Trophic Conditions and Planktonic Processes of Semi-arid Floodplain Lakes Inundated with Environmental Flows

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Published on 12 August 2021 at https://openjournals.library.sydney.edu.au/index.php/LIN/index

Kobayashi, T., Hunter, S.J., Ralph, T.J., Maguire, J. and Wolfenden, B. (2021). Trophic conditions and planktonic processes of semi-arid floodplain lakes inundated with environmental flows. *Proceedings of the Linnean Society of New South Wales* **143**, 37-49.

Shallow floodplain lakes are critical components of semi-arid floodplain wetland systems. Delivery of environmental flows that aim to sustain ecological processes of semi-arid floodplain wetlands has enhanced inundation of shallow lakes in inland Australia. To maximise environmental flow outcomes to support floodplain productivity and ecosystem functions, environmental managers would benefit from knowing whether semi-arid floodplain lakes function as a sink or source of atmospheric carbon. We investigated abiotic conditions, and rates of planktonic respiration and primary productivity of phytoplankton during summer under environmental flow conditions in three floodplain lakes of the lower Murrumbidgee River, Australia. All lakes showed mesoeutrophic to hypereutrophic characteristics and significant within- and between-lake variability in abiotic conditions, planktonic processes, and associated carbon balance. Nevertheless, the mean net primary productivity of phytoplankton in the lakes (364-1,674 mg C m^{-2} day^{-1}) were up to about three times greater than in other semi-arid floodplain wetlands of southeast Australia. Therefore, shallow floodplain lakes in semi-arid regions have great potential to function as a sink of atmospheric carbon through planktonic metabolism during summer. A spatial hierarchical framework for lake functional response to inundation is proposed to support decision-making and to maximise the benefits of environmental flow regimes for floodplain lakes.

Manuscript received 28 January 2021, accepted for publication 24 July 2021.

KEYWORDS: environmental water regime, limnological conditions, planktonic respiration, primary productivity, wetlands in drylands.

INTRODUCTION

Floodplain lakes constitute an integral part of inland floodplain wetland systems. They provide ecosystem services for agriculture and livestock grazing and are habitat for a diverse range of terrestrial and aquatic organisms that are adapted to intermittent and ephemeral wetland environments (Rogers and Ralph 2011). In Australia, many inland floodplain wetlands have been affected by river regulation including the construction of flood works with levee banks and roads, which have altered flood behaviour and flood connectivity (Kingsford 2000; Kingsford et al. 2004; Gell et al. 2007). Some inland floodplain lakes have experienced reduced frequencies and spatial extent of flooding, relative to those in pre-regulation periods (Kingsford 2000; Kingsford and Thomas 2004).

Recently, the delivery of water that is allocated and managed specifically to maintain or enhance the biological components, ecosystem functions, processes and resilience of aquatic ecosystems (i.e. water for the environment or environmental flows) has helped inundate and improve the health and resilience of inland floodplain lakes (Arthington 2012; COA 2014). For example, in New South Wales (NSW), Australia, the delivery of environmental flows has been used to inundate inland floodplain lakes in the lower Murrumbidgee floodplain in the Murray-Darling Basin to support fringing vegetation such as river red gums (*Eucalyptus camaldulensis*) and black box (*Eucalyptus largiflorens*), important aquatic vegetation such as tall spike rush (*Eleocharis sphacelata*), and to create and maintain feeding and breeding habitats for native fish, turtles, southern bell frogs (*Litoria raniformis*) and a variety of waterbird species (Spencer et al. 2010; OEH 2015).

In semi-arid regions of south-eastern Australia, inland floodplain lakes are often ephemeral, shallow and exposed to the effects of wind (promoting mixing of surface and bottom waters of the lakes) (Lieschke and Closs 1999; Kingsford 2000). Inland floodplain lakes are dynamic wetlands, and nutrients and carbon (C) accumulate on ephemeral-lake beds during the antecedent dry times, while lakes also receive influxes of nutrients and C transported through inflow channels during wet times (Knowles et al. 2012; Baldwin et al. 2013). Inland floodplain lakes are thought to display high levels of nutrients, algal biomass and productivity in semi-arid regions (Lieschke and Closs 1999; Robertson et al. 1999; Kobayashi et al. 2013). There are studies from other parts of the world indicating the eutrophic conditions of floodplain lakes, with variations due to catchment land uses and climate (e.g. Wissmar et al. 1981; Dong et al. 2012). Eutrophic lakes tend to be associated with high fish production, coupled with high primary production of phytoplankton and total phosphorus concentrations (Downing and Plante 1993). Inundation of eutrophic floodplain lakes may promote ecological productivity in semi-arid regions, especially when over-bank flooding from watercourses facilitates connectivity amongst floodplain wetlands to allow fish passage (see Ralph et al. 2011) and other forms of biotic transfer. Furthermore, there has been renewed attention on the functional role of lakes (oligotrophic to eutrophic) for C sequestering and storage in relation to increasing atmospheric concentrations of CO_2 (Alin and Johnson 2007; Tranvik et al. 2009; Anderson et al. 2014; Sanders et al. 2017). Eutrophic lakes contribute to C sequestering and storage through the CO_2 disequilibrium caused by extreme primary production; they are likely to absorb both landscape and atmospheric C, converting it into lake sediments and passing additional dissolved C (DOC) downstream (Pacheco et al. 2014).

In this study, we investigated the physical and chemical (abiotic) conditions and the rates of planktonic respiration and primary productivity of phytoplankton during summer in three inland floodplain lakes of the lower Murrumbidgee River, semi-arid Australia, that had been inundated with environmental flows. By measuring the water quality conditions and the rates of planktonic process, we aimed to determine if these inland floodplain lakes would be eutrophic with high planktonic metabolism (production and respiration), and act as a C sink or source in terms of net planktonic processes. In order to maximise environmental outcomes of environmental flows to support floodplain productivity and ecosystem functions, it would be of benefit to environmental water managers to know if inland floodplain lakes in semi-arid regions have the potential to function as a sink or source of atmospheric C. Results are discussed in the context of informing water resource management planning for floodplain lakes using environmental flows by considering individual and collective lake responses found in this study.

