Primining the productivity pump: flood pulse driven trends in suspended algal biomass distribution across a restored floodplain

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SUMMARY

1. Chlorophyll a (Chl a) distribution across a 0.36 km² restored floodplain (Cosumnes River, California) was analysed throughout the winter and spring flood season from January to June 2005. In addition, high temporal-resolution Chl a measurements were made in situ with field fluorometers in the floodplain and adjacent channel.

2. The primary objectives were to characterise suspended algal biomass distribution across the floodplain at various degrees of connection with the channel and to correlate Chl a concentration and distribution with physical and chemical gradients across the floodplain.

3. Our analysis indicates that periodic connection and disconnection of the floodplain with the channel is vital to the functioning of the floodplain as a source of concentrated suspended algal biomass for downstream aquatic ecosystems.

4. Peak Chl a levels on the floodplain occurred during disconnection, reaching levels as high as 25 μg L⁻¹. Chl a distribution across the floodplain was controlled by residence time and local physical/biological conditions, the latter of which were primarily a function of water depth.

5. During connection, the primary pond on the floodplain exhibited low Chl a (mean = 3.4 μg L⁻¹) and the shallow littoral zones had elevated concentrations (mean = 4.6 μg L⁻¹); during disconnection, shallow zone Chl a increased (mean = 12.4 μg L⁻¹), but the pond experienced the greatest algal growth (mean = 14.7 μg L⁻¹).

6. Storm-induced floodwaters entering the floodplain not only displaced antecedent floodplain waters, but also redistributed floodplain resources, creating complex mixing dynamics between parcels of water with distinct chemistries. Incomplete replacement of antecedent floodplain waters led to localised hypoxia in non-flushed areas.

7. The degree of complexity revealed in this analysis makes clear the need for high-resolution spatial and temporal studies such as this to begin to understand the functioning of dynamic and heterogeneous floodplain ecosystems.

Keywords: Cosumnes River, flood pulse, floodplain, phytoplankton, restoration

Introduction

A floodplain can be envisioned as a physical and chemical sieve through which river water and associated dissolved and particulate matter move. High surface roughness and slow water velocities across the floodplain not only create conditions favourable for retention of coarse woody debris and particulate...
matter, but also increase transient storage and so enhance the biological processing of dissolved and particulate constituents. As such, many floodplains have been shown to be sediment and particulate organic carbon sinks while simultaneously exporting autochthonous carbon (e.g. dissolved organic carbon, algal biomass, leaf litter) to the river (Robertson et al., 1999; Tockner et al., 1999; Valett et al., 2005). The importance of this resource exchange and transformation between the river and its floodplain is widely acknowledged (Cuffney, 1988; Junk, Bayley & Sparks, 1989; Ward, 1989; Thorp & Delong, 1994). Furthermore, it is the dynamic nature of this exchange that makes natural floodplains among the most productive and diverse ecosystems on earth (Mitsch & Gosselink, 2000; Tockner & Stanford, 2002). Maintaining ecosystem productivity/diversity and resource exchange mechanisms in floodplains has thus been promoted as a central element in the justification for a growing number of floodplain restoration projects in California (CALFED, 2000; Stromberg, 2001), and globally (Patten, 1998).

In California, there has been a 91% reduction in wetland habitat – from just over 2 million ha before 1800 to 184,000 ha in 1986 (Dahl, 1990). The large majority of these wetlands were floodplain habitats (Faber et al., 1989), which once carpeted California’s Central Valley. Historical accounts attest to networks of floodplain forests up to 10 km wide (Jepson, 1893). A large portion of the Central Valley was essentially a shallow lake for a few months each year. Today the world’s most elaborate network of impoundments, levees, and canals route flow through confined riverine areas (Mount, 1995) transporting water upwards of 900 km for consumptive uses and reducing forested floodplain habitat to <4% of the valley floor (Katibah, Drummer & Nedeff, 1984; Hunter et al., 1999). The alteration of this once extensive linkage between terrestrial and aquatic environments has subsequently impacted the ecological services that floodplains provide the Central Valley, such as transforming nutrients (Hubbard & Lowrance, 1996), exporting organic matter (Wetzel, 1992), providing freshwater habitat for the migration, reproduction and rearing of native fishes (Moyle et al., 2003; Crain, Whitner & Moyle, 2004) and mitigating flood damage to human settlements (Sommer et al., 2001).

The ecological effects of river–floodplain disconnection are multi-faceted and are particularly pronounced in complex food webs, such as those in large floodplain rivers. In the California Bay–Delta (the confluence of the Sacramento and San Joaquin rivers draining the Central Valley) declines in biota abundance, from zooplankton (Kimmerer & Orsi, 1996) to native fish (Bennett & Moyle, 1996), have been linked to a shortage of food resources (Foe & Knight, 1985; Jassby & Cloern, 2000). Mitigation strategies for reinvigorating the base of the food web have included recommendations for restoring floodplain habitat (Jassby & Cloern, 2000; Schemel et al., 2004). This habitat, it is thought, was once very productive and exported large quantities of high quality (i.e. rich in algae) organic matter to the Delta (Jassby & Cloern, 2000).

