Tracking a century of change in trophic structure and dynamics in a floodplain wetland: integrating palaeo-ecological, and palaeo-isotopic, evidence

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SUMMARY

1. The palaeoecological assessment, and the use of stable isotopes of carbon in subfossils of herbivores and omnivores, represents a novel approach to understand transitions in past food-web structure and the dynamics of lake ecosystems in response to natural perturbations and human impacts. Combined with records of subfossil assemblages of cladocerans and chironomids, it may be possible to decipher whether changes are attributable to external forces or internally derived system shifts.

2. A sediment record taken from the shallow (2.3 m depth) Kings Billabong in the River Murray floodplain (Australia) was analysed to explore changes in trophic dynamics over the past century.

3. The palaeoecological assessment revealed that littoral assemblages of cladocerans and benthic diatoms were gradually replaced by planktonic (planktonic and facultative planktonic) assemblages after river regulation in the 1920s.

4. The stable isotopic composition of carbon ($d^{13}C$), derived from chironomid head capsules, was relatively constant down-core, ranging between -26.1‰ and -24.0‰, and coincided largely with the $d^{13}C$ of bulk sediment samples (-25.6‰ to -22.0‰). The $d^{13}C$ values of pelagic (*Daphnia*) and ubiquitous (*Bosmina*, *Alona*) cladocerans, however, varied markedly, with that for *Daphnia* between -29.8‰ (10–20 cm) and -23.2‰ (60–70 cm), and for ubiquitous cladocerans, between -29.4‰ (20–30 cm) and -24.5‰ (80–70 cm).

5. The temporal changes in the $d^{13}C$ values of cladocerans also suggest a gradual transition from a macrophyte-dominated state to a phytoplankton-dominated state after river regulation and further indicate changes in the horizontal migration behaviour of *Daphnia* depending on macrophyte abundance and predation risk.

6. Our study demonstrates the potential of reconstructing, more precisely, the trophic dynamics of large river floodplain lakes and their ecological resilience by combining subfossil analyses with stable isotope analyses of selected subfossil groups.

Keywords: Kings Billabong, palaeo-food-web structure, River Murray system Australia, stable carbon isotope, subfossil cladocerans and chironomids

Introduction

In large river floodplains, the patterns of river flow and flood pulses are highly variable, resulting in pronounced variation in exchange rates of nutrients, organic matter (OM) and organisms between the river and its associated wetlands over space and time (Vannote *et al.*, 1980). Locally derived algae can be a significant source of

carbon at the base of the food web, but the carbon derived from the riparian vegetation can also add to local autochthonous production at degree that depends on the frequency and duration of the flood pulse (Thorp & Delong, 1994; Wehr & Descy, 1998). Flooding further brings terrestrial-derived plant and animal biomasses to the total carbon pool of the wetland (Burford *et al.*, 2008). Any natural or anthropogenic alterations in the connectivity between rivers and wetlands are, therefore, expected to influence riverine food webs significantly.

The natural flood pattern of the River Murray in south-east Australia has been disrupted following the arrival of Europeans around 1850. An extensive network of dams, weirs and locks was built on the river, mostly from the 1920s, and its catchment has been transformed for agriculture (Ogden, 2000; Gell *et al.*, 2009). The construction of dams, originally to facilitate navigation but now mostly to provide water for irrigation, has disrupted downstream flow, altering nutrient transport and the exchange of fixed carbon between the river and its wetlands (Gehrke & Harris, 2000; King, Humphries & Lake, 2003; Frazier & Page, 2006). In sites closely to the weir pools, permanent inundation has led to the disappearance of invertebrates and plants adapted to low water, and the loss of floodplain vegetation, such as river red gum (*Eucalyptus camaldulensis*) and lignum *Muehlenbeckia florulenta* (Kingsford, 2000), characteristic of early succession after drawdown. In wetlands distant from the channel, prolonged drought has forced herbivores and fish to feed on filamentous algae confined to small waterholes (Bunn, Davis & Winning, 2003; Burford *et al.*, 2008). Prolonged flooding, on the other hand, has reduced the density of submerged vegetation and led to the establishment of the emergent Cumbungi-*Typha* spp. vegetation (Nielsen *et al.*, 2000). Evidence for this also comes from palaeoecological investigations in billabongs across the middle reaches of the River Murray (Reid *et al.*, 2002). As a result of the switch in the density of submerged aquatic macrophytes, the sources of carbon to floodplain wetlands of the River Murray are also thought to have been altered internally by river regulation.