METHODS AND MATERIALS

Study area and sites

The three lakes investigated are Paika, Tala, and Yanga Lakes, located on the lower Murrumbidgee River floodplain near Balranald, NSW, Australia (Fig. 1). All three lakes are situated on Late Quaternary alluvial plains of the Murrumbidgee River, and isolated lunettes and dunes border the main lake beds (Butler et al. 1973). Paika Lake is located 20 km north of Balranald on the western edge of the lower Murrumbidgee floodplain. In contrast to Paika Lake, Tala and Yanga Lakes are located east of the Murrumbidgee River in the South Redbank floodplain system. Paika and Tala Lakes are semi-circular in shape, while Yanga Lake is kidney-shaped with two distinct basins, east and west (Fig. 1).

The semi-arid region receives a mean annual rainfall of about 300 mm (BOM 2018). Due to the high conservation value of wetlands in this dryland region, Yanga Lake and the surrounding extensive floodplain wetlands are protected within Yanga National Park, which is situated on the southern side of the Murrumbidgee River from just north of Redbank Weir to just south of Balranald township. Prior to being gazetted as a national park by the NSW Government in 2005, the area was predominantly used for grazing sheep and river red gum timber production. Since 2005, the area has been the focus of ecological restoration, with the provision of environmental flows to key wetland areas as one of the principal restoration methods (Knowles et al. 2012).

Historical hydrology of the lakes

To gain an understanding of the temporal dynamics of lake surface water extents, we reviewed the available literature and satellite image archive from 1986 to present in the Digital Earth Australia

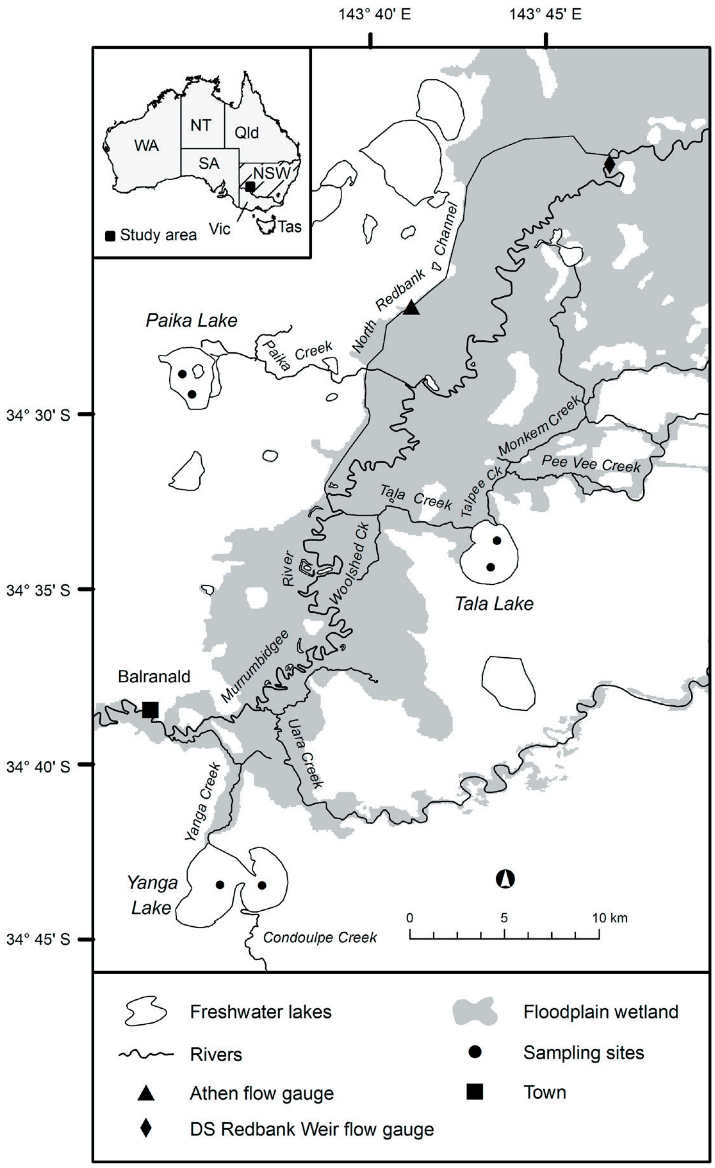

Figure 1. Location of sampling sites in Paika, Tala and Yanga Lakes at the terminal end of the Murrumbidgee River on the lower Murrumbidgee floodplain. WA: Western Australia; NT: Northern Territory; SA: South Australia; Qld: Queensland; NSW: New South Wales; Vic: Victoria; Tas: Tasmania.

Waterbodies interface (particularly the wet surface area of waterbodies data), which relied on imagery from Landsat 5 Thematic Mapper, Landsat 7 Enhanced Thematic Mapper Plus, Landsat 8 Operational Land Imager and Sentinel 2 sensors (Krause et al. 2021).

Historically, Paika Lake has been dry and isolated for about 100 years to flooding from the Lower Murrumbidgee floodplain until 2011 when the lake received its first environmental flow (McGinness et al. 2016). Such a long dry period of the lake was due to the construction of the Paika levee, a 23-km bank, and associated access roads between 1907 and 1911 (McGinness et al. 2016). Yanga Lake has been an important wetland habitat, predominantly receiving water from the Murrumbidgee River via Yanga Creek, or from Uara Creek. However, as water development in the Murrumbidgee catchment progressed, especially following the completion of Burrinjuck Dam in the late 1920s, Yanga Lake had less chance to be flooded and became increasingly episodic with dry periods in 1938 and again in 1967 (TZGA 2013). Yanga Lake dried up for eight years from July 2002 and remained dry until it filled in August 2010 at the end of the Millennium Drought (2001-2009) in southeast Australia (TZGA 2013; Van Dijk et al. 2013; Krause et al. 2021). Yanga Lake dried up again during the most recent drought from November 2019 until October 2020. Tala Lake is surrounded by river red gums and it receives floodplain inflows from Monkem, Deadmans and Pee Vee Creeks via water from the Yanga floodplain to the north, from the Gayini (Nimmie-Caira) floodplain to the east or directly from the Murrumbidgee River via Tala Creek to the west. Tala Lake has been used as an irrigation water storage (Wen et al. 2012). In contrast to Yanga Lake, the satellite image archive from 1986 to present indicated that Tala Lake maintained its permanent state at relatively high-water levels until February 2007 when the lake receded during the Millennium Drought and remained dry for three years until it filled again in July 2010 (Krause et al. 2021). Tala Lake remained filled during the most recent drought, in contrast to Yanga Lake which dried out in late 2019.

