

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

DYLAN S. AHEARN,\* JOSHUA H. VIERS,<sup>†</sup> JEFFREY F. MOUNT<sup>‡</sup> AND RANDY A. DAHLGREN\*

\*Department of Land, Air, Water, Resources, University of California, Davis, CA, U.S.A.

<sup>†</sup>Department of Environmental Science and Policy, University of California, Davis, CA, U.S.A.

<sup>‡</sup>Department of Geology, University of California, Davis, CA, U.S.A.

## SUMMARY

1. Chlorophyll *a* (Chl *a*) distribution across a 0.36 km<sup>2</sup> 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<sup>-1</sup>. 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<sup>-1</sup>) and the shallow littoral zones had elevated concentrations (mean = 4.6 µg L<sup>-1</sup>); during disconnection, shallow zone Chl *a* increased (mean = 12.4 µg L<sup>-1</sup>), but the pond experienced the greatest algal growth (mean = 14.7 µg L<sup>-1</sup>).
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 asso-

ciated 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

Correspondence: Dylan S. Ahearn, Department of Land, Air, Water, Resources, University of California, Davis, CA 95616, U.S.A.

E-mail: dsahearn@ucdavis.edu

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 pro-

nounced 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 (Delgiorgio & 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 &

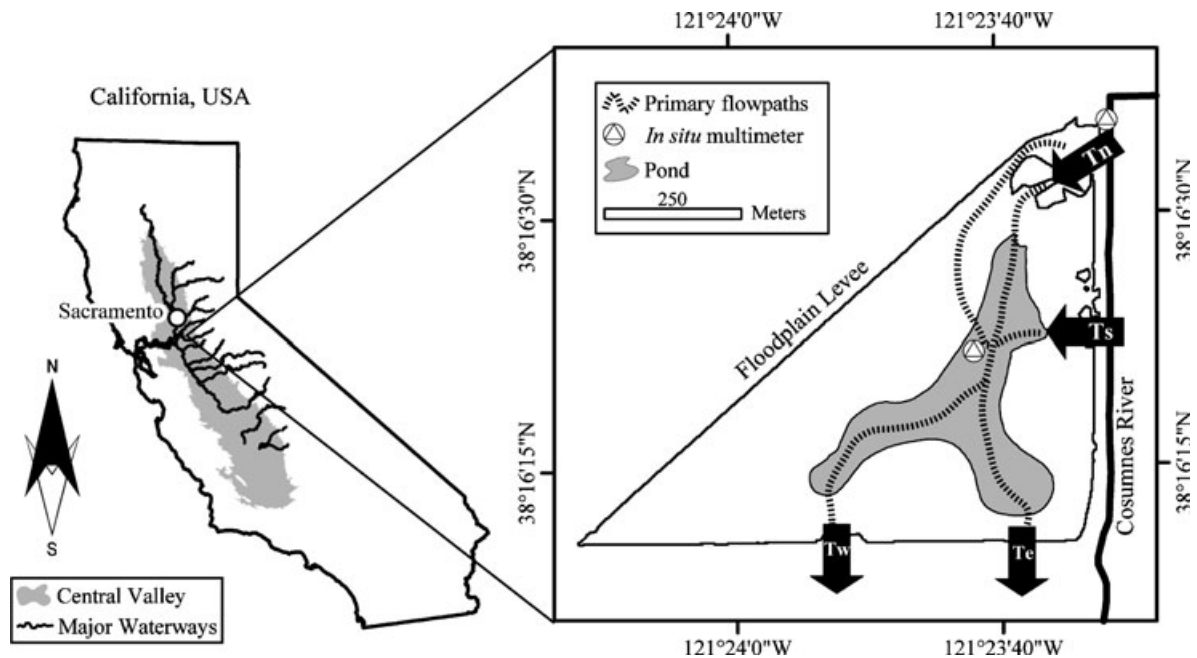


Fig. 1 Map of the study site in Central California. The inset shows the restored triangle floodplain with location and direction of flow through primary breaches in the levees. The inset also displays the location of the *in situ* data collection sondes and the paths of primary flow through the floodplain pond.

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 km<sup>2</sup> 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<sup>-1</sup> 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  $14.4 \text{ m}^3 \text{ s}^{-1}$  (USGS gage no. 11335000). Average precipitation in the upper watershed is  $804 \text{ mm year}^{-1}$  and  $445 \text{ mm year}^{-1}$  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 collect 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* ( $\mu\text{g L}^{-1}$ ). 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,

$$Z = \frac{\sum_{i=1}^N \frac{Z_i}{d_i^p}}{\sum_{i=1}^N \frac{1}{d_i^p}} \quad (1)$$

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  $d$ , 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 concentra-

tion 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 ( $\leq 5$  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.