The notion of floodplains as ‘productivity pumps’ has been previously proposed (Junk et al., 1989) and characterised (Furch & Junk, 1992; Tockner et al., 1999; Baldwin & Mitchell, 2000). Periodic river–floodplain connection and disconnection isolates and subsequently mobilises parcels of water on the floodplain. These waters – depending upon residence time, antecedent hydrologic conditions, and river–floodplain system biogeochemistry – are often more productive than adjacent channel waters (Junk et al., 1989; Schemel et al., 2004). As such floodplains can ‘feed’ the channel with valuable food resources in much the same way that littoral zones in lakes subsidise pelagic food webs (Deligiorgio & Gasol, 1995; Lucas et al., 2002; Larmola et al., 2004). Although it is widely accepted that floodplains are productive ecosystems, considerably less is known about where on the floodplain productivity is greatest and what controls the distribution of these highly productive areas.

Results from research on a Danubian floodplain by Hein et al. (1999, 2004), revealed the importance of hydrologic controls on the spatial distribution of phytoplankton biomass. They found that sections of the floodplain intermittently connected with the river had higher productivity than isolated areas of the floodplain, which shifted toward prevailing bacterial secondary production. Van den Brink et al. (1993) found similar results in the Lower Rhine where floodplain lake proximity to the nutrient-rich main channel determined lake productivity. Of the 100 lakes studied, those most directly connected to the main channel via flood flows and seepage exhibited the greatest suspended algal biomass. These studies and others (see Hamilton & Lewis, 1990; Knowlton &
Jones, 1997; Pithart, 1999; Izaguirre, O’Farrell & Tell, 2001) show that the distribution of suspended algal biomass on floodplains is, in large part, a function of residence time which is in turn controlled by riverine hydrology.

The objective of this study was to identify the environmental variables that control suspended algal biomass concentration and distribution across the surface of a restored floodplain. Additionally, it was our aim to identify what role the flood pulse played in importing, exporting, and redistributing algal biomass on the floodplain. Understanding the spatial and temporal dynamics of floodplain biogeochemistry is vitally important if river managers and scientists are to be successful in creating and maintaining the ecological services provided by these complex habitats.

Methods

Study area

Our study site is located within the confines of the Cosumnes River Preserve, a restored floodplain habitat located 34 km south of Sacramento, CA, that is managed by a consortium of federal, state and non-governmental agencies. A former agricultural field dedicated to tomato production, the study site is now a 0.36 km² triangular floodplain surrounded by levees (Fig. 1). In 1997, four breaches were engineered along the east and south levees to reconnect the riparian floodplain with the adjacent Cosumnes River. Additionally, a Y-lobed pond and isolated smaller pond were constructed to foster habitat heterogeneity. When connected with the river, water flows from north to south, moving onto the floodplain through breaches Triangle North (Tn) and Triangle South (Ts) and off the floodplain through breaches Triangle East (Te) and Triangle West (Tw) (Fig. 1). Since completion of the restoration, floodwater has carried large woody debris, sediment, coarse and fine particulate organic matter, and the occasional piece of farming equipment onto the restored floodplain. Sand accumulation rates measured in 1999 and 2000 were estimated between 0.19 and 0.39 m yr⁻¹ near the breaches (Florsheim & Mount, 2002). As the sediment-laden floodwaters have moved across the floodplain in successive stages (1997–present), substrate differentiation, topographic changes, and vegetation recruitment have occurred. The floodplain is still in early successional stages of riparian vegetation establishment, with dominant species of cottonwood (Populus fremontii), willow (Salix...
spp.) and oak (Quercus lobata) covering <10% of the floodplain (Trowbridge, Kalmanovitz & Schwartz, 2005). Without a dominant overstory, the floodplain has a very productive community of aquatic macrophytes and epiphytic algae, which thrive in shallow areas. As flooding initiates in the winter the annual shallow water vegetation is absent, but as the season progresses these macrophytes come to dominate all areas on the floodplain save the ponds. Although not the focus of this study, macrophytes and epiphytic algae play an important role in floodplain biogeochemistry (Scheffer, 1999), hydrogeomorphology (Hughes, 1997), ecology (Petry, Bayley & Markle, 2003) and productivity (dos Santos & Esteves, 2004).