In shallow lakes, a transition from a clear-water, macrophyte-rich state to a phytoplankton-dominated, turbid regime is often accompanied by a shift in floral and faunal assemblages and from littoral–benthic to pelagic carbon pathways and energy flow (Vadeboncoeur *et al.*, 2003). In the sediment record of subfossils, this is evident in an increase in the littoral to planktonic (L:P) ratios of consumers, such as cladocerans (Jeppesen *et al.*, 2001). The disruption in wetland connectivity, and the

implications for the quantity and quality of external inputs of carbon and nutrients to floodplain wetlands of south-east Australia, has been well investigated (Bunn *et al.*, 2003; Burford *et al.*, 2008). However, how the associated loss of benthic-periphytic submerged floral community has affected the internal dynamics of carbon is not well known. Stable isotope ratios of carbon ($d^{13}C$) in organic matter, and in remains of various organisms, may be useful to study changes in the internal C dynamics (Perga, 2010), as $d^{13}C$ values are reported to vary among primary producers, but to change little with trophic transfer, thereby allowing the ultimate sources of dietary carbon to be determined (Post, 2002).

The purpose here was to investigate how the trophic dynamics changed in a floodplain wetland in south-east Australia, before and after human disturbance. It is assumed that a clear-water, littoral-benthic-derived food web collapsed following river regulation during the late 1920s and that the base of the food web switched as a result of a shift to a phytoplankton-dominant pelagic regime. We aimed to describe the ecosystem in the past: changes in habitat diversity were documented from diatom and cladoceran subfossil assemblages (Ogden, 2000; Reid *et al.*, 2007), while changes in the carbon source fuelling the riverine food web were investigated from the $d^{13}C$ values of sediments and invertebrate subfossils.

Recently, the $d^{13}C$ values derived from subfossil chironomid head capsules and cladocerans have been used successfully to map the energy flow and to infer palaeo-food-web dynamics in European lakes (Perga, 2010; Frossard *et al.*, 2014). This has been possible due to the isotope ratio mass spectrometry (IRMS) technique enabling measurement of $d^{13}C$ values from small samples of the head capsules of subfossil chironomids and of cladocerans (Perga, 2010; Van Hardenbroek *et al.*, 2010).

For this study, $d^{13}C$ measurements were performed on subfossil taxa selected based on their abundance, food preferences and the capacity to separate their remains. *Bosmina* and *Alona* produce single eggs that can be relatively easily isolated from the sediment. The feeding of *Bosmina* and small *Alona* is not well studied, but their ubiquity, in terms of habitat, suggests they are not food specialists (DeMott, 1989). For instance, at the time of food shortage, *Bosmina* thrives by eating non-photosynthetic organisms, including protozoa and eubacteria (as does *Alona*) in the near-shore littoral environment, more efficiently than *Daphnia* (Smiley & Tessier, 1998). Their stable isotopic composition of carbon was, therefore, considered as representative of that of the source dominating the carbon pool (phytoplankton and/or the

terrestrial and littoral aquatic primary producers) at the time of sampling. In contrast, *Daphnia* is a typical pelagic filter-feeder (Lampert, 1989) producing eggs that can be easily distinguished from those of *Bosmina*/*Alona*. Their isotope composition has been repeatedly shown to reflect pelagic primary production (Perga & Gerdeaux, 2006; Francis *et al.*, 2011). Lastly, the ^{13}C of chironomid head capsules was expected to reflect benthic carbon sources. A comparison of the d^{13}C values between pelagic *Daphnia* and ubiquitous (e.g. *Bosmina,* small *Alona*) cladocerans and benthic chironomids in the system, over a 100-year timescale, should reveal any changes in the food web before, during and after a transition from a clear-water, littoral–benthic regime (high diversity in d^{13}C values among taxa) to a turbid water, phytoplankton-dominated regime (homogeneity of d^{13}C between taxa).

