April, and the floodplain was inundated for a month or longer in about half of those years.

Four streams that discharge to the west side of the Yolo Bypass can be important sources of local water to the floodplain. Ridge Cut is a large canal that delivers substantial discharge to the Yolo Bypass from an extensive agricultural basin, but it is not gauged (California Department of Water Resources, CDWR, 1964; Fig. 1). Cache and Putah creeks (both gauged) carry discharge from upstream reservoirs and storm runoff from their lower basins. Discharges from Willow Slough, a much smaller stream, were not significant during this study (Schemel et al., 2002).

Materials and methods

Water samples were collected from late January through April 2000 at three sites along the eastern margin of the Yolo Bypass (HWY5, HWY80, and Lower Bypass) and at upstream sites on three local streams (Ridge Cut, Cache Creek, and Putah Creek) that discharge to the west side of the floodplain (Fig. 1). Sampling intervals varied over the study, in most cases ranging from a few days to about 2 weeks. Near-surface waters were collected in acid-cleaned polyethylene bottles for dissolved inorganic analytes and chlorophyll *a* and in combusted glass bottles for particulate carbon and nitrogen. Samples were transported in ice chests to the laboratory where they were processed on the same day for chlorophyll *a* and usually on the following day for the other analytes.

Samples for dissolved inorganic analytes were filtered through 0.45 μm-pore-size membrane filters (Millipore Corp. type HA). Suspended particles (seston) were collected on glass fiber filters for chlorophyll *a* and combusted glass fiber filters for carbon and nitrogen. Filtrates for dissolved inorganic nutrients: nitrate, nitrite, and ammonium (the total is reported here as dissolved inorganic nitrogen, DIN), dissolved reactive phosphate (DRP), and dissolved silica (DSi), were frozen in polyethylene bottles and then thawed overnight before analysis on a Technicon Corp. Autoanalyzer II (Hager & Schemel, 1997). Samples for sulfate were refrigerated in polyethylene bottles until analysis on a Dionex LC20 ion chromatograph. Samples for sodium were acidified and stored at room temperature in polyethylene bottles before analysis on a Thermo Jarrell Ash Corp. IRIS Advantage inductively coupled plasma optical emission spectrophotometer. Seston carbon and nitrogen were measured with a Carlo Erba Instruments Model NA 1500NC analyzer. Chlorophyll *a* was used as the measure of phytoplankton biomass in this study. Chlorophyll *a* was extracted with methanol and measured using a Turner Designs Model 10 AU fluorometer (Marker et al. 1980). Specific conductance was measured by electrode at 25C in the laboratory. Additional details of the methods are described by Schemel et al. (2002).

Discharge and water level data for the Sacramento River, Cache and Putah creeks, and the Yolo Bypass were obtained from the U.S. Geological Survey (USGS) annual report (Anderson et al., 2001) or from the USGS (http://water.usgs.gov/nwis/discharge/) and CDWR (http://cdec.water.ca.gov) internet sites. Flow through Ridge Cut was not gauged, but its discharge depended on water levels in the Colusa Basin Drain and the Sacramento River that were provided by the CDWR Northern District Office (Sutter, CA). All gauge heights were adjusted to the National Geodetic Vertical Datum.

The fraction of the flow in the Yolo Bypass that was supplied by Ridge Cut, the local stream that was not gauged, was estimated from sulfate and sodium concentrations during a period when local streams were the major sources of water to the floodplain. These estimates, which assume that observed concentrations result largely from the mixing of two sources, have been used in studies of floodplain lakes (e.g., Fors-