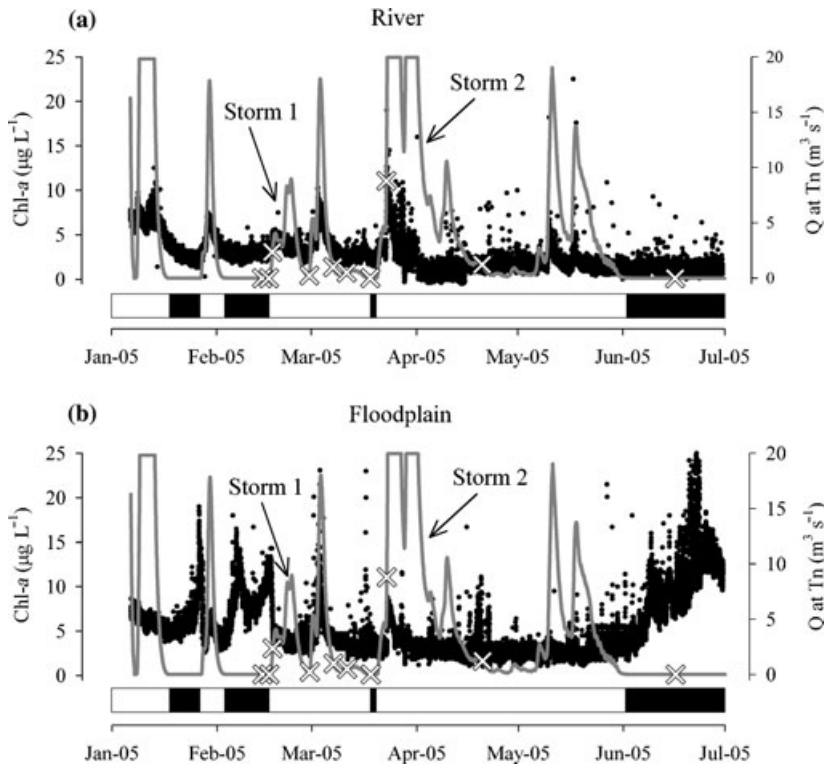
### Statistical analysis

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 1** Comparison between mean values for five constituents from the pond and shallow littoral regions of the floodplain (average  $n = 60$ ) for 10 days during 2005

Date	Hydrologic phase	Mean DO (%)		Mean Chl <i>a</i> ( $\mu\text{g L}^{-1}$ )		Mean turbidity (NTU)		Mean TDS ( $\text{mg L}^{-1}$ )		Mean temperature ( $^{\circ}\text{C}$ )	
		Pond	Littoral	Pond	Littoral	Pond	Littoral	Pond	Littoral	Pond	Littoral
14-Feb-05	Stagnant	102.7*	97.4	13.4*	10.9	5.7	6.7*	83.1	101.0*	14.0	14.2*
16-Feb-05		91.9	97.2	15.3*	12.4	5.8	7.4*	82.6	89.3*	13.4	14.4*
16-June-05		115	114.7	15.4	14.0	14.9*	13.1	35.3	38.3	21.7	21.7
17-Feb-05	Rising limb	91.5*	81.2	9.2	10.4*	16.9*	13.1	83.8	84.6*	11.4	11.8*
23-Mar-05		92.4	90.7	11.6*	9.9	86.4*	69.0	59.6	59.5	11.3	11.9*
23-Feb-05	Falling limb	117.8*	104.0	2.4	3.2*	17.0*	13.8	65.1	67.5*	12.4	13.8*
7-Mar-05		84.2	100.4*	5.0	6.6*	9.4*	8.6	79.3	80.4	17.9	18.9*
11-Mar-05		126.0	124.9	3.5	4.0*	9.0	9.5	73.1	80.3*	21.5	21.2
18-Mar-05		134.6*	119.4	3.7	6.0*	5.4	6.4*	52.0	78.0*	16.1	16.0
20-Apr-05		125.3*	96.3	2.4	3.2*	7.9	8.3	46.2	52.5*	16.2*	15.2

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



**Fig. 2** Chl *a* concentration time series from (a) the river and (b) the floodplain pond. Dates on which Chl *a* distribution across the floodplain was measured are marked on the hydrograph with an (×). Black bars above the *x*-axis represent periods of disconnection with the river. The hydrograph plateaus on the three largest storms are because of river discharge exceeding the rating curve. Note the increase in Chl *a* on the floodplain when the river and floodplain are disconnected.

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 include 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 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 storm 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  $\mu\text{g L}^{-1}$  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  $\mu\text{g L}^{-1}$  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*