The study site is near the mouth of the unimpounded Cosumnes River at 2 m above mean sea level. The river has a long-term (1907–2002) mean daily discharge of 14.4 m$^3$ s$^{-1}$ (USGS gage no. 11335000). Average precipitation in the upper watershed is 804 mm year$^{-1}$ and 445 mm year$^{-1}$ in the lowlands, with the majority of the rainfall occurring between December and March. Rainfall-induced flooding occurs on the floodplain during this period, after which time flooding is primarily driven by snowmelt in the upper basin (Ahearn et al., 2004). By June the flood season has ended and the floodplain steadily dries until the floodwaters return (usually the following December). During 2005 the floodplain and river were connected for 123 days between January 1 and June 1, with only 23 days of disconnection.

**Field methods and materials**

The majority of the data were collected with YSI 6600 multiparameter sondes (Yellow Springs Instruments, Yellow Springs, OH, U.S.A.). The sondes were capable of simultaneous acquisition of values for dissolved oxygen (DO), total dissolved solids (TDS), temperature, turbidity, and fluorescence (a proxy for Chl a). Uniformly calibrated sondes were placed in the river at Tn and in the main floodplain pond (Fig. 1). A third sonde was interfaced with a Global Positioning System unit (Garmin Rino 120; WAAS enabled; Garmin International Inc., Olathe, KS, U.S.A.) and used to rove across the floodplain logging position and water quality parameters every 40 m on average. The sonde was submerged (approximately 0.5 m) and lashed to a canoe in order to facilitate roving in the ponds (average maximum depth = 3.17 m); in the shallow areas (littoral zones) a calibration cup was used to skim water off the surface without disturbing the benthos. This roving process was conducted 22 times between 02 February 2005 and 16 June 2005 with an average of 120 spatial data points recorded on each campaign. Rising limb, peak and falling limb dynamics were characterised multiple times; in this study we present data from 10 days on the rising and falling limb of the flood hydrograph and during periods of river-floodplain disconnection. These 10 days were selected after data analysis revealed that 12 sampling days produced incomplete or corrupt data (because of disturbance of the benthos during sampling, equipment malfunctions and improper coverage of the floodplain surface). Autosamplers (ISCO 3600; Teledyne ISCO Inc., Lincoln, NE, U.S.A.) were located at Tn, Te, and Tw and set to collected water samples every 2 h during storms. Water from these samples, as well as from grab samples, were filtered for Chl a analysis within 48 h of collection. Chl a was measured from a 300 mL subsample using standard extraction and fluorometry techniques (Clesceri, Greenberg & Eaton, 1998). When sonde measurements and water sampling were simultaneous, extracted Chl a values were regressed against fluorescence values from the YSI sondes ($r^2 = 0.93$). The converted fluorescence values are reported herein as Chl a (µg L$^{-1}$). Stage gages were positioned at each breach and set to collect data every 10 min. The resultant information was used to generate hydrographs and determine when the floodplain and the river were connected.

**Computing methods and materials**

We conducted our spatial analysis using a geographical information system (ArcGIS v. 9.0; ESRI, Redlands, CA, U.S.A.) to utilise a number of inherent spatial analysis tools (compilation, visualisation, interpolation and extraction). We assembled field data into a personal geodatabase and generated a number of spatial descriptors from independent spatial data layers. These descriptors included depth, determined as an inverse correlate to a high-resolution digital elevation model (2 m, see Florsheim & Mount, 2002) and perpendicular distance to primary flow path. Flow paths were delineated and digitised on-screen using the field observations and ancillary data, such as orthorectified aerial photographs, as backdrops. An analysis mask was created by segmenting the digital

elevation model at the 3.9 m (above mean sea level) contour, which best approximated the high water mark of the seasonal flood regime.

We employed inverse-distance weighting (IDW) as an interpolation technique to spatially infer water quality at unsampled locations within the floodplain. IDW is a simple, exact surface interpolator taking the form of eqn 1,

\[
Z = \frac{\sum_{n=1}^{N} Z_i d_i^{-P}}{\sum_{n=1}^{N} d_i^{-P}}
\]

where \( Z \) is the value of the interpolated point, \( Z_i \) is a known value at a fixed point, and \( N \) is the total number of points used in the interpolation. Spatial determinants in the equation are \( d_i \), the distance between fixed and interpolated points evaluated in the neighbourhood and \( P \), a neighbourhood weighting term. We used values of \( N = 12 \) and \( P = 0.5 \) for all interpolated surfaces, which in effect lessens the influence of immediate neighbours on the interpolated value. IDW, as employed in ArcGIS Spatial Analyst Extension (see Watson & Philip, 1985 for specific implementation notes), takes advantage of spatial boundaries, such as our analysis mask of the triangle floodplain, by using a variable neighbourhood. The output surface is sensitive to clustering and the presence of outliers (Watson & Philip, 1985). To minimise these potential errors, our field collection strategy centred on observed transitions in concentration and we eliminated post hoc numerical outliers from our geodatabase. Comparatively, IDW has been used to infer plankton concentrations in lakes (Winder & Schindler, 2004), nutrient concentrations in soil (Arhonditsis et al., 2002) and depth to groundwater in riparian zones (Merritt & Cooper, 2000), among many applications. Additionally, IDW has also been shown to perform well over small areas (<100 ha) using a fine raster resolution (≤5 m; Robinson & Metternicht, 2005).