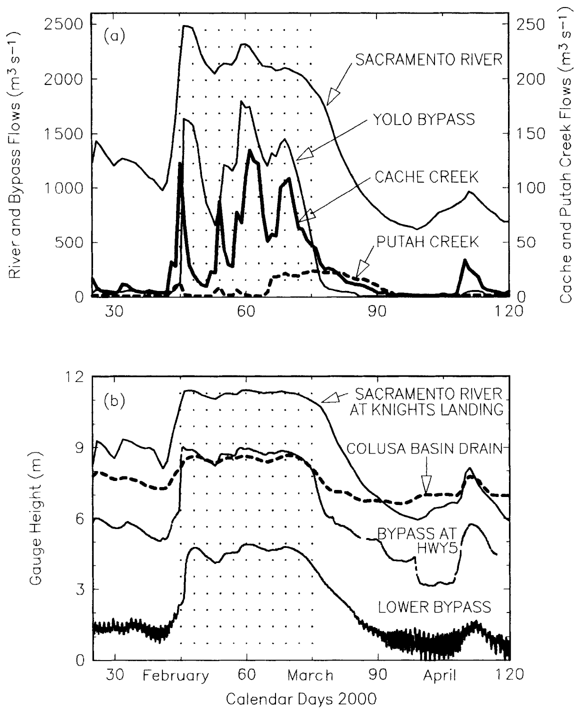

Figure 2. Flows (a) in the Sacramento River, Yolo Bypass, Cache Creek and Putah Creek and gauge heights (b) in the Sacramento River at Knights Landing, Colusa Basin Drain, and Yolo Bypass during late-January through April 2000. The stippled area indicates inundation of the floodplain by Sacramento River inflow.

berg et al., 1988; Carrignan & Neiff, 1992). This technique is particularly useful when differences in concentrations between the two sources are relatively large. In the calculations, transports of sulfate and sodium (products of flows and concentrations) at the floodplain sites were equal to the sum of the local stream transports to the floodplain. By rearranging the equations, the ratio of flow from Ridge Cut to the total flow (RCQ) at each floodplain site could be calculated from the concentration data. Local stream concentrations from Ridge Cut [RC] and Cache Creek [CC] were used in the calculations for the HWY5 and HWY80 sites. For example: RCQ at HWY5 = ([HWY5]−[CC])/([RC]−[CC]). Estimated concentrations for the mixture of Cache and Putah creeks based on their measured flows were used in place of [CC] in calculations for the Lower Bypass site.

Table 1. Specific conductance (μS cm^{-1}), dissolved inorganic nutrients (μM), sulfate (mg l^{-1}), sodium (mg l^{-1}), chlorophyll *a* (μg l^{-1}), and seston C:N ratio in the Sacramento River at Fremont Weir during the inundation period

Analyte	March 7	March 17
Specific conductance	121	147
Dissolved silica	308	339
Nitrate	10.9	14.0
Nitrite	0.1	0.1
Ammonium	0.9	0.3
Dissolved reactive phosphate	1.1	0.7
Sulfate	9.2	10.4
Sodium	6.3	7.2
Chlorophyll *a*	3.5	4.0
Seston C:N ratio (by moles)	11.2	11.2

Results

Hydrology

Water levels and discharges in the Sacramento River had increased with the onset of winter storms by late January 2000 (Fig. 2a,b). Water levels in the Sacramento River first exceeded the elevation of Fremont Weir on February 14 (Fig. 2b), and the river continued to discharge into the Yolo Bypass until March 17 (the inundation period). Water levels in the river remained below the elevation of Fremont Weir for the remainder of winter and spring, and there was no discharge over the Sacramento Weir during this year. The floodplain drained to the level of the perennial channel by mid-April, but water levels increased briefly following a small storm in late April (Fig. 2b).

Discharges from Cache and Putah creeks were an order of magnitude smaller than discharges through the Yolo Bypass during the inundation period, but both creeks and Ridge Cut were significant sources of water to the floodplain before and after the inundation period (Fig. 2a,b). Although not gauged, discharge levels observed during site visits at Ridge Cut appeared similar to or greater than those at Cache Creek from late January to early April. Floodwaters discharged through Ridge Cut primarily when water levels in the Sacramento River at Knights Landing exceeded those in the Colusa Basin Drain (Fig. 2b). This included a few days following the late-April storm, when a flow pulse from Cache Creek also was observed.