Environmental flows

In the southern-hemisphere spring-early summer of 2011 and 2012, Paika, Tala and Yanga Lakes were inundated by environmental flows delivered primarily via the Murrumbidgee North Redbank Channel (Fig. 1), with a maximum flow rate of 5,975 Ml day^{-1} on 21 December 2011 at the downstream Redbank Weir gauging site to the lower Murrumbidgee River floodplain (OEH 2011, 2012a, 2012b) (Fig. 2). The

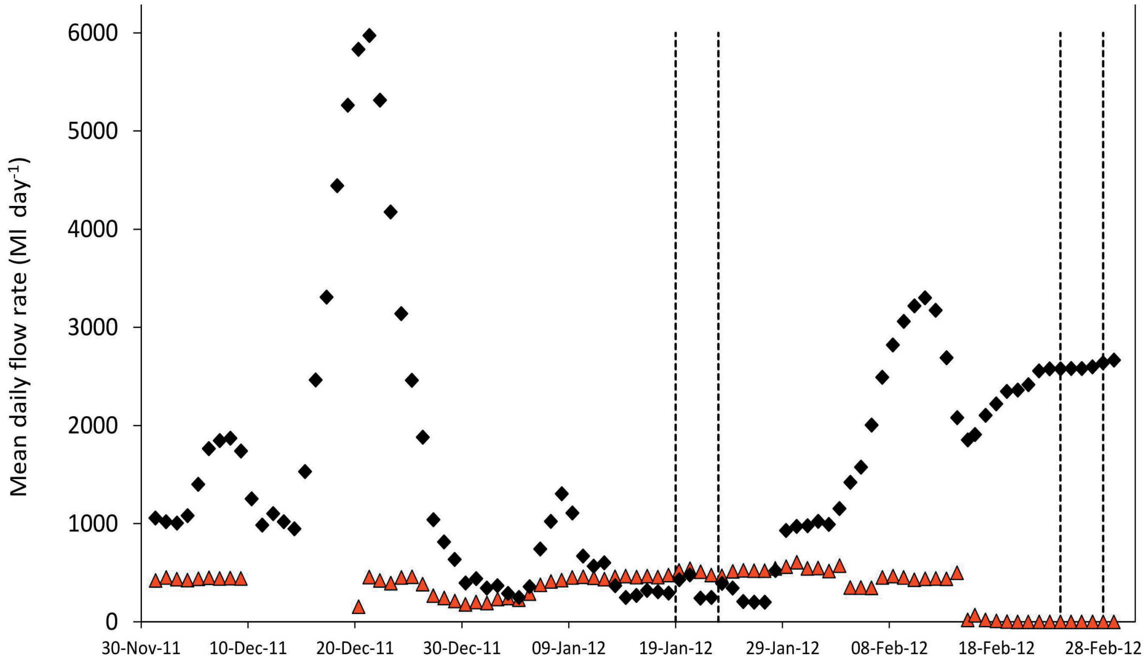

Figure 2. Mean daily flow rate (Ml day^{-1}) between December 2011 and February 2012. ◆, Murrumbidgee River downstream Redbank gauging site; △, North Redbank Channel downstream Athen gauging site. The two sampling periods (19-23 January and 24-28 February 2012) are indicated by vertical broken lines.

study was carried out in the three lakes between 19 and 23 January 2012, and again between 24 and 28 February 2012. During the January sampling period, the environmental flow rate was in the range 240-477 Ml day^{-1} at the downstream Redbank Weir gauging site and in the range 471-540 Ml day^{-1} at the downstream Athen gauging site. During the February sampling period, the environmental flow rate was in the range 2,578-2,641 Ml day^{-1} at the downstream Redbank Weir gauging site, while there was no flow at the downstream Athen gauging site (Fig. 2). Hydrological conditions during the study are related to these flow rates and the approximate inundated surface area (A, m^2), maximum water depth (z_{max}, m) and mean water depth (z, m) of each lake during January and February 2012, that were estimated to be: $A = 5 \times 10^6$, $z_{max} = 5.5$ and $z = 3$ for Paika, $A = 6.3 \times 10^6$, $z_{max} = 2.5$ and $z = 1.5$ for Tala, and $A = 13.5 \times 10^6$, $z_{max} = 3.5$ and $z = 2$ for Yanga (McGinness et al. 2016; S. Jacobs, pers. comm.).

Abiotic conditions

For the measurement of water transparency, a 25-cm Secchi disc was lowered at each site of each lake to express the water transparency as Secchi transparency depth (STD, m). For the measurement of water temperature (WT, °C) and concentrations of dissolved oxygen (DO, mg l^{-1}), two independent water samples were collected in January 2012 using a Haney-type water sampler (4.1 l volume) at depths of 0.15 and 2 m at each site of each lake (n = 8 for each lake), and at depths of 0.15, 2 and 5 m at each site of Paika Lake (n = 12) and at depths of 0.15 and 2 m at Tala and Yanga Lakes (n = 8 for each lake). From each water sample, water temperature and DO concentrations were immediately measured using a YSI Model 5100 Dissolved Oxygen/Temperature Meter (YSI Inc., Ohio, USA). For the measurement of all other abiotic conditions, five independent depth-integrated water samples (0.15 and 2 m depths) were collected using the water sampler at each site of each lake in both January and February 2012 (n = 10 for each lake in each month). From each water sample, a single subsample (100 ml) was taken and stored at 4 °C for laboratory measurements of pH (ORION Thermo Model 720A pH meter, Orion Research Inc., Massachusetts), conductivity (µS cm^{-1}) (ORION Model 160 conductivity meter, Orion Research Inc., Massachusetts, USA), turbidity (NTU) (HACH 2100AN turbidimeter, Hach Company, Colorado, USA). Another subsample (30 ml), taken from each of the five depth-integrated water samples using a sterilised syringe (Termo, USA), was stored at –20 °C for the determination of total nitrogen (TN, mg l^{-1}) and total phosphorus (TP, mg l^{-1}). A further three subsamples taken (30 ml each) were immediately filtered through a membrane filter (pore size: 0.45 µm) and stored at −20 °C for the determination of dissolved ammonia (NH_3-N, mg l^{-1}), dissolved oxydised nitrogen (NO_x-N, mg l^{-1}), dissolved reactive phosphorus (PO_4-P, mg l^{-1}), dissolved silica (SiO_2-Si, mg l^{-1}), total dissolved nitrogen (TDN, mg l^{-1}), total dissolved phosphorus (TDP, mg l^{-1}) and DOC (mg l^{-1}). Nutrient analysis methods followed Hosomi and Sudo (1986) and Eaton et al. (2005). Dissolved organic nitrogen (DON, mg l^{-1}) was estimated as [TDN – (NH_3-N + NO_x-N)] (Wiegner et al. 2006), and dissolved organic phosphorus (DOP, mg l^{-1}) was approximated as [TDP – (PO_4-P)] (Saunders et al. 2006; Baldwin 2013).