Methods

Study site

Kings Billabong, a shallow (maximum depth *c.* 2.3 m) wetland, is located adjacent to the lower River Murray near the city of Mildura (north-west Victoria) (Kattel, Dong & Yang, 2014). Historically, Kings Billabong was closely associated with the *Nyeri Nyeri* aboriginal community. The remarks of William Splatt in 1853, that '*The aboriginal inhabitants of the lower Murray are more numerous and a finer race than any other native tribe I have seen in Australia. The comparatively warm, short winter of this neighbourhood, and the abundance of fish and game, may in part account for this*' reveal the value of fish in Kings Billabong to the economy of the aboriginal community (McBride, 1898). A variety of fish species, including the endemic Murray cod (*Maccullochella peelii peelii*), golden perch (*Macquaria ambigua*), Australian smelt (*Retropinna semoni*), fly-specked hardyhead (*Craterocephalus stercusmuscarum fulvus*), flat-headed gudgeon and bony herring (*Nematalosa erebi*), as well as introduced species such as mosquito fish (*Gambusia holbrooki*), has been collected by the Murray Darling Freshwater Research Centre (MDFRC) from Kings Billabong during their routine monitoring programme.

In its natural condition, Kings Billabong was intermittently filled at times of high flows in the Murray River. However, since the intensification of the early European migrant settlement in the Victorian Mallee region from 1891 to 1923 (www.murrayriver.com.au), the landscape across the catchment has changed substantially (MCMA, 2006). The natural flow of the Murray has been signifi-

cantly modified by the construction and operation of a series of locks, weirs and upstream storages (Gippel & Blackham, 2002). These changes have affected the hydrology and, in particular, the variability, duration and frequency of flows in the river (Gippel & Blackham, 2002). While Kings Billabong was first used as a water storage basin for irrigation in 1896, major river regulation was imposed on the system through the commissioning of a network of impoundments between 1922 and 1937, and these are likely to have modified the connectivity of Kings Billabong to the river (Gippel & Blackham, 2002). Artificial flooding linked to the nearby weir pool of Lock 9 at Mildura, transformed Kings Billabong to a permanently waterlogged area, leading to the dieback of river red gum forests and the establishment of fringing Cumbungi (*Typha* sp.) vegetation. The loss of river red gum continued until the 1950s, as their timber was used to fuel steam-operated pumps and paddle boats on the river (Parks Victoria, 2008).

^{210}Pb dating

A 94-cm-long, 80-mm-diameter piston sediment core was collected from the deepest point (*c.* 2.3 m) of the wetland in September 2011 and used for analyses of subfossil cladocerans, chironomids and diatoms, stable isotopes of carbon and nitrogen, as well as age modelling. The ^{210}Pb age modelling (Appleby, 2001) was based on CIC (constant initial concentration) and CRS (constant rate of supply) models using a total of 9 subsamples showing ^{210}Pb activity down to 51 cm. The samples were analysed at the Australian Nuclear Science and Technology Organisation (ANSTO), Lucas Heights following the methods described by Harrison, Heijnis & Caprarelli (2003).