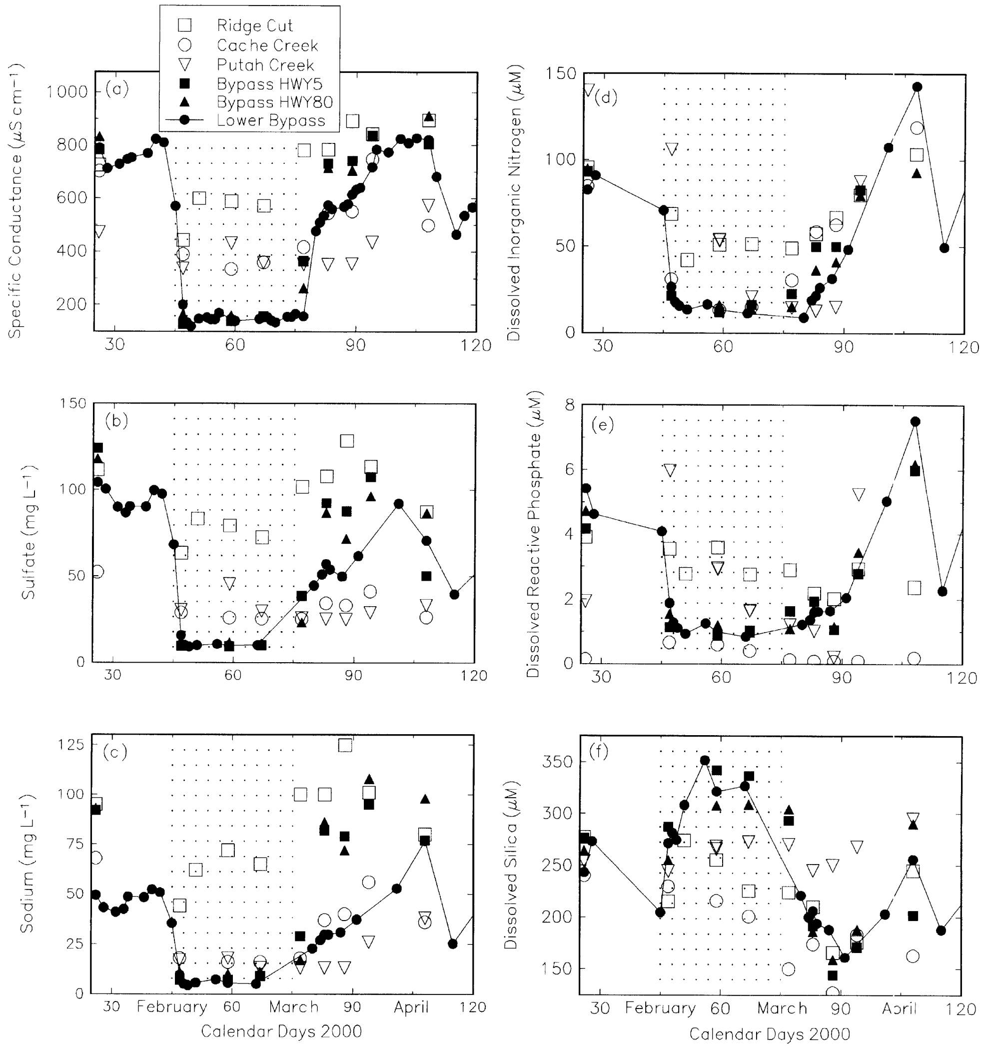

Figure 3. Specific conductance (a), sulfate (b), sodium(c), dissolved inorganic nitrogen (d), dissolved reactive phosphate (e) and dissolved silica (f) in the Yolo Bypass (HWY80, HWY5, Lower Bypass) and local streams (Ridge Cut, Putah Creek, Cache Creek) during late-January through April 2000. The stippled area indicates inundation of the floodplain by Sacramento River inflow.

Water chemistry

Variations in specific conductance in the Yolo Bypass floodwaters indicated major changes in water sources and chemistry upon inundation by the Sacramento River and during the subsequent draining of the floodplain (Fig. 3a). Specific conductance dropped sharply at the beginning and remained low during the inundation period at all three sites in the Yolo Bypass. At that time, specific conductance in the Yolo Bypass was similar to the Sacramento River (Table 1), whereas specific conductances in the local streams were greater by factors of two to four (Fig. 3a). When inflow from the Sacramento River stopped, there was a rapid increase in specific conductance that continued for several weeks at all three sites in the draining floodplain. Specific conductance in the upper Yolo Bypass at HWY5 and HWY80, the sites nearest to inflows from Ridge Cut and Cache Creek, was higher than at the Lower Bypass site until early April. The decrease in specific conductance at the Lower Bypass site in late April coincided with increased water levels from local stream inflows.

Concentrations of sulfate and sodium were lowest in the Sacramento River and at all three Yolo Bypass sites during the inundation period (Table 1, Fig.