We constructed IDW surfaces for 10 dates, interpolating values for Chl \( a \), DO, TDS, turbidity and temperature, resulting in 50 individual raster datasets.

**Statistical analysis**

In order to analyse differences in constituent concentrations in the pond and littoral areas of the floodplain the field data were categorised into pond and littoral samples (\( n \) approximately 60 in each category). A Student’s \( t \)-test was applied to characterise the significance of any differences in mean concentration between samples in the littoral area and pond area (Zar, 1984). Statistica data analysis software was used for this purpose and the results are reported in Table 1. In order to determine which chemical and physical parameters were driving Chl \( a \) concentrations during a representative falling limb and disconnection day, multiple linear regression was used. Independent variables included temperature, TDS, turbidity, DO, elevation and distance from primary

<table>
<thead>
<tr>
<th>Date</th>
<th>Hydrologic phase</th>
<th>Mean DO (%)</th>
<th>Mean Chl ( a ) (µg L(^{-1}))</th>
<th>Mean turbidity (NTU)</th>
<th>Mean TDS (mg L(^{-1}))</th>
<th>Mean temperature (°C)</th>
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<tr>
<td></td>
<td></td>
<td>Pond</td>
<td>Littoral</td>
<td>Pond</td>
<td>Littoral</td>
<td>Pond</td>
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<td>14-Feb-05</td>
<td>Stagnant</td>
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<td>97.4</td>
<td>13.4*</td>
<td>10.9</td>
<td>5.7</td>
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<td></td>
<td>91.9</td>
<td>97.2</td>
<td>15.3*</td>
<td>12.4</td>
<td>5.8</td>
</tr>
<tr>
<td>16-June-05</td>
<td></td>
<td>115</td>
<td>114.7</td>
<td>15.4</td>
<td>14.0</td>
<td>14.9*</td>
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<tr>
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<td>Rising limb</td>
<td>91.5*</td>
<td>81.2</td>
<td>9.2</td>
<td>10.4*</td>
<td>16.9*</td>
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<td></td>
<td>92.4</td>
<td>90.7</td>
<td>11.6*</td>
<td>9.9</td>
<td>86.4*</td>
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<td>Falling limb</td>
<td>117.8*</td>
<td>104.0</td>
<td>2.4</td>
<td>3.2*</td>
<td>17.0*</td>
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<td>84.2</td>
<td>100.4*</td>
<td>5.0</td>
<td>6.6*</td>
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<td>124.9</td>
<td>3.5</td>
<td>4.0*</td>
<td>9.0</td>
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<td>18-Mar-05</td>
<td></td>
<td>134.6*</td>
<td>119.4</td>
<td>3.7</td>
<td>6.0*</td>
<td>5.4</td>
</tr>
<tr>
<td>20-Apr-05</td>
<td></td>
<td>125.3*</td>
<td>96.3</td>
<td>2.4</td>
<td>3.2*</td>
<td>7.9</td>
</tr>
</tbody>
</table>

*Indicates that the mean constituent concentration within the pond and littoral areas are significantly different as determined by a Student’s \( t \)-test (\( P > 0.05 \)).

flowpath. The data were checked for normality and log transformations were applied where necessary. Next a stepwise regression analysis was conducted with only significant independent variables included in the model (Helsel & Hirsch, 1992).

Results

*Priming the productivity pump*

Water year 2005 (October 2004 to September 2005) was an above average year for precipitation with 525 mm of rain falling on the lower Cosumnes River Watershed, 134% of normal. The resulting high flows connected the river with the restored floodplain for a total of 128 days beginning on 01 January 2005. In contrast in 2002, a dry year, the floodplain was not connected with the river for only 22 days. Because of above normal precipitation, disconnection time between flood events was reduced. When the floodplain did disconnect, however, water chemistry on the floodplain began to diverge from river chemistry. Most notably temperature (data not shown) and Chl $a$ concentration on the floodplain began to rise while the river remained unchanged (Fig. 2). There were three periods of brief disconnection in 2005, (i) 20 January 2005 to 28 January 2005, (ii) 05 February 2005 to 18 February 2005 and (iii) 18 March 2005 to 20 March 2005 (Fig. 2), with intervening storms events; the final disconnection between the river and floodplain in 2005 occurred on 05 June 2005. The first two periods of disconnection were marked by elevated levels of Chl $a$ on the floodplain, peaking at 19 and 18 $\mu$g L$^{-1}$ Chl $a$, respectively, before being flushed out by the subsequent storms (Fig. 2). During these same periods Chl $a$ in the river averaged 4.8 $\mu$g L$^{-1}$ and showed little variation about the mean. The first two periods of disconnection both exhibited a lag time between the point of disconnection and the point at which Chl $a$ levels on the floodplain began to rise: in January the lag was 5 days, in February it was 2 days. The last period of disconnection in March was apparently too brief for floodplain chemistry to diverge from river chemistry (1.5 days), so Chl $a$ values in the floodplain and the river remained comparable. It should be noted that the sonde measuring Chl $a$ on the floodplain was located in the pond and that Chl $a$ patterns differed significantly between the pond and the shallows, but despite variation across the floodplain Chl $a$ levels at all floodplain locations were almost always higher than channel Chl $a$ concentrations.
**Intra-floodplain resource redistribution**