Subfossil diatom analyses

High-resolution subsampling (every 1-cm interval) was carried out on the core for subfossil diatom analyses. Samples were digested in 10% HCl and 10% H_2O_2 (Battarbee *et al.*, 2001). Aliquots of 400 lL and 800 lL were dried on coverslips and mounted on microscope slides using Naphrax. Approximately 200 valves were counted per slide, which is considered adequate to characterise a diatom community (Bate & Newall, 1998). Broken valves were counted if the central area was present. Counting was undertaken on a Nikon Eclipse E600 microscope under differential interference contrast using 91000 magnification (oil immersion lens). Diatom taxa were identified following standard texts (e.g. Krammer &

Lange-Bertalot, 1986, 1988, 1991a,b). The counts for each diatom taxon were expressed as a percentage of the total valves counted. Littoral to planktonic ratios of diatoms were calculated based on the littoral and planktonic (planktonic and facultative planktonic) species counts. Diatom taxa known to inhabit both the plankton and benthos were regarded as opportunistic–facultative planktonic taxa and grouped under planktonic taxa.

Subfossil cladoceran analysis

High-resolution subsampling (every 1-cm interval) was carried out on the core for subfossil cladoceran analyses. Approximately 3–4 g wet sediment was treated with 100 mL 10% KOH solution and heated at 60 °C on a hotplate for at least 45 min. The subsample mixture was sieved through a 38-mm mesh with running tap water. A few drops of safranin were added to stain the remains. Slides were then prepared by pipetting 50 lL of each subsample onto microscopic slides. One hundred or more cladoceran remains (carapaces, headshields, post-abdomen, ephippia and post-abdominal claws) were counted at 400× magnification. Badly fragmented remains were counted provided that they remained identifiable. The dry mass percentage of each sediment sample was measured to calculate the counted portion of remains present per gram of dry sediment (Kattel *et al.*, 2008). Cladoceran taxa were identified following standard texts (e.g. Shiel & Dickson, 1995; Szeroczyńska & Sarmaja-Korjonen, 2007). Littoral to planktonic ratios of cladocerans were calculated based on the littoral and planktonic species counts.

The cladoceran species feeding exclusively in the pelagic habitats, such as *Daphnia* were grouped as 'Preferentially Pelagic'; species known to switch their feeding habits with changes in food source were regarded as ubiquitous or 'Opportunistic' cladocerans; and those species that feed exclusively on food derived from shoreline and/or submerged littoral and benthic vegetation were grouped as 'Preferentially Littoral' cladocerans.

Stable isotope of carbon analyses of subfossil cladocerans, chironomids and bulk sediment

To extract sufficient numbers of cladoceran subfossil ephippia and chironomid head capsules, a total of nine subsamples, from depths comprising 0–10, 10–20, 20–30, 30–40, 40–50, 50–60, 60–70, 70–80 and 80–94 cm, were taken from the same core and treated with 10% KOH, as described previously. Subfossil cladoceran ephippia were sorted into two groups based on the number of embryos

in a resting egg. Any ephippium with two embryos was assigned to *Daphnia* (Vandekerkhove *et al.*, 2004). In contrast, eggs with single embryos are produced mostly by cladocerans such as chydorids (*Alona* sp., *Biapertura* sp.) and *Bosmina* (Gannon & Stemberger, 1978). For chironomids, only five depth strata (0–10 cm, 20–30 cm, 30–40 cm, 40–50 cm and 50–60 cm) contained the required number of head capsule. Both cladoceran ephippia and head capsules of chironomids were picked manually using fine forceps and placed separately under a binocular microscope. From each subsample, at least 50–200 ephippia of both groups of Cladocera, and 80 chironomid head capsules (van Hardenbroek, 2010), were needed to achieve a mass of 0.2 mg dry mass. All dry subfossil ephippia and chironomid head capsules were packed into a tin capsule before submitting them for determination of carbon stable isotope composition in SINLAB, New Brunswick, Canada (http://www.unb.ca/cri/sinlab). SINLAB used both a Costech 4010 Elemental Analyser coupled to the Finnigan Delta Plus XP Mass Spectrometer via the Conflo III and a NC2500 Elemental Analyser coupled to the Finnigan Delta Plus Mass Spectrometer via the Conflo II for $d^{13}C$ analysis of subfossil biota. Data were normalised using internal standards that had been calibrated against external standards from the International Atomic Energy Agency (IAEA). The $d^{13}C$ standard deviations on external standards were 0.1&. This is close to instrumental error, although these external standards were not 'normalised samples'. The results for the subfossil cladoceran and chironomid samples are from a single analysis of each sample.