Biotic conditions

Concentrations of chlorophyll (Chl) *a* (µg l^{-1}) were determined, using a fluorometric analysis (Eaton et al. 2005). At each site in each lake, two independent water samples (100 ml each) were collected at depths of 0.15 m and 2 m using the water sampler and were filtered through a glass fibre filter (47 mm in diameter: ~0.45 µm in pore size). Each filter was then placed into a plastic tube, wrapped with aluminium foil, frozen at −20 °C and kept in the dark at −80 °C until analysis. For each sample, Chl *a* was extracted using an aqueous acetone solution and their concentrations were determined by using a Trilogy Laboratory Fluorometer 7200-000 (Turner Designs, Sunnyvale, CA) calibrated with a known concentration of chlorophyll solution.

For the determination of planktonic respiration and primary productivity of phytoplankton, two independent water samples were collected at depths of 0.15 and 2 m (total four samples) at each site in each lake. Using each water sample, two glass biological oxygen demand (BOD) bottles (300 ml volume each) were filled without air bubbles: one bottle fully wrapped with aluminium foil ('dark' bottle) and the other bottle remained unwrapped ('light' bottle). In each lake, a total of four BOD bottles (two dark and two light) were suspended at each depth at each site. Planktonic respiration (PR, mg C m^{-3} day^{-1}) and gross primary productivity (GPP, mg C m^{-3} day^{-1}) of phytoplankton were estimated from changes in DO concentrations between the dark and light bottles at the beginning and the end of *in situ* incubation using the equations in Wetzel and Likens (1991):

(1)

$$PR = [(IB - DB) \times 1{,}000 \times RQ \times 0.375] \times (t / 24)$$

(2)

$$GPP = [(LB - DB) \times 1{,}000 \times 0.375] / [PQ \times (t / 24)]$$

where *IB* is the concentration of dissolved oxygen (DO, mg l^{-1}) at the beginning of the incubation. *LB* and *DB* are the concentration of DO (mg l^{-1}) in light and dark bottles respectively at the end of the incubation. A factor of 1,000 was used to convert the volume of water from litres to cubic meters. A factor of 0.375 is the ratio of moles of C to moles of oxygen (12 mg C ÷ 32 mg O_2 = 0.375) and was used to convert the mass of oxygen to mass of C (Wetzel and Likens 1991). *PQ* is the photosynthetic quotient and *RQ* is the respiratory quotient. *PQ* and *RQ* indicate the relative amounts of oxygen and C involved in the process of photosynthesis and respiration respectively. A *PQ* of 1.2 and *RQ* of 1.0 were used in this study (Wetzel and Likens 1991). *t* is the incubation time (h).

Lake characteristics

A principal component analysis (PCA) with a correlation biplot was used to summarise lake characteristics with respect to water quality as descriptors to a dimensionally reduced space. The principal components (PCs) were extracted from Pearson's correlation matrices, so that the descriptors were standardised and contributed equally in the clustering of samples. This was necessary as the variables (descriptors) were measured on different scales. Prior to analysis, all variables except pH were $\log_{10}$-transformed to reduce skewness. The Jolliffe cut-off value was used as an indication of how many PCs should be considered significant (Jolliffe 1986). PAST (paleontological stastics) stastical computer software version 2.17 (Hammer et al. 2001) was used for the PCA and the correlation biplot.

In this study, the water-column GPP/PR of each lake (i.e., local-level GPP/PR) was approximated for each month simply as:

(3)

$$\text{Water-column GPP/PR} = \text{mean } GPP_i / \text{mean } PR_i$$

where mean GPP_i and PR_i are the arithmetic mean of GPP and PR respectively in lake *i*. The water column of a lake is considered to be autotrophic and a C sink if a water-column GPP/PR > 1, but heterotrophic and a C source if a water-column GPP/PR < 1, in terms of the C balance through the process of planktonic metabolism.

In addition, the three-lake GPP/PR was estimated for each month as the summation of the local-level planktonic metabolism of Paika, Tala and Yanga Lakes, weighted by lake volumes:

(4)Three-lake

$$\text{GPP/PR} = \sum_{i=1}^{3}(\text{mean } GPP_i \times A_i \times z_i) / \sum_{i=1}^{3}(\text{mean } PR_i \times A_i \times z_i)$$

where mean GPP_i and PR_i are the same as those defined in equation (3), A_i is surface area and z_i is mean depth of lake *i*, respectively.

RESULTS

Abiotic conditions

The three lakes Paika, Tala and Yanga had relatively low STD and a high level of turbidity and high concentrations of nutrients in both January and February 2012 (Table 1). There were relatively small differences in WT and DO concentrations with depth in each lake (difference between depths: < 0.5 °C and < 2 mg l^{-1} respectively for all three lakes), with a minimum WT and DO concentration of 25.5 ± 0.03 °C and 8.3 ± 0.4 mg l^{-1} (mean ± SE, n = 4) recorded at 5 m depth in Paika Lake in February 2012. A principal component analysis with a correlation biplot projected observations of the three-lake samples and the descriptors (all abiotic variables excluding STD, WT and DO shown in Table 1) onto a two-dimensional plane (Fig. 3). The first two PCs had eigenvalues above an estimated Jolliffe cut-off value of 0.7 and accounted for 89 % of total variance (64 % by the first PC alone). The results of PCA showed that the three lakes were distinguished from one another with respect to abiotic conditions in both January and February 2012, especially with respect to relatively high turbidity in Paika and Tala Lakes, and relatively high total and dissolved nutrients in Yanga Lake. For Yanga Lake, there were marked differences in abiotic conditions between the east and the west basins in February 2012. This was primarily due to large within-lake differences in concentrations of NH_3-N (6.1 ± 0.3 µg l^{-1} for the east basin and 981 ± 2 µg l^{-1} for the west basin, n = 5), and NO_x-N (2.7 ± 0.6 µg l^{-1} for the east basin and 144 ± 7 µg l^{-1} for the west basin) and to a lesser extent PO_4-P (167 ± 6 µg l^{-1} for the east basin and 297 ± 8 µg l^{-1} for the west basin) and SiO_2-Si (2,284 ± 30 µg l^{-1} for the east basin and 7,453 ± 68 µg l^{-1} for the west basin). No such large within-lake differences in abiotic conditions were observed for Tala and Paika Lakes in both January and February 2012 (Table 1).