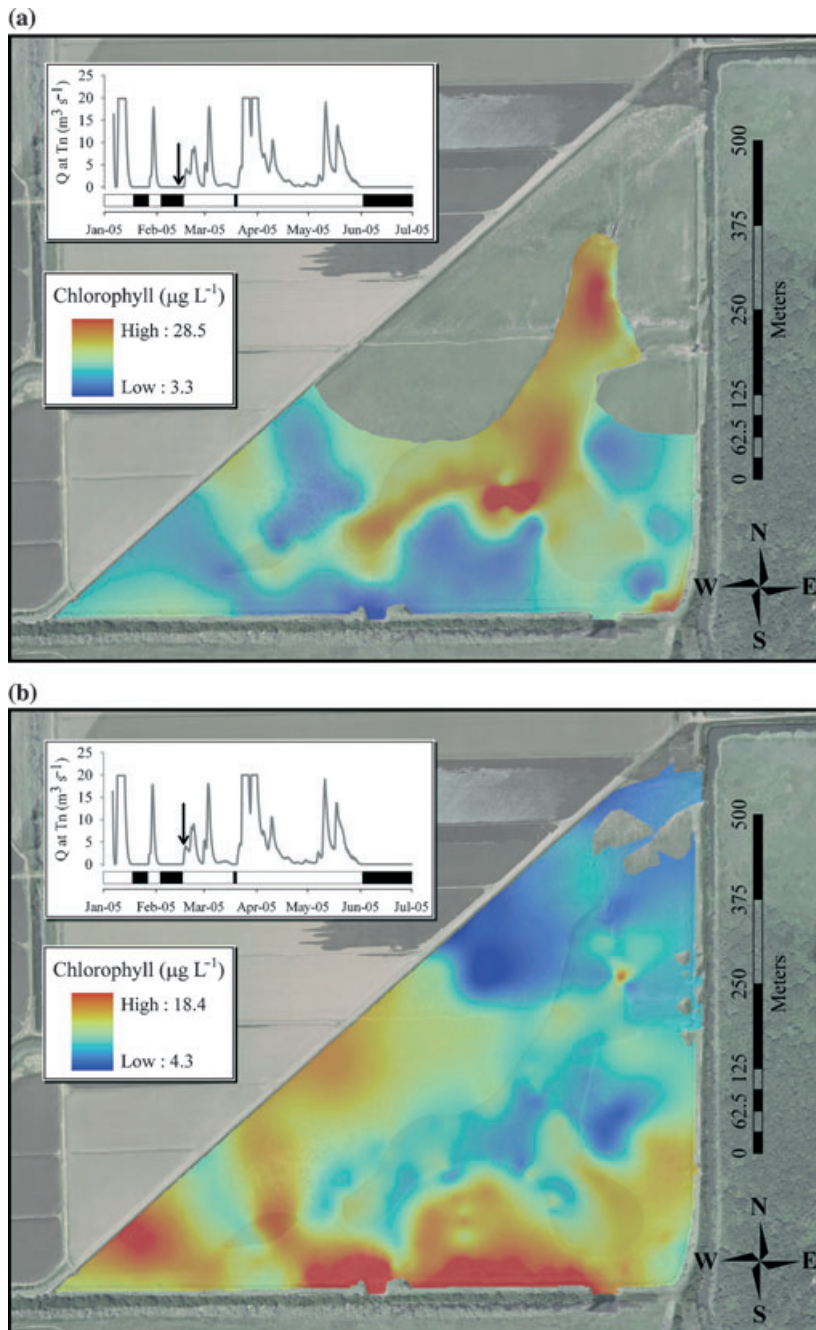
*Storm 1.* In order to characterise the effect of the flood pulse on Chl *a* distribution on the floodplain, we conducted water quality mapping before, during and after storm events. There were seven significant storms in the 2005 flood season but for this analysis we focus on two (Fig. 2). The first 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<sup>-1</sup>) to approximately 30% saturation (3.0 mg L<sup>-1</sup>) on 23 February 2005 (Fig. 3e). A concomitant fish (*Oncorhynchus tshawytscha*) 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<sup>-1</sup>) 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<sup>-1</sup>) while the shallows had significantly lower concentrations (3-day mean = 12.4 µg L<sup>-1</sup>; 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 ( $\text{Chl } a_{16 \text{ February}} = 0.75 \text{ turbidity} - 0.33 \text{ elevation} + 0.31 \text{ DO} - 0.22 \text{ TDS} - 0.21 \text{ flow distance} + 20.6$ ,  $r^2 = 0.66$ ,  $P < 0.001$ ; 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 evapoconcentration 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 ( $\text{Chl } a_{18 \text{ March}} = 0.56 \text{ TDS} + 0.39 \text{ flow distance} + 2.14$ ,  $r^2 = 0.60$ ,  $P < 0.001$ ; 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



**Fig. 3** Water quality distribution maps depicting Chl *a*, turbidity, and DO at different stages of flooding. Each map is accompanied by an inset hydrograph with an arrow showing the hydrograph position when the data were collected. During disconnection on 16 February 2005 (a) Chl *a* was greatest in the pond and the floodplain was only partially inundated. When a subsequent storm arrived the (b) high Chl *a* water was pushed off the floodplain and into the south-westerly corner by (c) turbid flood water. The algal biomass from the pond was then (d) trapped in the south-westerly corner where it augments respiration and (e) contributed to a decrease in DO. Later in the season there was a brief period of disconnection before a large storm (f–h). Unlike on 16 February 2005, Chl *a* on 18 March 2005 was (f) concentrated in the shallows and low in the pond. The rising limb of the subsequent storm pushed this (g) low Chl *a* water into the shallows and flushed them out, trapping some vestiges of high Chl *a* littoral water against the far south-westerly corner. A rising limb turbidity distribution map (h) clearly shows the mixing front between antecedent floodplain waters and flood waters from the river. Note that the scale bars on the various maps are optimised to show the full spectrum of colours for each day (spatially normalised) and so are not equal between maps (temporally normalised)

quantified, the distal littoral areas had significantly greater suspended algal biomass (5-day mean =  $4.6 \mu\text{g L}^{-1}$ ) than the deep flowing zones (5-day mean =  $3.4 \mu\text{g L}^{-1}$ ) 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