**Storm 1.** In order to characterise the effect of the flood pulse on Chl $a$ distribution on the floodplain, we conducted water quality mapping before, during and after storm events. There were seven significant storms in the 2005 flood season but for this analysis we focus on two (Fig. 2). The first storm analysed (18–28 February 2005) was preceded by a 13 day period of river-floodplain disconnection (Fig. 2); as such Chl $a$ levels in the pond were high (Fig. 3a). Floodwaters brought low Chl $a$ (Fig. 3b), turbid water (Fig. 3c) onto the floodplain, and displaced antecedent water with high Chl $a$ from the pond. The majority of the antecedent waters were flushed out of the floodplain (0.53 kg Chl $a$), but Fig. 3d,e indicate that some algal biomass was transported into the south-westerly corner, where it apparently augmented respiration rates. DO percent saturation in this zone subsequently dropped from a previous 3-day mean of 60% (6.2 mg L$^{-1}$) to approximately 30% saturation (3.0 mg L$^{-1}$) on 23 February 2005 (Fig. 3e). A concomitant fish (*Oncorhynchus tschawytscha*) enclosure study on the floodplain observed 100% mortality of the juvenile salmonids in this low DO zone (C. A. Jeffres, unpubl. data). Our combined observations indicate that the redistribution of suspended algal biomass, and subsequent impact on respiration rates, can contribute to the creation of dynamic hypoxic zones that have adverse impacts on some aquatic fauna.

**Storm 2.** The storm on 23 March 2005 to 07 April 2005, exhibited a different pattern, as it was preceded by a period of river-floodplain disconnection of only 1.5 days, not long enough for Chl $a$ to increase in the pond (Fig. 3f). Instead of displacing high Chl $a$ water out of the pond, this storm moved the relatively low Chl $a$ pond waters into the shallow littoral areas (Fig. 3g), in the process flushing most of the littoral waters while trapping some against the far south-westerly corner. This storm was the largest of the season and was characterised by high Chl $a$ (16.7 µg L$^{-1}$) concentrations in the channel water during the rising limb. The combination of high Chl $a$ inflowing water, low Chl $a$ displaced pond water, and high Chl $a$ displaced littoral water, created a complex mixing front as patches of antecedent floodplain waters stacked up against encroaching floodwaters (Fig. 3g).

**Alternating zones of phytoplankton production**

The distribution of phytoplankton across the floodplain was dependent upon river connectivity and hydrograph position. We detail here the three patterns in Chl $a$ distribution, which emerged during the rising limb, falling limb and disconnection. During periods of disconnection, the pond exhibited elevated Chl $a$ concentration (3-day mean = 14.7 µg L$^{-1}$) while the shallows had significantly lower concentrations (3-day mean = 12.4 µg L$^{-1}$; Table 1). Fig. 3a shows the spatial distribution of Chl $a$ on 16 February 2005, a representative disconnection day. A multiple linear regression analysis of all the measured and calculated parameters (Chl $a$, turbidity, temperature, TDS, DO, depth, distance from primary flowpath) revealed that variation in the Chl $a$ content of these standing waters could be explained by a linear combination of water depth (expressed as the inverse of elevation), distance from primary flowpaths, TDS, DO, and turbidity (Chl $a_{16\text{ February}}$ = 0.75 turbidity $- 0.33$ elevation $+ 0.31$ DO $- 0.22$ TDS $- 0.21$ flow distance $+ 20.6$, $r^2 = 0.66$, $P < 0.001$; Table 2). DO and turbidity are not Chl $a$ drivers in this system, rather they are by-products of phytoplankton concentration and distribution. Phytoplankton growth or decomposition can control DO concentrations, while algal cells can interfere with optical turbidity reading. TDS and distance from flowpath are metrics of residence time as evapo-concentration and material dissolution on the floodplain increased TDS in those waters which were not flushed and the degree of flushing was dependant on the distance from the primary flowpaths. Thus, this analysis indicates that there is a relationship between water depth (inverse of elevation), residence time and Chl $a$ concentration distribution across the floodplain.