Stable carbon isotopes of bulk sediment were analysed in the ANSTO laboratories using an Elemental Analyser (Elementar VarioMICRO) and Isotope Ratio Mass Spectrometer (GV Instruments IsoPrime) on a total of 45 samples (2 cm intervals). After acid treatment using 1M HCl, rinsing and drying at 60 °C, the samples were loaded into tin capsules and analysed in duplicates, with further replicates if the standard deviations between duplicates exceeded 0.4&. The samples were analysed with both internal and external standards, and the data were normalised using the external standard IAEA C8 with a consensus value of $d^{13}C_{V-PDB}$ = -18.31& (Le Clercq, van der Plicht & Groning, 1998). The average standard deviation between replicates was 0.2& for both standards and samples.

Measurement of loss-on-ignition (LOI)

About 2 g of wet sediment from each depth sample was heated at 105 °C in pre-weighted crucibles to determine

dry mass. The percentage LOI was calculated after placing the crucibles in a furnace (Carbolyte) at 550 °C for 2 h (Meyers & Teranes, 2001).

Numerical analysis

The diatom and cladoceran stratigraphic diagrams were zoned using CONISS (Grimm, 1987). Taxa were grouped to show the stratigraphy of zonations corresponding with the changes in pelagic, littoral and ubiquitous (pelagic *Bosmina* plus littoral chydorids) assemblages over time. In each stratigraphy, the littoral:planktonic ratios are also presented. PCA axis 1 in subfossil diatom and cladoceran samples was derived from principal components analysis (PCA), a linear ordination technique in CANOCO 4.5 (ter Braak & ◆Smilauer, 2002).

Results

Age model

The unsupported ^{210}Pb activities from the Kings Billabong sediment core samples were relatively low, and the chronology should thus be treated with caution. The CIC and CRS models showed close agreement in chronology (Fig. 1a,b). The CRS model suggested that 51 cm depth is 42 ± 6 years old so is dated to *c.* 1969 ± 6 AD (Fig. 1b). The CRS model also suggested an increased mass accumulation rate (MAR) in recent years from 0.5 g^{-1} cm^2 year^{-1} in 1976 to 0.8 g^{-1} cm^2 year^{-1} in 2009. These changes in MAR suggest that the CRS model is more reliable. The CIC model should only be used for sediment cores showing constant MARs. The dating below 60 cm only represents rough estimates as it is derived from a simple extrapolation based on the sedimentation rates calculated at 60 cm (MAR = *c.* 0.6g^{-1} cm^2 year^{-1}), and should therefore be treated with caution.

Subfossil diatom stratigraphy

The L:P ratios of diatoms also revealed that the basal zone (Zone 1 − 70–94 cm, possibly prior to the 1930s) of the diatom stratigraphy is dominated by benthic and periphytic taxa such as *Epithemia adnata* and *Cocconeis placentula* (Fig. 2). However, there was a temporary large peak in the total planktonic assemblage at 90 cm (Fig. 2). Epiphytic taxa decreased gradually from the bottom of the core to the top (Fig. 2). Facultative planktonic taxa, such as *Staurosira construens* var. *construens* and *Staurosira construens* f. *venter*, began to increase from 70 cm to 35 cm (Zone 2 and 3 − *c.* 1985 AD), showing the transition from benthic, clear-water conditions to a turbid water regime (Fig. 2). Facultative planktonic species, particularly *Pseudostaurosira brevistriata*, *S. construens* var. *construens* [Ehrenberg (Hustedt)] and *S. construens* f. *venter* [Ehrenberg (Hustedt)], continued to dominate the system until the upper section (Zone 4 & 5) of the core (Fig. 2).