3b,c). Sulfate and sodium increased at all three Yolo Bypass sites over the month following the inundation period, but concentrations at the HWY5 and HWY80 sites were typically higher that those at the Lower Bypass site. Among the local streams, sulfate and sodium were most concentrated in Ridge Cut throughout this study. During the second week following the inundation period in late March, two-source mixing calculations using sulfate and sodium concentrations estimated that an average of 75% of the water at HWY5, 66% of the water at HWY80, and 31% of the water at the Lower Bypass site was from Ridge Cut.

Dissolved inorganic nutrient concentrations at all three Yolo Bypass sites were similar to values in the Sacramento River during the inundation period (Table 1, Fig. 3d–f). Concentrations of DIN and DRP increased at the Yolo Bypass sites following the inundation period, whereas concentrations of DSi decreased by 50%, and then increased during April. The ratio of DSi to DIN decreased by a factor of ten to an average value of 3 at the Yolo Bypass sites by late March. Concentrations of DIN, DRP, and DSi at the HWY5 and HWY80 sites in late March were lower than estimates based on supplies from the local streams, but the apparent losses were small (<22%). Similar calculations for the Lower Bypass site indicated a 36% loss of DIN, but no loss of DRP or DSi. Estimates at the Lower Bypass Site did not account for a potentially significant amount of Sacramento River water draining from the floodplain, which was a source of DSi.

The highest nutrient concentrations in mid-April coincided with the lowest water levels along the perennial channel and tidal flow at the Lower Bypass site (Fig. 2b). Nitrate accounted for >90% of the DIN during most of this study. Ammonium was more concentrated in Ridge Cut (10–20% of DIN) compared to the other streams, and ammonium increased at the Yolo Bypass sites in April. Concentrations of all three nutrients decreased at the Lower Bypass site following the small storm in late April.

Chlorophyll a *and C:N ratio*

Concentrations of chlorophyll *a* in the Yolo Bypass increased briefly in early February, when local streams were discharging to the floodplain, but then decreased and remained low (<4 μg l^{-1}) until the end of the inundation period (Fig. 4a). Water elevations and flows in the Yolo Bypass began decreasing 1 week before discharge from the Sacramento River stopped (Fig. 2a,b). This also began a month-long period with no

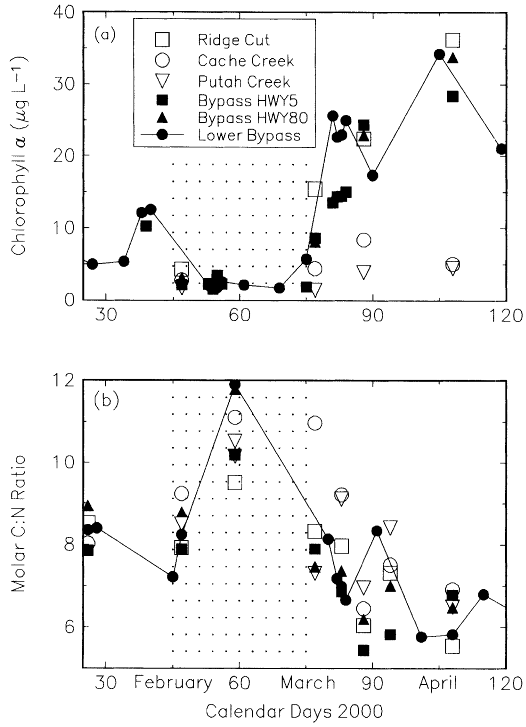

Figure 4. Chlorophyll *a* (a) and molar C:N ratio (b) in the Yolo Bypass (HWY80, HWY5, Lower Bypass) and local streams (Ridge Cut, Putah Creek, Cache Creek) during late-January through April 2000. The stippled area indicates inundation of the floodplain by Sacramento River inflow.

rainfall and increasing sunlight (Schemel et al., 2002). Chlorophyll *a* had increased at all three Yolo Bypass sites (6–9 μg ;$^{-1}$) by March 17, the end of the inundation period. Over the following week, Chlorophyll *a* rapidly increased at the Lower Bypass site to concentrations (23 μg l^{-1} ave.) that were higher than at HWY5 (14 μg l^{-1}). Chlorophyll *a* also increased in Ridge Cut, but concentrations were much lower in Cache and Putah creeks. Chlorophyll *a* remained high at all three Yolo Bypass sites and in Ridge Cut through mid-April, and then decreased at the Lower Bypass site after the small storm in late April.