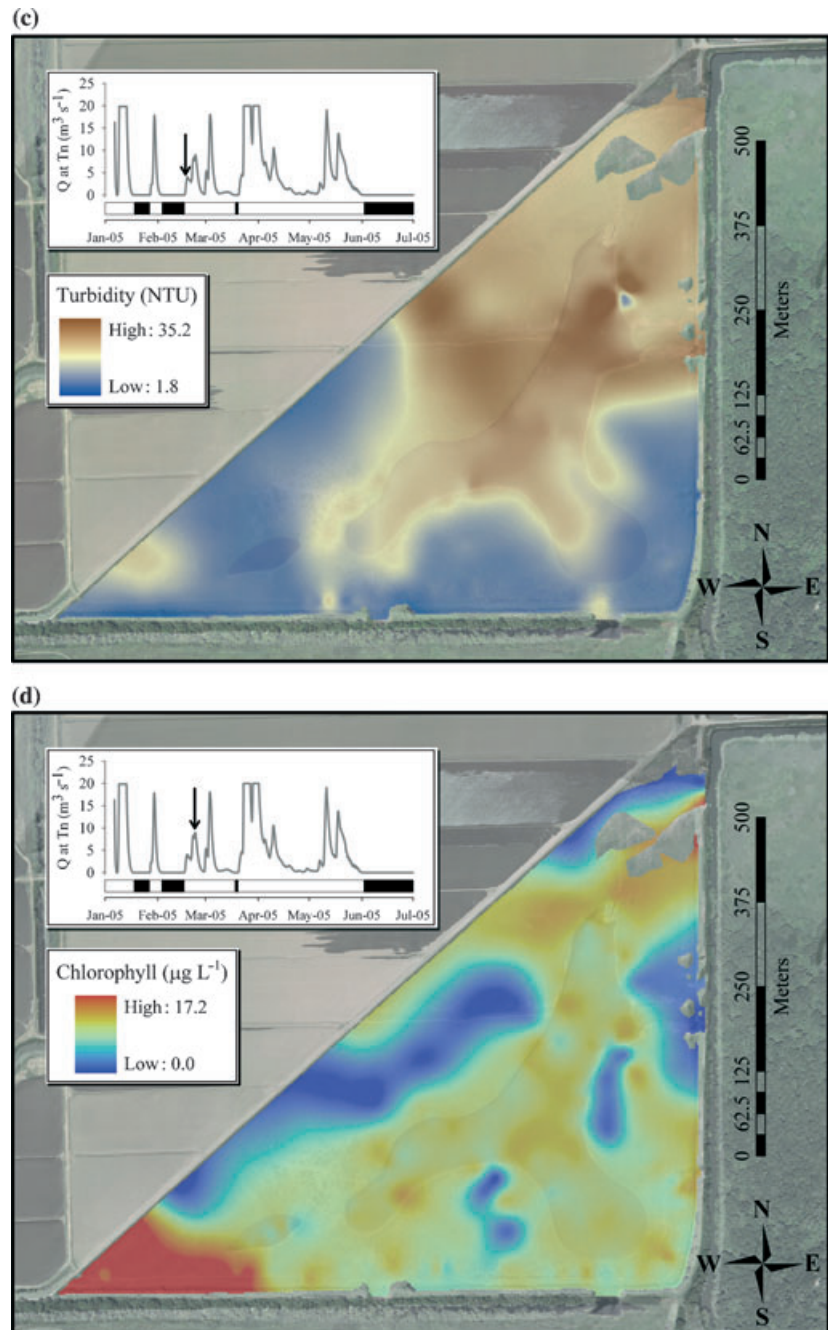


Fig. 3 (Continued)

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

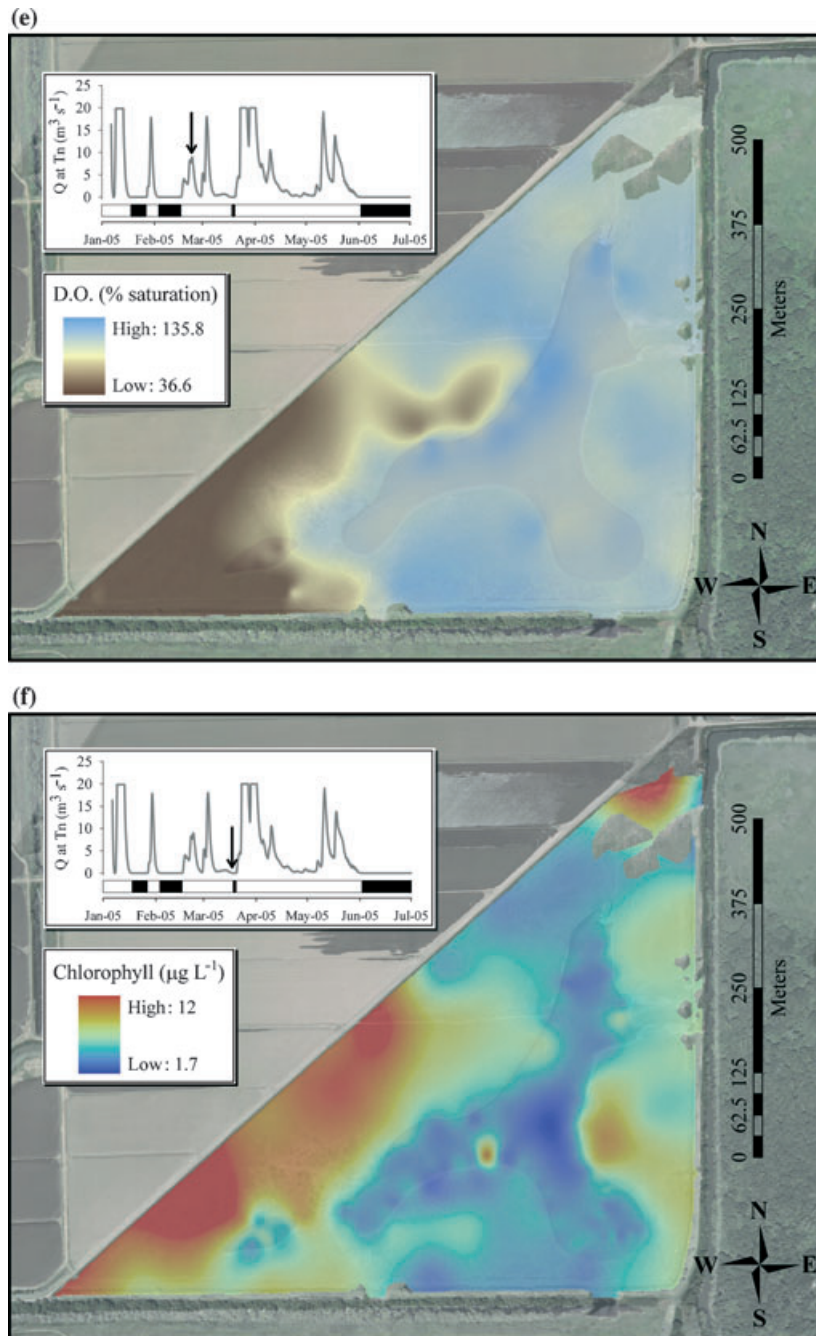


Fig. 3 (Continued)