Subfossil cladocerans stratigraphy

Littoral to planktonic (L:P) ratios revealed that the basal zone (Zone 1 − 70–94 cm, possibly prior to 1930s) of the cladoceran stratigraphy is dominated by littoral species (Fig. 3). The littoral taxon *Dunhevedia crassa* was the only littoral species to influence the total littoral assemblage and the cluster in CONISS (Fig. 3). Above this zone (Zone 2), the cladoceran assemblage was associated with more ubiquitous or opportunistic species such as *Alona guttata* and *Bosmina meridionalis* with a gradual decline in L/P ratios (Fig. 3). Ratios did not change further from 40 cm and upwards. Several opportunistic species, including *B. meridionalis*, *Chydrous sphaericus*, *Alona quadrangularis* and *Biapertura longispina*, continued to dominate the cladoceran community. Mostly, post-abdominal
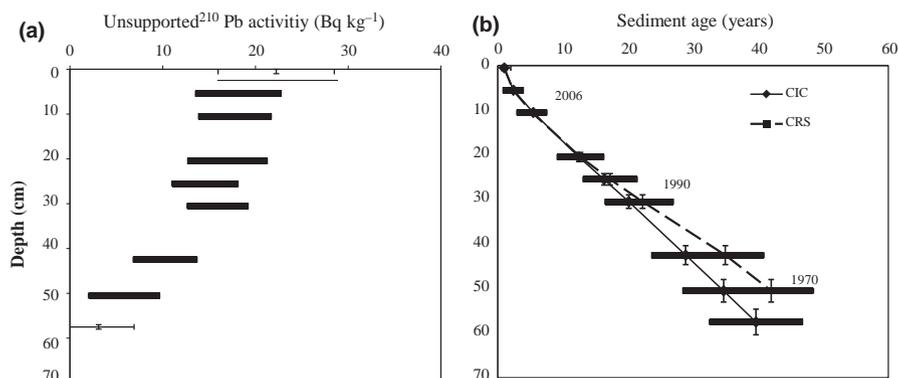