Biotic conditions

In both January and February 2012, Tala Lake had the greatest mean rates of PR and GPP both at depths of 0.15 and 2 m among the three lakes, together with the greatest mean Chl *a* concentration at both depths in February 2012 (Table 2). For the three lakes, the mean rates of GPP at 0.15 m depth were 3-14 times greater than those at 2 m depth while the mean rates of PR and the mean Chl *a* concentrations were similar between the two depths. The GPP/PR values were ≥ 1 at 0.15 m depth but was < 1 at 2 m depth for the three lakes in both January and February 2012 (Fig. 4). The estimated water-column (i.e., local-level) GPP/PR value for Paika Lake was 0.63 in January and 2.23 in February 2012. For Tala Lake, the values were 1.64 in January and 1.78 in February. For Yanga Lake, the values were 1.64 in January and 0.94 in February. The estimated three-lake GPP/PR value was 1.53 in January and 1.40 in February. By converting the volume-based hourly rate to area-based daily rate using mean water depth of lake (z), the overall mean rate of net primary productivity of phytoplankton was estimated as 533, 1,674 and 364 mg C m^{-2} day^{-1} for Paika, Tala and Yanga Lakes respectively, with an overall three-lake mean NPP rate of 857 mg C m^{-2} day^{-1} in this study.

DISCUSSION

Trophic state and carbon dynamics

There are different criteria and thresholds using a set of biotic and abiotic variables available to classify the trophic conditions of lakes (Carlson 1977; OECD 1982; Galvez-Cloutier and Sanchez 2007). The biomass and primary productivity of phytoplankton and concentrations of macronutrients such as N and P are often used as criteria for the determination of trophic conditions of lakes (Likens 1975; OECD 1982; Galvez-Cloutier and Sanchez 2007). More complex approaches use mathematically-modelled indices instead of measured concentrations per se (e.g. Vollenweider 1975; Carlson 1977; Brezonik 1984; Markad et al. 2019). Based on the classification by Wetzel (2001:389, Table 15-13) which uses primary productivity of phytoplankton (approximately equivalent to NPP in this study) and concentrations of Chl *a* and macronutrients, all three lakes (Paika, Tala and Yanga) show, on average, the characteristics of mesoeutrophy with respect to NPP and Chl *a* and hypereutrophy with respect to TN and TP (Fig. 5).

There were notable differences in water quality among the lakes: relatively high turbidity in Paika and Tala Lakes, and relatively high total and dissolved nutrients in Yanga Lake. The high turbidity in Paika Lake is likely to be attributed to the transition of the lake from a dry system which had been previously grazed and not been flooded for about 100 years and the accumulation of abiotic matter such as sediments in the lake bed and its primary inflow Paika Creek. In addition, there was a marked within-lake difference in concentrations of dissolved nutrients in the east and west basins of Yanga Lake in February 2012,

Table 1. Summary statistics for Secchi transparency depth (STD) and depth-integrated (0.15 and 2 m depths) abiotic conditions in Paika, Tala and Yanga Lakes in January and February 2012. WT: water temperature; DO: dissolved oxygen; COND: conductivity; TURB: turbidity; NOx-N: oxidised nitrogen: NH_3-N, ammonia nitrogen: PO_4-P: dissolved inorganic phosphorus: SiO_2-Si, dissolved silica: TN, total nitrogen: TP, total phosphorus: DOC, dissolved organic carbon: DOC, dissolved organic nitrogen: DON, dissolved organic phosphorus: DOP. Mean ± SE are shown for each observation (n = 10) apart from WT and DO (n = 8), and Secchi transparency depth for which median values are shown (n = 2).

	Paika Lake		Tala Lake		Yanga Lake	
	January	February	January	February	January	February
STD (m)	0.4	0.4	0.4	0.3	0.9	0.8
WT (°C)	25.5±0.1	25.5±0.08	25.5±0.6	27.6±0.1	28.6±0.4	27.1±0.1
DO (mg l^{-1})	6.7±0.1	9.6±0.3	7.0±0.6	10.8±0.3	4.7±0.2	9.1±1.3
pH	8.1±0.02	8.8±0.04	9.2±0.03	9.5±0.02	8.1±0.02	8.8±0.09
COND (µS cm^{-1})	321.9±0.8	319.4±1.1	320.3±1.2	330.2±0.6	509.3±0.7	536.8±6.0
TURB (NTU)	42.9±1.0	49.5±3.0	45.4±0.9	30.5±0.5	10.0±1.1	23.1±1.9
NO_x-N (µg l^{-1})	125.4±7.0	4.8±1.3	7.3±1.4	1.8±0.3	49.6±8.1	73.4±23.8
NH_3-N (µg l^{-1})	82.1±7.3	10.4±4.1	12.4±0.7	5.1±0.1	1,329.7±78.7	493.6±162.5
PO_4-P (µg l^{-1})	120.6±1.9	39.6±0.7	3.3±0.6	2.3±0.1	468.2±12.3	232.1±22.2
SiO_2-Si (µg l^{-1})	3,925.5±30.3	270.9±27.3	107.3±29.4	779.4±22.1	14,797.0±150.2	4,868.2±862.2
TN (µg l^{-1})	1,413.2±25.3	1,298.3±12.5	2,789.2±22.2	2,905.4±9.3	4,086.0±116.9	3,398.2±134.8
TP (µg l^{-1})	253.4±2.3	176.3±1.2	219.8±4.5	203.8±1.5	659.2±12.0	409.1±22.7
DOC (mg l^{-1})	11.1±0.1	10.1±0.1	28.5±0.2	27.5±0.2	32.9±0.2	30.9±0.2
DON (µg l^{-1})	838.3±27.4	746.9±6.0	1,095.3±24.9	1,186.8±3.7	2,386.9±10.1	2,143.7±9.2
DOP (µg l^{-1})	45.7±1.9	26.8±0.6	28.4±3.6	24.4±0.1	122.4±11.8	91.8±7.2

especially NH_3-N and NO_x-N (~160 and 50 times respectively greater in the west basin than the east basin). The reason for such large differences in dissolved nutrients is unclear but may include possible differing sediment characteristics, restricted mixing of lake water between the two basins due to its kidney-shaped morphology, and external sources of dissolved nutrients entering the west basin of Yanga Lake, for example via Yanga Creek (Fig. 1). Further detailed studies are warranted to elucidate the causal mechanism for the spatial heterogeneity of dissolved nutrients in Yanga Lake.