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’)  $158 \text{ m}^3$  was held in the pond and  $208 \text{ m}^3$  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  $0.32 \text{ kg ha}^{-1}$  of Chl *a* and the littoral zones exported  $0.075 \text{ kg ha}^{-1}$  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*

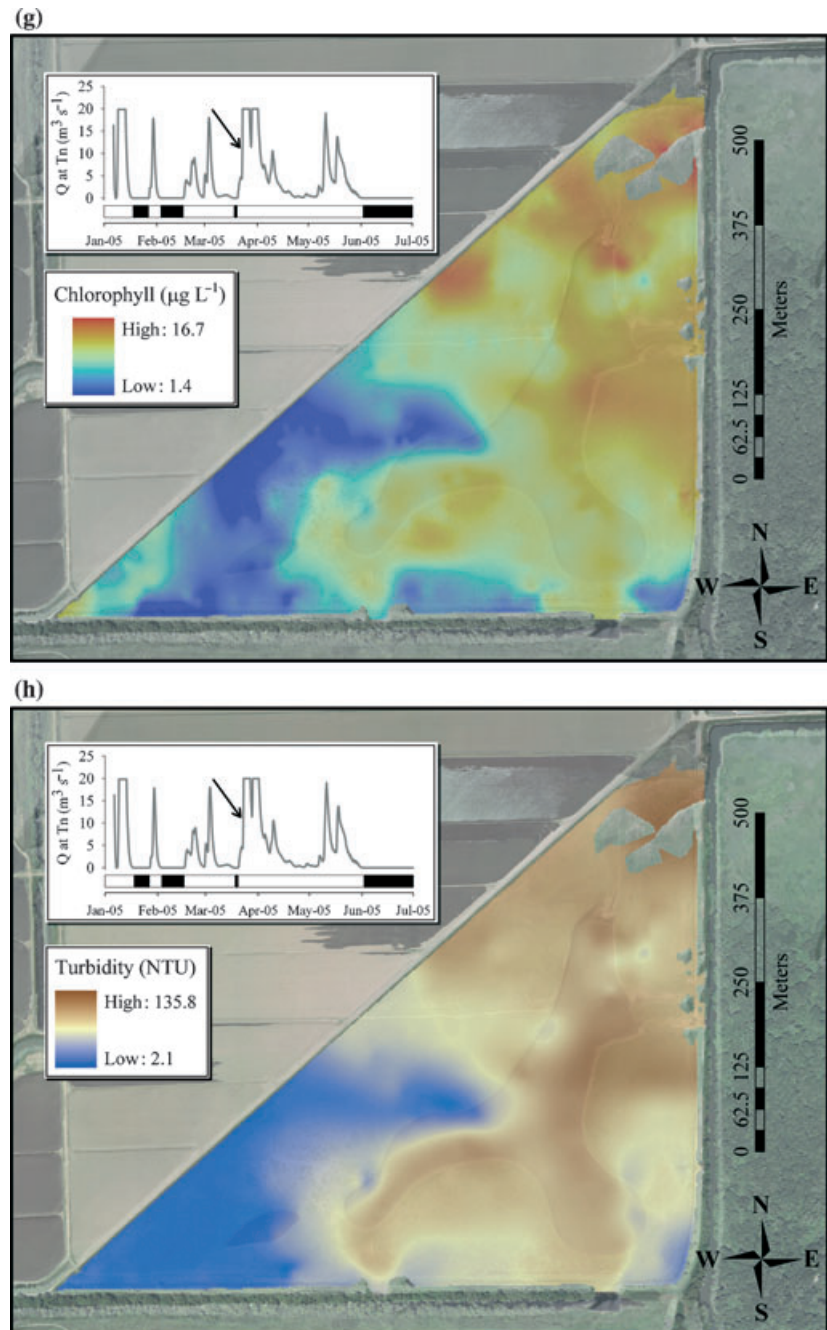


Fig. 3 (Continued)

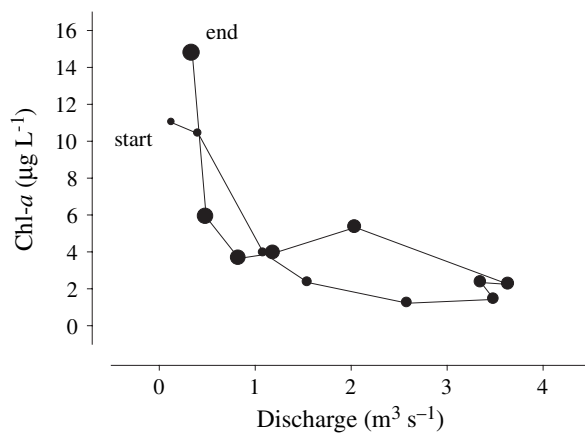
export from the floodplain. A similar calculation for the 23 March 2005 flood reveals  $0.08 \text{ kg ha}^{-1}$  Chl *a* exported from the ponds and  $0.07 \text{ kg ha}^{-1}$  from the shallows. This phenomenon intimates that the relationship between deep and shallow water habitat across the inundated 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

Date	<i>n</i>	<i>r</i> <sup>2</sup>	SE	Independent variables	$\beta$	<i>P</i> -level
16-Feb-05	156	0.66	2.03	Intercept	20.57	<0.001
				Turbidity	0.75	<0.001
				Elevation	-0.33	<0.001
				DO	0.31	<0.001
				TDS	-0.22	0.014
				Flow distance	-0.21	0.001
18-Mar-05	222	0.60	0.78	Intercept	2.14	<0.001
				TDS	0.56	<0.001
				Flow distance	0.39	<0.001

\*Flow distance is analogous to the perpendicular distance from the primary flowpaths across the floodplain.