Seston C:N ratios decreased after the inundation period at all three Yolo Bypass sites, coinciding with the increase in chlorophyll *a* (Fig. 4b). This general pattern was also observed in the local streams, but C:N ratios for Cache and Putah creeks were typically higher than those for Ridge Cut after mid-March.

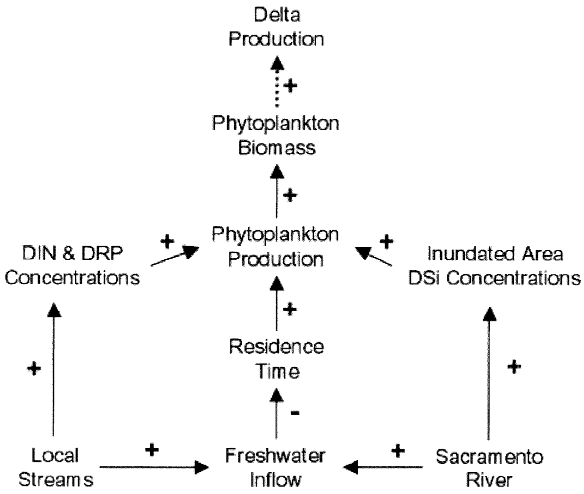

Figure 5. Diagram of a conceptual model for the Yolo Bypass floodplain. Plus symbols represent factors that enhance phytoplankton biomass.

Discussion

This study identified hydrologic conditions that affected transport processes, water chemistry, and phytoplankton biomass in an engineered floodplain of a large temperate river. Likely cause–effect relationships between hydrologic conditions and observed variables are summarized in the following conceptual model (Fig. 5). The Yolo Bypass floodplain receives water from the Sacramento River and several local streams. Flooding of the Yolo Bypass by the Sacramento River greatly increases the inundated area available for phytoplankton production. However, phytoplankton biomass and concentrations of several dissolved chemical constituents are low in the floodplain during major inundation events. This is likely due to low concentrations in the source waters and physical processes such as short (hydraulic) residence times at increased flows. Inundation events are followed by rapid increases in phytoplankton production and biomass as residence times and concentrations of DIN and DRP increase. Although not measured in our study, we believe that floodplain phytoplankton production subsequently supports primary consumers in the seasonal habitat, and provides high quality organic carbon to the downstream San Francisco Estuary. Because our study shows that phytoplankton levels are highest during floodplain drainage, we suggest that years with multiple inundation and drainage events would yield greater production than years with just one inundation event. Here we discuss our results within the context of this conceptual model, provide additional supporting evidence, and identify some uncertainties.

The apparent inverse relationship between flow and concentrations of chlorophyll *a* and some dissolved chemical constituents indicates that hydrologic variability is a dominant factor. Similar links between flows and chlorophyll *a* concentrations have been reported in tropical and temperate floodplains and floodplain lakes (Hamilton & Lewis, 1987; Knowlton & Jones, 1997; Tockner et al., 1999; Lewis et al., 2000; Castillo, 2000). The mechanism by which flow affects these variables was not specifically addressed in this study; however, source water concentrations and residence time provide reasonable explanations for many of our observations. Residence time likely affected phytoplankton biomass through several mechanisms. For example, if residence time during flood events is much shorter than the growth rate of floodplain phytoplankton, there is insufficient time for biomass accumulation. Recent hydrologic modeling of the Yolo Bypass has shown that large flood events result in substantial decreases in an index of residence time (Sommer, 2002). Other flow and residence-time-related variables that could help explain the observed trends in phytoplankton biomass include variations in water temperature and light availability as mediated by turbidity or water depth.

While inflow from the Sacramento River was the largest input to the floodplain, our evidence shows that smaller tributaries (local streams) can have an important effect on floodplain phytoplankton and water chemistry. Influences of local sources of water (streams, groundwaters, precipitation, etc.) have been recognized primarily in floodplain lakes during periods of isolation or reduced river inflow (e.g., Forsberg et al., 1988; Lesack & Melack, 1995). However, local waters can create variability in floodwater characteristics across floodplains during inundations by the river (Mertes, 1997). This was documented in the Yolo Bypass during 1998 by aerial photographs showing that discharges from four local streams formed broad bands that extended the length of the floodplain during inundation by the Sacramento River (Sommer et al., 2001a).