In terms of planktonic processes, the metabolic functioning of the floodplain lakes varies both spatially and temporally. Within lake, the planktonic processes were highly heterogenous with depth: autotrophy (GPP/PR ≥ 1) in the near-surface layer and heterotrophy (GPP/PR < 1) in the near-bottom layer during the two study periods (Fig. 4) even though all three lakes are relatively shallow. This seems to be attributed to large reductions in GPP with depth, relative to PR at each lake (Table 2), suggesting that the primary production of phytoplankton may chiefly be limited by light in these semi-arid floodplain lakes.

Between lakes, Paika Lake was a source for atmospheric C in January 2012 but a sink in February 2012; Tala Lake was a sink for atmospheric C in both January 2012 and February 2012; and Yanga Lake was a sink for atmospheric C in January 2012 but a source in February 2012. The observed heterotrophic conditions imply that there are occasions when the inundated floodplain lakes receive an external, most likely terrestrial supply of organic matter (e.g. from upstream or higher elevation floodplain areas) that are actively respired within the lakes, as have been observed in lakes in the northern-hemisphere (Staehr and Sand-Jensen 2007; Cole 2013). The external (or allochthonous) source of C is also thought to be important in regulating the functional process of

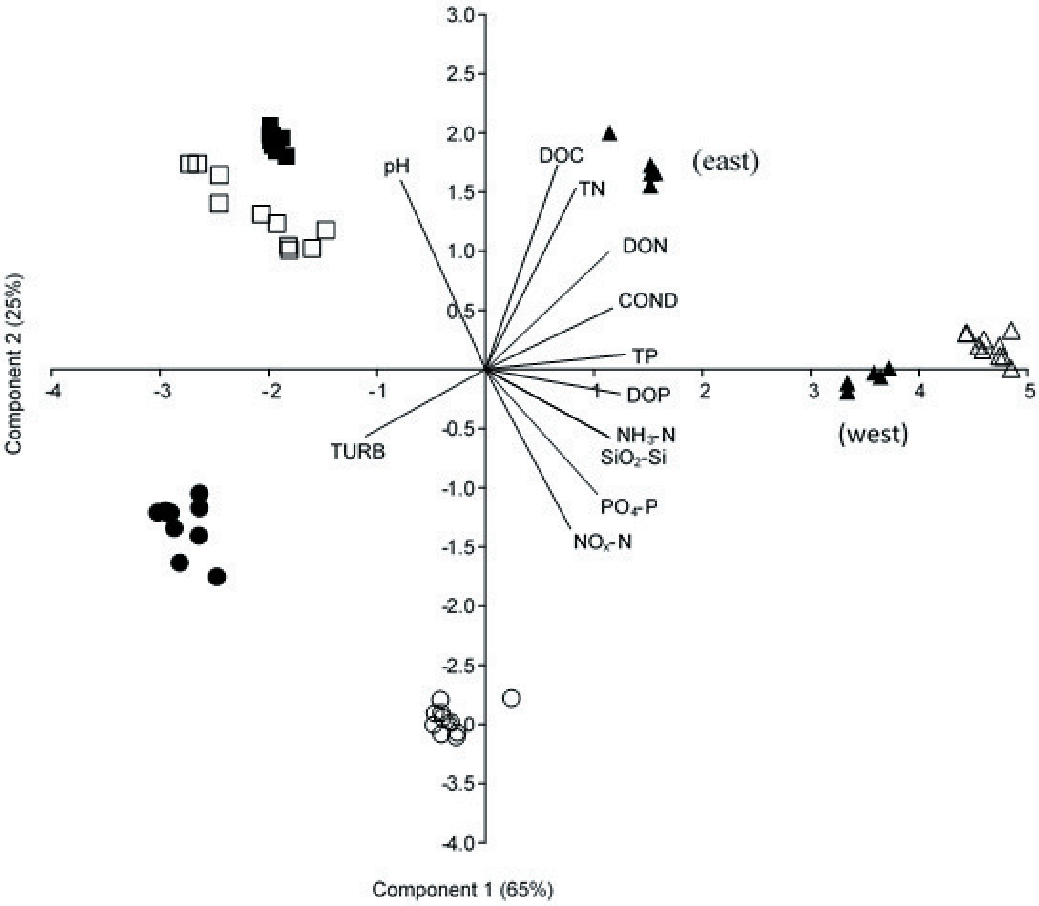

Figure 3. Principal component analysis with a correlation biplot projecting observations of the samples and the descriptors: conductivity (COND), turbidity (TURB), oxidised nitrogen (NOx-N), ammonia nitrogen (NH_3-N), dissolved inorganic phosphorus (PO_4-P), dissolved silica (SiO_2-Si), total nitrogen (TN), total phosphorus (TP), dissolved organic carbon (DOC), dissolved organic nitrogen (DON) and dissolved organic phosphorus (DOP). Paika Lake: ○, January 2012; ●, February 2012. Tala Lake: □, January 2012; ■, February 2012. Yanga Lake: △, January 2012; ▲, February 2012. For Yanga Lake, the observations in February 2012 showed a significant separation between the east (east) and the west (west) basin samples.

Australian inland floodplain-river systems (Robertson et al. 1999; Baldwin et al. 2013; Baldwin et al. 2016). Nevertheless, the mean NPP rates for the three lakes are about 0.7 to 3.0 times greater than the mean NPP rate (554 mg C m^{-2} day^{-1}) estimated for inland floodplain wetlands of southeast Australia (Kobayashi et al. 2013) and correspond to about 9 to 43 % (three-lake mean: 22 %) of the mean ecosystem-level NPP estimated for temperate-zone inland freshwater marshes (3.9 g C m^{-2} day^{-1}, Mitsch and Gosselink 2000). These comparisons, though approximate, indicate the substantial potential of semi-arid inland floodplain lakes to function as a sink of atmospheric C through planktonic metabolism during summer.

Lake functional response framework

By applying a spatial hierarchical framework to lake functional response, we define an individual lake response as a local-level response, and a response combining multiple lakes as an area-level response. Using this framework, the results of this study show that as an area-level response, the three-lakes were a sink for atmospheric C in terms of the planktonic processes in both January and February 2012 (three-lake GPP/PR = 1.53 and 1.40 respectively), even though one of the three lakes (Paika) was considered a source for atmospheric C in January (local-level GPP/PR = 0.63).