**Fig. 4** Chlorophyll *a* hysteresis loop from storm 1 at a floodplain exit breach (Tw). As an indication of the temporal trend of the loop the data points increase in size from 16 February 2005 23:00 to 27 February 2005 20:00. The loop indicates that Chl *a* concentrations leaving the floodplain are elevated on the early rising and late falling limbs of the storm.

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

**Table 2** Results from a multiple linear regression analysis of Chl *a* (dependent variable) with a suite of physical (elevation, flow distance\*) and chemical (DO, TDS, temperature, and turbidity) independent variables. Only significant and independent predictor variables were included in the model.

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.*,

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 floodplains 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  $0.5 \text{ kg ha}^{-1} \text{ year}^{-1}$  of Chl *a* and  $21 \text{ kg ha}^{-1} \text{ year}^{-1}$  of CPOM and  $240 \text{ kg ha}^{-1} \text{ year}^{-1}$  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 that the floodplain exported  $20 \text{ kg C ha}^{-1} \text{ year}^{-1}$  as Chl *a* and  $10.5 \text{ kg C ha}^{-1} \text{ year}^{-1}$  as CPOM and  $240 \text{ kg C ha}^{-1} \text{ year}^{-1}$  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 (Keckeis *et al.*, 2003). Indeed, in laboratory experiments moderate populations of the cladoceran *Simocephalus vetulus* (biomass  $1.6 \text{ mg L}^{-1}$ ) 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 ecotone (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 flood water 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* flood water 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 than 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.

## Acknowledgments

Research on the Cosumnes River Floodplain was made possible by The Nature Conservancy and was financially supported by the CALFED Bay-Delta project [grant no. 01-N01 (Amend no. 1)]. The authors would like to acknowledge Erwin Van Nieuwenhuysse for the use of the data sondes, and Erika L. Gallo and Xien Wang for their sweat and support. We are especially grateful to Carson A. Jeffres for providing flow data, field support and limitless common sense.

## References

- Ahearn D.S., Sheibley R.W., Dahlgren R.A. & Keller K.E. (2004) Temporal dynamics of stream water chemistry in the last free-flowing river draining the western Sierra Nevada, California. *Journal of Hydrology*, **295**, 47–63.
- Arhonditsis G., Giourga C., Loumou A. & Koulouri M. (2002) Quantitative assessment of agricultural runoff and soil erosion using mathematical modeling: applications in the Mediterranean region. *Environmental Management*, **30**, 434–453.
- Baldwin D.S. & Mitchell A.M. (2000) The effects of drying and re-flooding on the sediment and soil nutrient dynamics of lowland river-floodplain systems: a synthesis. *Regulated Rivers-Research & Management*, **16**, 457–467.
- Bennett W.A. & Moyle P.B. (1996) Where have all the fishes gone? Interactive factors producing fish declines in the Sacramento-San Joaquin Estuary. In: *San Francisco Bay: the Ecosystem* (Ed. J.T. Hollibaugh), pp. 519–542. AAAS, San Francisco, CA.
- Bunn S.E., Davies P.M. & Winning M. (2003) Sources of organic carbon supporting the food web of an arid zone floodplain river. *Freshwater Biology*, **48**, 619–635.
- CALFED (2000) *Strategic Plan for Ecosystem Restoration*, pp. 75. CALFED Bay-Delta Program, Sacramento, CA.
- Cellot B., Mouillot F. & Henry C.P. (1998) Flood drift and propagule bank of aquatic macrophytes in a riverine wetland. *Journal of Vegetation Science*, **9**, 631–640.
- Clesceri L.S., Greenberg A.E. & Eaton A.D. (Eds) (1998) *Standard Methods for the Examination of Water and Wastewater*. APHA, AWWA, WEF, Baltimore, MD.
- Cloern J.E., Grenz C. & Vidregar-Lucas L. (1995) An empirical model of the phytoplankton chlorophyll/carbon ratio – the conversion factor between productivity and growth rate. *Limnology and Oceanography*, **40**, 1313–1321.
- Crain P.K., Whitner K. & Moyle P.B. (2004) Use of a restored central California floodplain by larvae of native and alien fishes. *American Fisheries Society Symposium*, **39**, 125–140.
- Cuffney T.F. (1988) Input, movement and exchange of organic-matter within a sub-tropical coastal blackwater river floodplain system. *Freshwater Biology*, **19**, 305–320.
- Dahl T.E. (1990) *Wetland Losses in the United States, 1780s to 1980s*, pp. 21. U.S. Fish and Wildlife Service, Washington, DC.
- Delgiorgio P.A. & Gasol J.M. (1995) Biomass distribution in fresh-water plankton communities. *American Naturalist*, **146**, 135–152.
- Engle D.L. & Melack J.M. (1993) Consequences of riverine flooding for seston and the periphyton of floating meadows in an Amazon floodplain lake. *Limnology and Oceanography*, **38**, 1500–1520.
- Faber P.A., Keller E., Sands A. & Masser B.M. (1989) *The Ecology of Riparian Habitats of the Southern California Coastal Region: a Community Profile*. pp. 152. Fish and Wildlife Service, Washington, DC: U.S.
- Florsheim J.L. & Mount J.F. (2002) Restoration of floodplain topography by sand-splay complex formation in response to intentional levee breaches, Lower Cosumnes River, California. *Geomorphology*, **44**, 67–94.
- Foe C. & Knight A. (1985) The effect of phytoplankton and suspended sediment on the growth of *Corbicula fluminea* (Bivalvia). *Hydrobiologia*, **127**, 105–115.
- Furch K. & Junk W.J. (1992) Nutrient dynamics of submersed decomposing Amazonian herbaceous plant species *Paspalum fasciculatum* and *Echinochloa polystachya*: 1. *Revue D'Hydrobiologie Tropicale*, **25**, 75–85.
- Hamilton S.K. & Lewis W.M.J. (1990) Basin morphology in relation to chemical and ecological characteristics of lakes on the Orinoco River floodplain Venezuela. *Archiv Fur Hydrobiologie*, **119**, 393–426.
- Hein T., Baranyi C., Reckendorfer W. & Schiemer F. (2004) The impact of surface water exchange on the nutrient and particle dynamics in side-arms along the River Danube, Austria. *Science of the Total Environment*, **328**, 207–218.
- Hein T., Baranyi C., Heiler G., Holarek C., Riedler P. & Schiemer F. (1999) Hydrology as a major factor determining plankton development in two floodplain segments and the River Danube, Austria. *Archiv Fur Hydrobiologie*, **3**, 439–452.
- Helsel D.R. & Hirsch R.M. (1992) *Statistical Methods in Water Resources*. Elsevier, Amsterdam.
- Hubbard R.K. & Lowrance R.R. (1996) Solute transport and filtering through a riparian forest. *Transactions of the Asae*, **39**, 477–488.
- Hughes F.M.R. (1997) Floodplain biogeomorphology. *Progress in Physical Geography*, **21**, 501–529.
- Hunter J.C., Willett K.B., McCoy M.C., Quinn J.F. & Keller K.E. (1999) Prospects for preservation and