Local streams were significant sources of nutrients to the floodplain during this study. This is in contrast to river-floodplain systems where the river is a primary source of nutrients. In these systems, floodplain waters can become depleted in nutrients when connectivity is reduced and phytoplankton abundance increases (Van den Brink et al., 1993; Knowlton & Jones, 1997; Hein et al., 1999; Unrein, 2002). This was not observed in the Yolo Bypass, which in part might be attributed to the supply of nutrients by the local streams. Concentrations of DIN and DRP were low when the Yolo Bypass was flooded by the Sacramento River, but local streams and presumably other sources and processes (e.g., groundwater and mineralization of organic matter, as indicated by higher ammonium concentrations) supplied these nutrients after the inundation period. Utilization by phytoplankton was apparent during the last week of March because concentrations (particularly DIN) at the floodplain sites were lower than might be expected based on supplies from the local streams. Depletion of DSi in river-floodplain systems that are rich in DIN and DRP can cause changes in the community structure of phytoplankton and zooplankton (e.g., Van den Brink et al., 1994). DSi was not depleted to extremely low levels in the Yolo Bypass, but DSi concentrations were greatly reduced relative to DIN concentrations as phytoplankton biomass increased and Sacramento River water was replaced by local stream inflow.

As the floodplain drained, chlorophyll *a* concentrations reached levels that could be particularly beneficial to primary consumers in the Yolo Bypass. Even though detrital organic matter typically is abundant in this system, the high nutritional quality of phytoplankton organic carbon promotes growth of primary consumers that are important links in the food chain for fishes and other aquatic species (Orsi & Mecum, 1986; Sobczak et al., 2002). Recent research in the Yolo Bypass and at other locations in the Delta has shown that cladoceran growth rates are highest when concentrations of chlorophyll *a* exceed 10 μg l^{-1} and that detrital organic matter does not strongly enhance growth (Müller-Solger et al., 2002). Low seston C:N ratios during our study indicated that phytoplankton became a large fraction of the available particulate organic matter as the floodplain drained. Abundant food resources appear to be beneficial to aquatic species that inhabit the floodplain waters. For example, juvenile chinook salmon migrating through the Yolo Bypass have shown higher prey consumption and growth rates than salmon migrating in the adjacent Sacramento River (Sommer et al., 2001b).

The degree to which primary production from the Yolo Bypass benefits the downstream San Francisco Estuary is unclear. Although the floodplain was disconnected from the upstream Sacramento River after mid-March, the connection to the Delta was maintained at the southern outlet even at low water levels when river-floodplain exchanges were driven largely by tides. Because of its design, large areas of the Yolo Bypass drained over a few weeks following major inundation by the river, thereby transporting phytoplankton with the floodwaters to the Delta. A concurrent study which collected phytoplankton samples in water draining from the Yolo Bypass observed large increases in abundances of diatoms and other phytoplankton species in late March (Sobczak, W. V., pers. comm.). Transport to the Delta was confirmed by a downstream water quality monitor on the west bank of the Sacramento River channel at Rio Vista (Fig. 1), which detected a substantial increase in chlorophyll *a* fluorescence at that time (CDWR, unpublished data). During our study, chlorophyll *a* concentrations rarely exceeded 10 μg l^{-1} at most locations in the Delta, and the deep river channels had the lowest concentrations (Sobczak et al., 2002). The average chlorophyll *a* concentration at the Lower Bypass site during the last week of March was 23 μg l^{-1}, indicating that discharge from the draining Yolo Bypass was enriched in phytoplankton biomass relative to the Delta. In addition to their importance in providing nutrients for phytoplankton production and (in the case of Ridge Cut) phytoplankton biomass to the floodplain, local streams were also responsible for a substantial amount of the flow through the Yolo Bypass as the floodplain drained and after a small storm. These flows likely played an important role in transporting accumulated phytoplankton, other aquatic organisms, and dissolved nutrients from the floodplain to the Delta.