Fig. 1 (a) Unsupported ^{210}Pb activity plotted against depth, (b) sediment age estimated from CIC and CRS models plotted against depth.
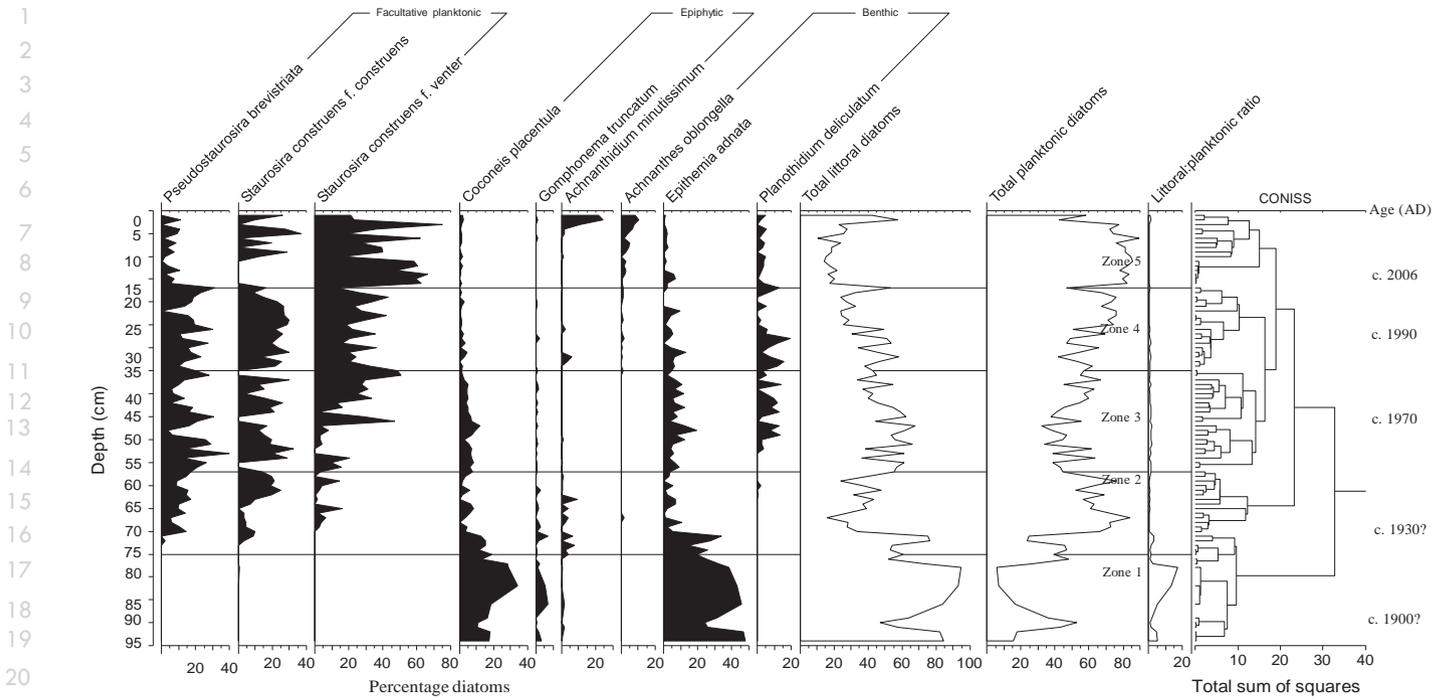
Fig. 2 Diatoms that indicate major food web change in Kings Billabong. The overall assemblage of diatoms was classified using the program CONISS. L:P ratios were calculated on the basis of total littoral diatoms divided by total planktonic (planktonic and facultative planktonic) diatom concentrations (individuals).
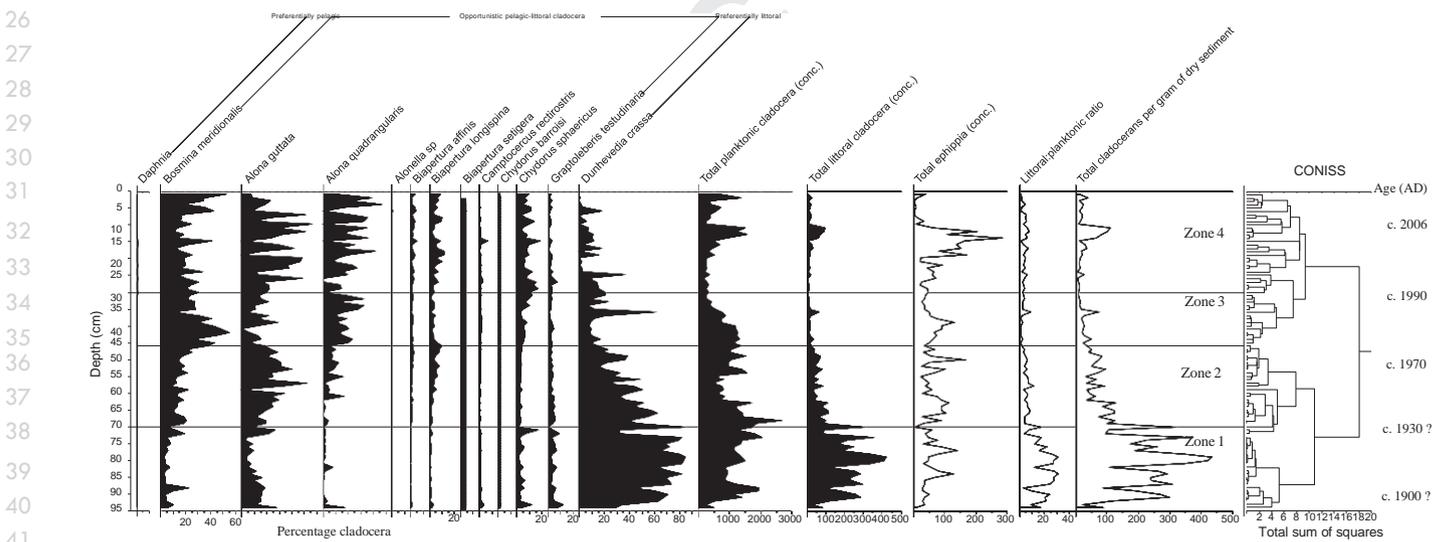