- restoration of riparian forests in the Sacramento Valley, California, USA. *Environmental Management*, **24**, 65–75.
- Izaguirre I., O'Farrell I. & Tell G. (2001) Variation in phytoplankton composition and limnological features in a water-water ecotone of the Lower Parana Basin (Argentina). *Freshwater Biology*, **46**, 63–74.
- Jassby A.D. & Cloern J.E. (2000) Organic matter sources and rehabilitation of the Sacramento-San Joaquin Delta (California, USA). *Aquatic Conservation-Marine and Freshwater Ecosystems*, **10**, 323–352.
- Jepson W.L. (1893) The riparian botany of the lower Sacramento. *Erythea*, **1**, 238–246.
- Junk W. J., Bayley P. B. & Sparks R. E. (1989) The flood pulse concept in river-floodplain systems. Proceedings of the International Large River Symposium, **106**, Canadian Special Publication of Fisheries and Aquatic Sciences, Ottawa, Canada.
- Kaldy J.E., Onuf C.P., Eldridge P.M. & Cifuentes L.A. (2002) Carbon budget for a subtropical seagrass dominated coastal lagoon: how important are seagrasses to total ecosystem net primary production? *Estuaries*, **25**, 528–539.
- Katibah E.F., Drummer K.J. & Nedeff N.E. (1984) Current condition of riparian resources in the Central Valley of California. In: *California Riparian Systems: Ecology, Conservation, and Productive Management* (Eds R.E. Warner & K.M. Hendrix), pp. 315–322. University of California Press: Berkeley, CA.
- Keckeis S., Baranyi C., Hein T., Holarek C., Riedler P. & Schiemer F. (2003) The significance of zooplankton grazing in a floodplain system of the River Danube. *Journal of Plankton Research*, **25**, 243–253.
- Kimmerer W.J. & Orsi J.J. (1996) Causes of long-term declines in zooplankton in the San Francisco Bay estuary since 1987. In: *San Francisco Bay: the Ecosystem* (Ed. J.T. Hollibaugh), pp. 403–424. AAAS: San Francisco, CA.
- Knowlton M.F. & Jones J.R. (1997) Trophic status of Missouri River floodplain lakes in relation to basin type and connectivity. *Wetlands*, **17**, 468–475.
- Larmola T., Alm J., Juutinen S., Saarnio S., Martikainen P.J. & Silvola J. (2004) Floods can cause large interannual differences in littoral net ecosystem productivity. *Limnology and Oceanography*, **49**, 1896–1906.
- Lucas L.V., Cloern J.E., Thompson J.K. & Monsen N.E. (2002) Functional variability of habitats within the Sacramento-San Joaquin Delta: restoration implications. *Ecological Applications*, **12**, 1528–1547.
- Merritt D.M. & Cooper D.J. (2000) Riparian vegetation and channel change in response to river regulation: a comparative study of regulated and unregulated streams in the Green River Basin, USA. *Regulated Rivers-Research & Management*, **16**, 543–564.
- Mertes L.A.K. (1997) Documentation and significance of the perirheic zone on inundated floodplains. *Water Resources Research*, **33**, 1749–1762.
- Mitsch W.J. & Gosselink J.G. (2000) *Wetlands*. John Wiley & Sons, New York, NY.
- Moncreiff C.A., Sullivan M.J. & Daehnick A.E. (1992) Primary production dynamics in seagrass beds of Mississippi Sound – the contributions of seagrass, epiphytic algae, sand microflora, and phytoplankton. *Marine Ecology-Progress Series*, **87**, 161–171.
- Mount J.F. (1995) *California Rivers and Streams: The Conflict between Fluvial Process and Land Use*. University of California Press, Berkeley, CA.
- Moyle P.B., Crain P.K., Whitener K. & Mount J.F. (2003) Alien fishes in natural streams: fish distribution, assemblage structure, and conservation in the Cosumnes River, California, USA. *Environmental Biology of Fishes*, **68**, 143–162.
- Muller-Solger A.B., Jassby A.D. & Muller-Navarra D.C. (2002) Nutritional quality of food resources for zooplankton (*Daphnia*) in a tidal freshwater system (Sacramento-San Joaquin River Delta). *Limnology and Oceanography*, **47**, 1468–1476.
- Patten D.T. (1998) Riparian ecosystems of semi-arid North America: diversity and human impacts. *Wetlands*, **18**, 498–512.
- Petry P., Bayley P.B. & Markle D.F. (2003) Relationships between fish assemblages, macrophytes and environmental gradients in the Amazon River floodplain. *Journal of Fish Biology*, **63**, 547–579.
- Pithart D. (1999) Phytoplankton and water chemistry of several alluvial pools and oxbows after the flood event – a process of diversification. *Algological Studies*, **130**, 93–113.
- Pogozhev P.I. & Gerasimova T.N. (2005) The role of filtering zooplankton in de-eutrophication of waterbodies. *Water Resources*, **32**, 337–345.
- Robertson A.I., Bunn S.E., Boon P.I. & Walker K.F. (1999) Sources, sinks and transformations of organic carbon in Australian floodplain rivers. *Marine and Freshwater Research*, **50**, 813–829.
- Robinson T.P. & Metternicht G. (2005) Comparing the performance of techniques to improve the quality of yield maps. *Agricultural Systems*, **85**, 19–41.
- dos Santos A.M. & Esteves F.D.A. (2004) Influence of water level fluctuation on the mortality and aboveground biomass of the aquatic macrophyte *Eleocharis interstincta* (VAHL) Roemer et Schults. *Brazilian Archives of Biology and Technology*, **47**, 281–290.
- Scheffer M. (1999) The effect of aquatic vegetation on turbidity; how important are the filter feeders? *Hydrobiologia*, **409**, 307–316.