Although phytoplankton-enriched discharges from the Yolo Bypass to the Delta appear limited to relatively brief periods during late winter and spring, these discharges might deliver food resources to areas of the Delta that typically have low densities of phytoplankton (CDWR, 1996). Even relatively small supplies might be beneficial to the Delta and downstream embayments of the San Francisco Estuary because recent studies have shown a long-term decline in phytoplankton biomass and productivity (Jassby et al., 2002) to levels that limit consumer growth (Müller-Solger et al., 2002; Sobczak et al., 2002). Moreover, hydrodynamic models suggest that discharge plumes from the Yolo Bypass flow along the west bank of the river channel toward embayments of the San Francisco Estuary that are important to life cycles of a variety of species (Monsen, 2000).

From a theoretical perspective, our study raises questions about what types of hydrologic variations can maximize phytoplankton production in temperate river-floodplain systems. Variation in flow regulates important floodplain processes and, according to current conceptual models of river-floodplain interactions (Bayley, 1995; Tockner et al., 2000), large, short-term variations might limit some benefits of inundation in temperate river systems. The 1-month-long inundation by the Sacramento River was short compared to seasonal-scale flooding in tropical river-floodplain systems. Shorter inundation periods and less-predictable flooding are common in many temperate systems (Tockner et al., 2000). However, we suggest that floodplains of temperate rivers might still yield high phytoplankton production provided that there are multiple flow pulses. Our rationale is that since phytoplankton biomass was highest during floodplain drainage, it is possible that years with multiple drainage events could result in high production. For example, during 1998 there were multiple sequences of floodplain inundation and draining as well as smaller flow pulses from the Yolo Bypass as late as June (Sommer et al., 2001a). Chlorophyll *a* was not measured in the Yolo Bypass in 1998, but large decreases in seston C:N ratios were observed during each of three periods when the floodplain was draining (Schemel & Cox, 1999). The chlorophyll *a* fluorescence record from Rio Vista during 1998 showed a distinct peak during each draining event (Sommer et al., 2001a). Additional peaks in chlorophyll *a* were associated with flow pulses, which flushed accumulated biomass from the floodplain to the Delta. These results suggest that hydrographs with multiple flow peaks, such as in 1998, may yield more phytoplankton production than years with less hydrologic variation, such as 2000.

The large variability in precipitation and river flow in northern California (Cayan & Peterson, 1989; Cayan et al., 1999) provides an excellent opportunity to test this hypothesis in future years. In addition, the CALFED Ecosystem Restoration Program supports habitat restoration projects in the Yolo Bypass that could provide some degree of control over the frequency and duration of floodplain inundation (CALFED, 2000). Future studies might also identify effects of hydrologic variability on higher trophic levels of floodplain biota, which likely require longer inundation periods than phytoplankton for maximum production.

Conclusion

Variations in flow and sources of water were major factors affecting phytoplankton biomass in floodplain waters and exports from the floodplain. Phytoplankton biomass was low when river flow through the floodplain was high, but it rapidly increased as flow decreased and the floodplain drained. This scenario, which has been observed in other temperate river-floodplain systems, suggests that the length of time that the floodplain was inundated by the river was not as important as the hydrologic processes affecting floodplain drainage. It also suggests that years with complex hydrologic variability involving multiple flooding and draining sequences might produce more phytoplankton biomass in the floodplain and increase export from the floodplain.

Sacramento River discharge was quantitatively the largest source of water to the floodplain, but local sources of water were particularly important influences on water chemistry as the floodplain drained and transported accumulated phytoplankton biomass and nutrients from the floodplain. Precipitation from storms and below-flood-stage variations in water level in the river were both factors affecting the discharge of local water to the floodplain. Nutrients were not depleted by phytoplankton uptake in the floodplain waters, which in part might be attributed to supply by the local streams.

This study and other studies of this system support the concept that both the quality and quantity of food resources are enhanced in the floodplain compared to the river. Inundations and exports of primary production from the floodplain, however, were limited to relatively short periods of time. Consequently, the overall value of floodplain production to the river-floodplain system is difficult to assess and is likely to vary greatly from year to year.

Acknowledgements

This study would not have been successful without the contributions of laboratory and field staff at USGS, CDWR, and the University of California, Davis. We owe particular thanks to Marisa Cox, Wendy Batham, Ryon Kurth, Stephen Hager, Stephen Graham, Mike Dempsey, and Hank Gephardt. We also appreciate very helpful comments from many of our colleagues and two anonymous reviewers. Funding was provided by the Interagency Ecological Program, the CALFED Ecosystem Restoration Program, and the USGS National Research Program.

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