Table 2. Summary statistics for planktonic respiration (PR, mg C m^{-3} day^{-1}), gross primary productivity (GPP, mg C m^{-3} day^{-1}) of phytoplankton and chlorophyll *a* (Chl *a*, mg m^{-3}) at 0.15 m and 2 m depths of Paika, Tala and Yanga Lakes in January and February 2012. Mean ± SE are shown for each observation (n = 4). Results of Chl *a* are available for February 2012 only.

	Paika Lake		Tala Lake		Yanga Lake	
	January	February	January	February	January	February
0.15 m depth						
PR	282.2±41.0	408.8±65.0	1,489.7±231.4	1,723.1±89.0	620.6±107.0	926.3±288.5
GPP	230.5±18.1	1,486.7±46.0	4,156.3±125.4	4,995.30±47.1	1,975.8±296.2	1,378.1±370.5
Chl *a*	-	70.3±2.8	-	147.8±1.9	-	31.5±12.0
2 m depth						
PR	215.6±27.2	315.9±19.4	1,425.9±239.5	1,584.4±31.1	673.1±57.5	798.8±206.8
GPP	85.2±16.2	131.3±13.8	632.8±90.8	903.9±64.3	146.1±49.0	246.1±98.9
Chl *a*	-	72.4±1.9	-	138.0±2.2	-	34.9±15.2

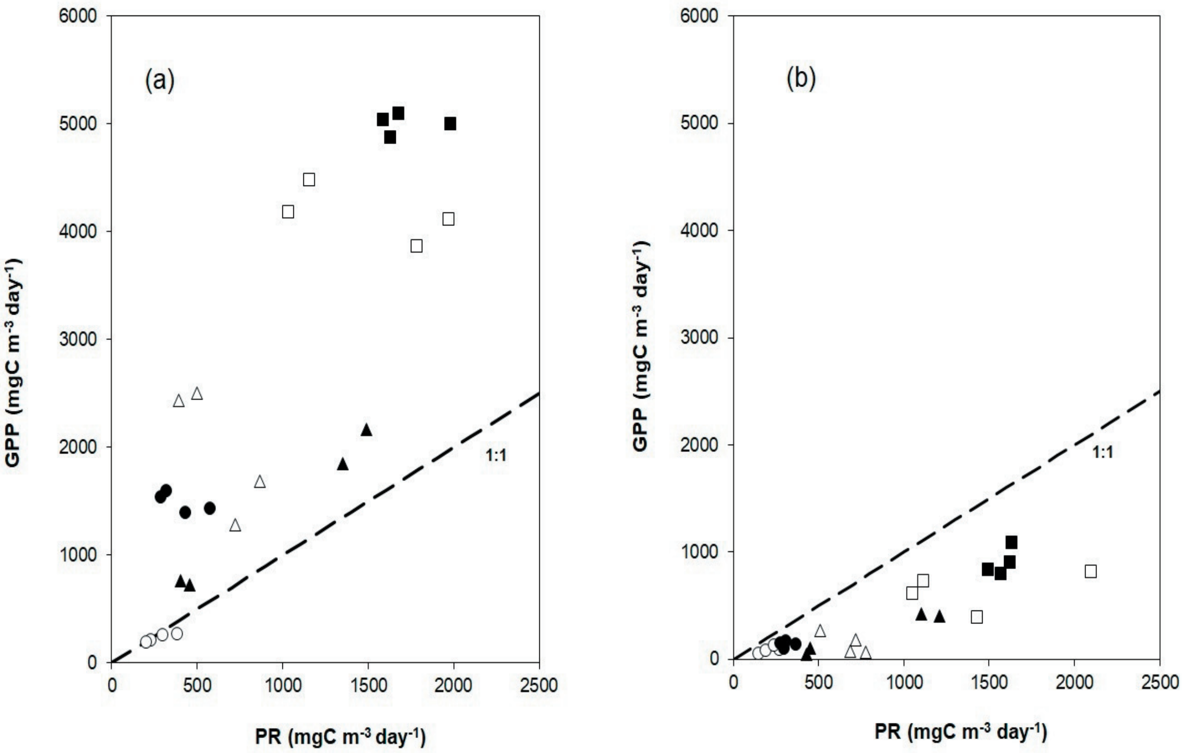

Figure 4. Gross primary productivity of phytoplankton (GPP, mg C m^{-3} day^{-1}) and planktonic respiration (PR, mg C m^{-3} day^{-1}) in Paika, Tala and Yanga Lakes. (a) 0.15 m depth; (b) 2 m depth. Paika Lake: ○, January 2012; ●, February 2012. Tala Lake: □, January 2012; ■, February 2012. Yanga Lake: △, January 2012; ▲, February 2012. Dotted lines indicate that GPP/PR = 1 (1:1 ratio). The measured values above the dotted lines indicate an autotrophic state (GPP>PR) and those below the dotted lines indicate a heterotrophic state (GPP<PR) in terms of planktonic processes in the lakes