During the falling limb, stable primary flowpaths developed across the floodplain and Chl $a$ distribution remained consistent until the next period of disconnection or flooding. Fig. 3f, shows a representative falling limb Chl $a$ distribution. On this day, 18 March 2005, 60% of the variance in Chl $a$ concentration could be explained by a linear combination of distance from flowpath and TDS (Chl $a_{18\text{ March}} = 0.56$ TDS $+ 0.39$ flow distance $+ 2.14$, $r^2 = 0.60$, $P < 0.001$; Table 2). This relationship indicates that during the falling limb Chl $a$ is most concentrated in those areas of high residence time (the distal littoral zones). During each falling limb
quantified, the distal littoral areas had significantly greater suspended algal biomass (5-day mean = 4.6 µg L⁻¹) than the deep flowing zones (5-day mean = 3.4 µg L⁻¹) on the floodplain (Table 1). This observed Chl a distribution is opposite the distribution characterised during periods of river-floodplain disconnection, during which time the deep primary flowpaths (pond) had higher Chl a concentrations than the littoral zones.

During the rising limb of the hydrograph Chl a distribution was a function of the position and concentration of inflowing waters versus those of antecedent floodplain waters. As the translation and mixing of waters on the rising limb is very dynamic, relative concentrations of Chl a in the deep and littoral areas are not so easily modelled. Of the 2 days in which Chl a was quantified on the rising limb of a storm each exhibited opposite spatial concentration...
patterns (Table 1) and we were not able to meaningfully model Chl $a$ concentration distribution with local environmental variables.

If phytoplankton-rich antecedent waters exist on the floodplain prior to flooding (as was the case with storm 1; Fig. 4), the rising limb of the hydrograph can be ecologically significant for downstream receiving waters. The two storms in 2005 that arrived after periods of stagnation on the floodplain exhibited elevated Chl $a$ on the rising as well as falling limbs (see Fig. 4 for an example of one), the other five storms had minimal Chl $a$ flushing associated with them. In this study we focused on two storms (storms 1 and 2; Fig. 2) where antecedent waters were pushed off the floodplain, one in which the ‘productivity pump’ was ‘primed’ – that is Chl $a$ levels on the
floodplain where five to six times higher than in the channel (Fig. 3a) – and one in which the pump was not primed, and Chl a levels on the floodplain and in the channel were similar (Fig. 3f). Water volume data from the floodplain revealed that prior to the 17 February 2005 flood (when the floodplain was ‘primed’) 158 m³ was held in the pond and 208 m³ in the shallows. If we take the average Chl a value and area of the ponds and littoral zones and assume that all the water was pushed out of the floodplain, a simple calculation reveals that the ponds exported 0.32 kg ha⁻¹ of Chl a and the littoral zones exported 0.075 kg ha⁻¹ of Chl a. So it would seem that when a flood arrives after a period of river-floodplain disconnection the pond is the dominant source of Chl a exported from the floodplain. If the floodplain is not ‘primed’ when flooding occurs, the shallows and deep zones of the floodplain equally contribute to Chl a export.
export from the floodplain. A similar calculation for the 23 March 2005 flood reveals 0.08 kg ha\(^{-1}\) Chl \(a\) exported from the ponds and 0.07 kg ha\(^{-1}\) from the shallows. This phenomenon intimates that the relationship between deep and shallow water habitat across the inundated floodplain is an important factor in determining the influence of the floodplain on channel material budgets during flooding events.

**Discussion**

The importance of the floodplain to the fluvial and ecological dynamics of the riverine ecosystem is rooted in the complexity of the ecotone, both hydrological (e.g. highly variable residence times and depths) and structural (e.g. complex topography and vegetative cover), relative to the nearby channel. Such
complexity gives rise to dynamic zones of phytoplankton production on the floodplain, which may be absent within the river channel itself. The complexity of floodplain systems, particularly the dynamic spatial and temporal dimensions, also gives rise to difficulties in conducting research in these ecosystems. For example, previous research (see Van den Brink et al., 1993; Hein et al., 2004) on floodplain phytoplankton distribution has had to focus on compartmentalised flooded riparian areas (because of study site size and complexity) without examining the hydro-ecosystem as a continuous unit of varying depth, residence time and vegetative cover. The relatively small area (36 ha) of our study site made such an analysis possible; and with high-resolution monitoring, we were able to characterise aspects of the floodplain which have been previously underappreciated.

Many floodplains, including the Cosumnes River Preserve, can be envisioned as a series of small ponds and floodplain channels with extensive and dynamic littoral zones (Junk et al., 1989). Flow from the river will invariably connect a number of these deep water zones before returning to the channel while distal areas (shallow littoral zones at our site) will not be as thoroughly flushed. This creates a condition whereby residence time at any given point on the floodplain is a function of distance from the primary flowpath through the floodplain. Concordantly, our data show that during flooding Chl $a$ is elevated in the littoral zones of the floodplain (Table 1), that is, the zones which are distal to primary flowpaths and where residence time is high. As such, the ‘inshore retention concept’ (Schiemer et al., 2001), which states that retention in littoral backwater areas is a major determinant of biological processes in large rivers, is also applicable to flow-through floodplains during flooding. Phytoplankton production in distal areas of the floodplain will be most significant for downstream environments and organisms when the littoral zones drain; indeed a hysteresis analysis of storm 1 indicates that Chl $a$ concentrations are elevated during the falling limb when the floodplain is draining (Fig. 4).