- Schemel L.E., Sommer T.R., Muller-Solger A.B. & Harrell W.C. (2004) Hydrologic variability, water chemistry, and phytoplankton biomass in a large floodplain of the Sacramento River, CA, USA. *Hydrobiologia*, **513**, 129–139.
- Schiemer F., Keckeis H., Reckendorfer W. & Winkler G. (2001) The “inshore retention concept” and its significance for large rivers. *Algological Studies*, **135**, 509–516.
- Schwarzenbach R.P., Gschwend P.M. & Imboden D.M. (2003) *Environmental Organic Chemistry*, 2nd Edn. John Wiley & Sons, Hoboken, NJ.
- Sommer T.R., Harrell W.C., Solger A.M., Tom B. & Kimmerer W. (2004) Effects of flow variation on channel and floodplain biota and habitats of the Sacramento River, California, USA. *Aquatic Conservation-Marine and Freshwater Ecosystems*, **14**, 247–261.
- Sommer T., Harrell B., Nobriga M., Brown R., Moyle P., Kimmerer W. & Schemel L. (2001) California’s Yolo Bypass: evidence that flood control can be compatible with fisheries, wetlands, wildlife, and agriculture. *Fisheries*, **26**, 6–16.
- Stromberg J.C. (2001) Restoration of riparian vegetation in the south-western United States: importance of flow regimes and fluvial dynamism. *Journal of Arid Environments*, **49**, 17–34.
- Thorp J.H. & DeLong M.D. (1994) The riverine productivity model – an heuristic view of carbon sources and organic processing in large river ecosystems. *Oikos*, **70**, 305–308.
- Tockner K. & Stanford J.A. (2002) Riverine flood plains: present state and future trends. *Environmental Conservation*, **29**, 308–330.
- Tockner K., Pennetzdorfer D., Reiner N., Schiemer F. & Ward J.V. (1999) Hydrological connectivity, and the exchange of organic matter and nutrients in a dynamic river-floodplain system (Danube, Austria). *Freshwater Biology*, **41**, 521–535.
- Trowbridge W.B., Kalmanovitz S. & Schwartz M.W. (2005) Growth of valley oak (*Quercus lobata* Nee) in four floodplain environments in the Central Valley of California. *Plant Ecology*, **176**, 157–164.
- Valett H.M., Baker M.A., Morrice J.A., Crawford C.S., Molles M.C., Dahm C.N., Moyer D.L., Thibault J.R. & Ellis L.M. (2005) Biogeochemical and metabolic responses to the flood pulse in a semiarid floodplain. *Ecology*, **86**, 220–234.
- Van den Brink F.W.B., Deleeuw J.P.H.M., Vandervelde G. & Verheggen G.M. (1993) Impact of hydrology on the chemistry and phytoplankton development in floodplain lakes along the lower Rhine and Meuse. *Biogeochemistry*, **19**, 103–128.
- Ward J.V. (1989) The 4-dimensional nature of lotic ecosystems. *Journal of the North American Benthological Society*, **8**, 2–8.
- Watson D.F. & Philip G.M. (1985) A refinement of inverse distance weighted interpolation. *Geo-Processing*, **2**, 315–327.
- Wetzel R.G. (1992) Gradient-dominated ecosystems – sources and regulatory functions of dissolved organic-matter in fresh-water ecosystems. *Hydrobiologia*, **229**, 181–198.
- Winder M. & Schindler D.E. (2004) Climatic effects on the phenology of lake processes. *Global Change Biology*, **10**, 1844–1856.
- Zar J.H. (1984) *Biostatistical Analysis*. Prentice Hall, Inc, Englewood Cliffs, NJ.

*Manuscript accepted 24 April 2006*