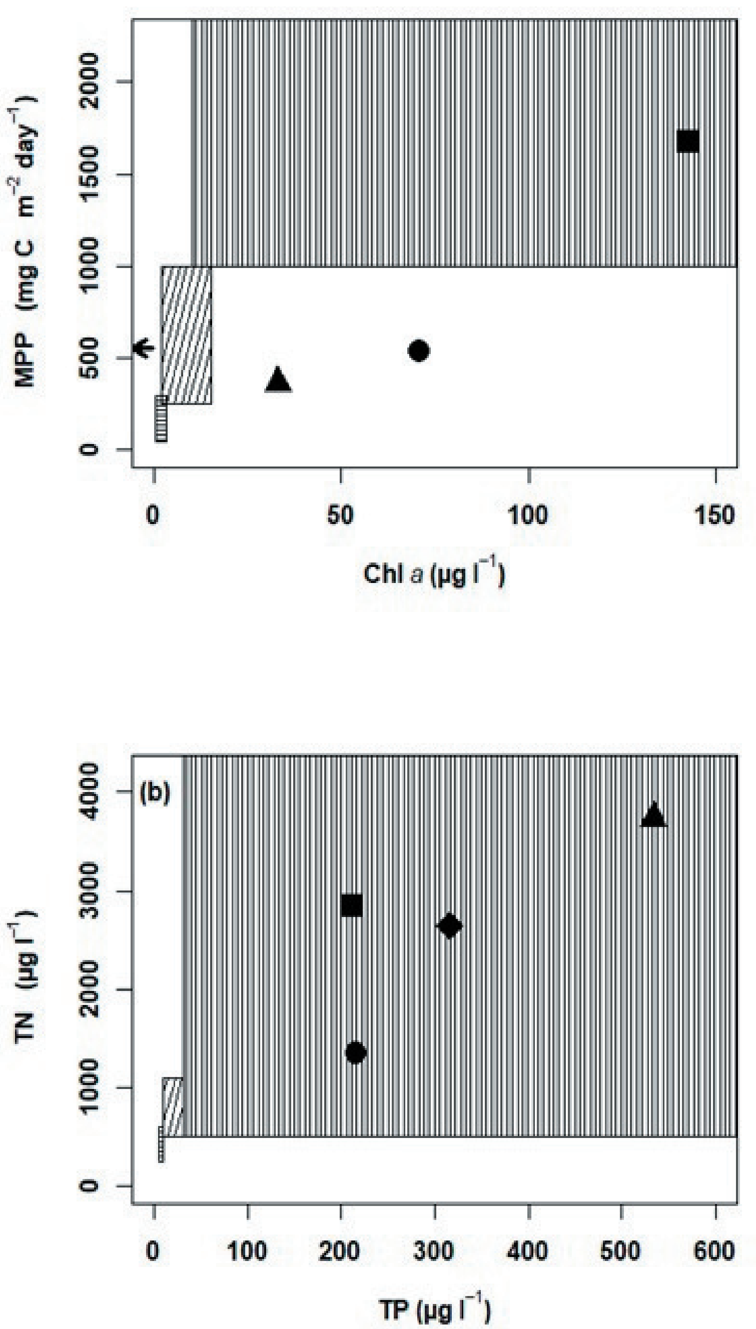

Figure 5. Comparisons of biotic and abiotic characterizes of Paika, Tala and Yanga Lakes with general ranges for lakes of different trophic categories. Values of the general ranges given in Wetzel (2001:389) were used to construct range boxes. (a) Mean primary productivity (MPP, mg C m^{-2} day^{-1}) and chlorophyll *a* (Chl *a*, µg l^{-1}). MPPs for Paika, Tala and Yanga Lakes were estimated as the mean net primary productivity (NPP = GPP-PR) based on average depth for each lake. General ranges of MPP and Chl *a*: oligotrophic (horizontal-line shade), mesotrophic (angle-line shade); eutrophic (vertical-line shade). An arrow at the bottom left corner indicates the mean NPP (554 mg C m^{-2} day^{-1}) for inland floodplain wetlands of southeast Australia (Kobayashi et al. 2013). ●, Paika Lake; ■, Tala Lake; ▲, Yanga Lake. (b) Mean concentrations of total nitrogen (TN, µg l^{-1}) and total phosphorus (TP, µg l^{-1}). General ranges of TN and TP: oligomesotrophic (horizontal-line shade), mesoeutrophic (angle-line shade), hypereutrophic (vertical-line shade). ●, Paika Lake; ■, Tala Lake; ▲, Yanga Lake: ◆, mean TN and TP concentrations for inland floodplain wetlands of southeast Australia (Kobayashi et al. 2013).

The spatial hierarchical framework in relation to lake functional response outlined in this study informs environmental water managers planning the delivery of environmental water to individual or multiple floodplain lakes. The framework helps optimise watering regimes to support ecosystem functions such as floodplain productivity and nutrient transport objectives. For example, if the water resource management objective is to attain a net-positive C storage of a floodplain lake in terms of planktonic processes, it would be beneficial to deliver environmental flows locally to a lake that is most likely to be highly autotrophic (e.g. Tala Lake in the present study) to achieve a local-level response. Conversely, in order to inundate a wide area including multiple lakes and attain a net-positive planktonic C storage as an area-level response, the delivery of environmental flows may be directed to lakes that are either autotrophic or heterotrophic provided the net C budget expressed as the whole inundated lake area is expected to be autotrophic.

It is worth noting that primary productivity and respiration of the three lakes decreased with increasing years of dry conditions before being inundated with environmental waters. In particular, since Paika Lake has not functioned as an inundated waterbody for about 100 years, the viable communities such as algae and bacteria on lake beds, which are important in forming a series of planktonic responses following inundation (e.g. Kobayashi et al. 2009, 2019; Rana et al. 2021), may have been impaired, relative to those in Tala and Yanga Lakes. The response of nutrients and carbon was similar but differed as Yanga Lake showed more positive response than Tala Lake, suggesting that other factors (e.g. episodic dry events, lake geomorphology) may also contribute to the magnitude of lake ecological response following inundation.

There are hydro-geomorphic constraints (e.g. connectivity and networks of inflow channels, lake elevations, weirs) and other considerations associated with any floodplain wetland systems to facilitate or hinder implementing such an adaptive environmental flow-delivery approach. Further, to assess the likelihood of autotrophic or heterotrophic response in the lakes, knowledge of recent inundation history, water requirements of biological communities including threatened species, current land use and other factors should be considered prior to an environmental watering event (Koster et al. 2017; Wolfenden et al. 2018). Nevertheless, it is highly important to identify general functional response patterns of each of the inland floodplain lakes that are focus for future managed environmental flows, based on lake monitoring, integrating both field based and remotely-sensed observations and reporting during and following environmental flows. This ensures that the likely environmental benefits or dis-benefits from the inundation of inland floodplain lakes, especially via the delivery of environmental flows, can be better understood and planned at varying management stages and scales (see also Dong et al. 2012).

CONCLUSION

The three inland floodplain lakes investigated in this study exhibited mesoeutrophic to hypereutrophic characteristics, with some notable between-lake and within-lake spatial variability in water quality and productivity. Each lake can be autotrophic or heterotrophic in terms of planktonic C balance. Nevertheless, there is the substantial potential of semi-arid inland floodplain lakes to function as a sink of atmospheric C through planktonic (or water-column) metabolism during summer. Further detailed studies at multiple lakes with higher sampling frequency and longer monitoring period at a range of environmental flow rates are warranted. The concept of a spatial hierarchical framework for lake functional response that we introduced can be further refined and considered by environmental water managers when planning the inundation of inland floodplain lakes with the delivery of environmental flows.

ACKNOWLEDGEMENTS

We thank Steve Jacobs for help in field work and Ed Czobik for analyses of nutrients and Chl *a*. We thank Li Wen for comments. Partial financial support was received from the Water, Wetlands and Coast Division, Office of Environment and Heritage (OEH) (OEH is predecessor organisation of the Department of Planning, Industry and Environment). We thank two anonymous reviewers for helpful comments. The views and conclusions expressed in this paper are those of the authors and do not necessarily represent the official policies, either expressed or implied, of the respective organisations.

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