The two primary factors, which explain this phenomenon are (i) export of algal biomass from littoral area and (ii) increased residence time on the falling limb promoting autochthonous production on the floodplain. Each of the seven storms in 2005 exhibited this same pattern of elevated Chl $a$ on the falling limb. Other studies (Schemel et al., 2004; Sommer et al.,

<table>
<thead>
<tr>
<th>Date</th>
<th>$n$</th>
<th>$r^2$</th>
<th>SE</th>
<th>Independent variables</th>
<th>$\beta$</th>
<th>$P$-level</th>
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<td>156</td>
<td>0.66</td>
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<td></td>
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<tr>
<td>18-Mar-05</td>
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<td></td>
<td></td>
<td></td>
<td>Flow distance</td>
<td>0.39</td>
<td>&lt;0.001</td>
</tr>
</tbody>
</table>

*Flow distance is analogous to the perpendicular distance from the primary flowpaths across the floodplain.
2004) have also shown that, on the falling limb of the hydrograph, water egressing from floodplains is enriched with organic material relative to river channel water.

We have postulated that the functioning of the floodplain productivity pump is contingent upon connection and disconnection between the floodplain and the channel. Indeed the data indicate that some of the highest Chl \(a\) concentrations are exported from the floodplain on the rising limb of storms after a period of disconnection (Fig. 2). It should be noted that the study floodplain was artificially small (because of constriction from bounding levees) and that in a natural lowland floodplain, flood water residence time on the floodplain would be much greater. A higher residence time during flooding may alter the relative importance of the connection–disconnection cycle for the generation of high concentrations of phytoplankton.

Of course, phytoplankton is not the only valuable carbon resource that is exported from floodplains. It has been shown that attached algae can account for a substantial portion of the biomass in productive shallow waters (Moncreiff, Sullivan & Daehnick, 1992; Kaldy et al., 2002) and be the primary foundation for floodplain aquatic food webs (Bunn, Davies & Winning, 2003). During large floods litter and attached algae – primarily transported as coarse particulate organic matter (CPOM) – may be disturbed and transported from the floodplain to the channel. Indeed, many studies that have quantified CPOM budgets for lowland floodplains have found the floodplain carbon to be CPOM sources (Cuffney, 1988; Cellot, Mouillot & Henry, 1998; Tockner et al., 1999). Tockner et al. (1999) found that a restored floodplain on the Danube, Austria exported 0.5 kg ha\(^{-1}\) year\(^{-1}\) of Chl \(a\) and 21 kg ha\(^{-1}\) year\(^{-1}\) of CPOM and 240 kg ha\(^{-1}\) year\(^{-1}\) of DOC. If we convert these values to equivalent carbon loading with an assumed C : Chl \(a\) of 40 (Cloern, Grenz & Vidergar-Lucas, 1995) and C : CPOM of 0.5 (Schwarzenbach, Gschwend & Imboden, 2003) then it would appear than the floodplain exported 20 kg C ha\(^{-1}\) year\(^{-1}\) as Chl \(a\) and 10.5 kg C ha\(^{-1}\) year\(^{-1}\) as CPOM and 240 kg C ha\(^{-1}\) year\(^{-1}\) as DOC. So it is apparent from this study (one of the few that have quantified Chl \(a\), CPOM and DOC export from floodplains) that DOC is the dominant form of carbon export followed by Chl \(a\) and CPOM. Of these three carbon resources Chl \(a\) has the highest nutrient content (Muller-Solger, Jassby & Muller-Navarra, 2002) and is considered a valuable subsidy to downstream aquatic ecosystems (Jassby & Cloern, 2000). Because of these factors (mass of carbon export and food resource quality) it would seem that a focus on Chl \(a\) dynamics is warranted. The form in which carbon is exported from the floodplain will be dependant on the relative contribution from different carbon pools. When the hydrology of an agricultural riparian habitat is restored the system will evolve from an open body of water dominated by macrophytes and algae to a riparian forest with a closed canopy; this will in turn shift the quality and source of food resources exported from the floodplain to the channel.

Alternating zones of phytoplankton production were a conspicuous feature within our data set. We characterised productive littoral zones during periods of flow-through when waters in the deep primary flow paths were being continually flushed with river water. When the channel hydraulically disconnected from the floodplain, Chl \(a\) levels across the entire floodplain increased, but it was the deep zones, which exhibited the highest Chl \(a\) concentrations. Aside from depth, the other primary difference between the shallow and the deep zones in our study system is residence time. Hein et al. (2004) compared side-arm channels of the Danube and examined relationships between residence time within the side-arms and Chl \(a\) values. They concluded that residence time is related to Chl \(a\) hyperbolically with maximum Chl \(a\) occurring when the water in the side-arm was approximately 10 days old. They attribute the Chl \(a\) decrease after 10 days to grazing pressure from a growing population of metazooplankton (Keckes et al., 2003). Indeed, in laboratory experiments moderate populations of the cladoceran Simocephalus vetulus (biomass 1.6 mg L\(^{-1}\)) have been shown to decrease phytoplankton biomass by a factor of 13.6 within 1 h (Pogozhev & Gerasimova, 2005). The variation in depth between the littoral and ponded zones exaggerates this grazing pressure as it has been shown that, in vegetated littoral zones, productivity reducing factors such as nutrient competition, shading and excretion of allelopathic substances by macrophytes can initiate top–down trophic control of phytoplankton by a relatively moderate population of filter feeders (Scheffer, 1999). A temporal analysis of the data indicates that these processes evolve through the flooding season. As
macrophyte communities grew rapidly beginning in March, the temperature differential between the deep and shallow zones decreased with the unshaded pond eventually growing warmer than the shallows (Table 1). So it would seem that a combination of residence time and depth variability between habitats creates distinct physical and biological conditions which (i) favour phytoplankton growth in the shallow habitat that is not actively flushed during connection and (ii) during disconnection favour phytoplankton growth in deep water areas where residence time is intermediate, and shading and competition from macrophytes are low.

One of the most novel aspects of this study was the fact that we were able to characterise the complex nature of resource redistribution across the floodplain during flooding. The creation of a water–water eco-tone (Izaguirre et al., 2001) or perirheic zone (Mertes, 1997) between antecedent water and river water moving onto the floodplain has been shown to have important ecological ramifications, as the encroaching river water imports nutrients and disturbs floodplain waters across the perirheic front (Engle & Melack, 1993). We have shown that the hydraulic push from the inflowing river water also redistributes patches of antecedent water on the floodplain causing translation, mixing and the creation of a complex perirheos between a shifting mosaic of antecedent waters, not merely between the river water and floodplain water. Mertes (1997) defined the perirheos by analysing variation in turbidity across a number of large floodplains. We believe that this may result in an over-simplified view of patch dynamics on the floodplain as adjacent patches may have equivalent suspended sediment content but differing Chl a concentration, nutrient status, temperature, etc. By comparing Fig. 3g,h we can see that a relatively simple turbidity map belies the underlying patch complexity, which is revealed in the Chl a coverage. Fig. 3h depicts two distinct patches of water, turbid floodwater originating from the channel and less turbid displaced floodplain waters. Fig. 3g however, clearly shows three patches of water on the floodplain, high Chl a floodwater from the channel, low Chl a water displaced from the pond (see Fig. 3f), and an isolated patch of high Chl a littoral water in the far south-westerly corner. Each of these patches were characterised with at least 20 sampling points and the concurrent data collected (temperature, TDS, DO) all support our assertion that there exists a complex mixing front as patches of antecedent floodplain waters are stacked up against encroaching floodwaters. Our data indicate that the interaction of patches during flooding – realised in the intra-floodplain transfer of suspended algal biomass from deep water habitat to warm, shallow water habitat – can contribute to a precipitous decline in DO and create local conditions unfavourable for floodplain fishes (Fig. 3b,d). We have also shown how clear, less productive, pond water can be pushed into the productive littoral zone and displace high Chl a water (Fig. 3g). Obviously, these intra-floodplain transfers play an important role in floodplain dynamics and as such, the perirheic zone may be more complex then originally envisioned.

It is widely acknowledged that floodplains play a vital role in lowland river ecology. The idea of the floodplain as a productivity pump which requires a two stroke connection–disconnection series in order to efficiently export resources to the channel has been previously hypothesised (Schemel et al., 2004), but never explicitly quantified. In the present paper we show how a disconnection period of at least 2 days is required for the ponded water on the floodplain to begin to produce elevated levels of Chl a. If a subsequent flood arrives when these levels are high there will be a substantial mass of Chl a exported from the floodplain (as high as 4.68 kg). Suspended algal biomass on the floodplain was correlated with residence time and depth. Zones of maximum phytoplankton production alternated between the pond and the littoral zone dependant upon residence time and local growth conditions (e.g. shading, competition). Storms entering the floodplain not only pushed antecedent floodplain waters off the floodplain but also redistributed floodplain resources creating areas of hypoxia in those areas that were not flushed. The composite perirheic front, which develops during storms on the floodplain adds another layer of complexity to the already diverse algal patch dynamics, which are driven by residence time and local physical and biological conditions. If, as it has been proposed (Jassby & Cloern, 2000), floodplains are to be managed as sources of high quality organic matter for deficient downstream aquatic ecosystems then the information garnered from studies such as these becomes vital to restoration efforts.
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