Fig. 3 Cladocerans that indicate major food web change in Kings Billabong. Based on previous studies, and their commonalities in lakes, cladoceran species present in Kings Billabong were grouped as 'Preferentially Pelagic', 'Opportunistic' and 'Preferentially Littoral'. The overall assemblage of cladocerans was classified using the program CONISS. L:P ratios were calculated on the basis of total littoral cladocerans divided by total planktonic cladocerans.

claws and ephippia of *Daphnia*, the 'preferentially' pelagic cladocerans, are preserved in sediment. From 40 cm (Zone 3 & 4), more *Daphnia* remains were recorded than non-pelagic remains (Fig. 3).

d^{13}C values in bulk sediments and percentage LOI

The LOI and d^{13}C values of the bulk sediment samples of the entire core were strongly correlated ($r^2 = 0.78$,

P = 0.0001). This reflects the changes in the carbon isotopic composition of the sediment OM (Fig. 4). The d^{13}C values of sedimentary carbon show a systematic depletion in ^{13}C of c. 3.2‰ up-core (Fig. 4). The most enriched d^{13}C values were recorded in sediment deposited prior to the 1920s (70 cm) with values ranging from -23.9‰ to -22.0‰ (Fig. 4). During this period, the percentage LOI was below 30% (Fig. 4). The period before the 1920s coincided with high littoral:planktonic ratios, which is also reflected in the PCA axis 1 of the cladoceran and diatom assemblages (Fig. 4). Following 1990, the d^{13}C values in the sediment depleted further to -25.6‰, and the LOI declined to values as low as 22.7% (Fig. 4).

d^{13}C values of chironomid head capsules

Values of chironomid head capsules were obtained for the years 1955–2011 at a time resolution of c. 15 years (Fig. 4). The d^{13}C values showed a relatively similar trend to that of d^{13}C values of bulk sediment samples, reflecting their dependency on profundal-sediment carbon sources (Fig. 4). The most enriched d^{13}C value (-24.0‰) of chironomids was recorded between c. 1940 and c. 1955 (Fig. 4). During the period 1955–1970, the head capsule d^{13}C values decreased to -26.0‰ and became enriched

again to -24.8‰ during 1970–1985 (Fig. 2). Between 1985 and 1990, the head capsule d^{13}C values declined to -25.73‰. Measurement of the d^{13}C values of head capsules, during 1990–2000, was not successful; however, there was an enrichment trend (-24, 69‰) in the head capsules between 2000 and 2006 (Fig. 4).

The d^{13}C values of pelagic *Daphnia* and ubiquitous cladocerans

The d^{13}C values of ubiquitous (*Bosmina*, *Alona*) and pelagic (*Daphnia*) cladocerans were obtained from nine sections, with a resolution of about 15 years, covering the period of more than 100 years from 1900 to 2006 (Fig. 4). The d^{13}C values of ubiquitous consumers ranged from -29.4‰ to -24.5‰, while the d^{13}C values of pelagic *Daphnia* ranged from -29.8‰ to -23.2‰ (Fig. 4). The d^{13}C values of ubiquitous and pelagic cladocerans were lower than those of bulk sediment and chironomid head capsules. Such differences between the d^{13}C values of consumers and that of bulk organic matter are rather typical. They are attributed to feeding selectivity or preferential assimilation of algae or fresh material within seston or sediment that are usually ^{13}C depleted as compared to the bulk organic matter (Del Giorgio &
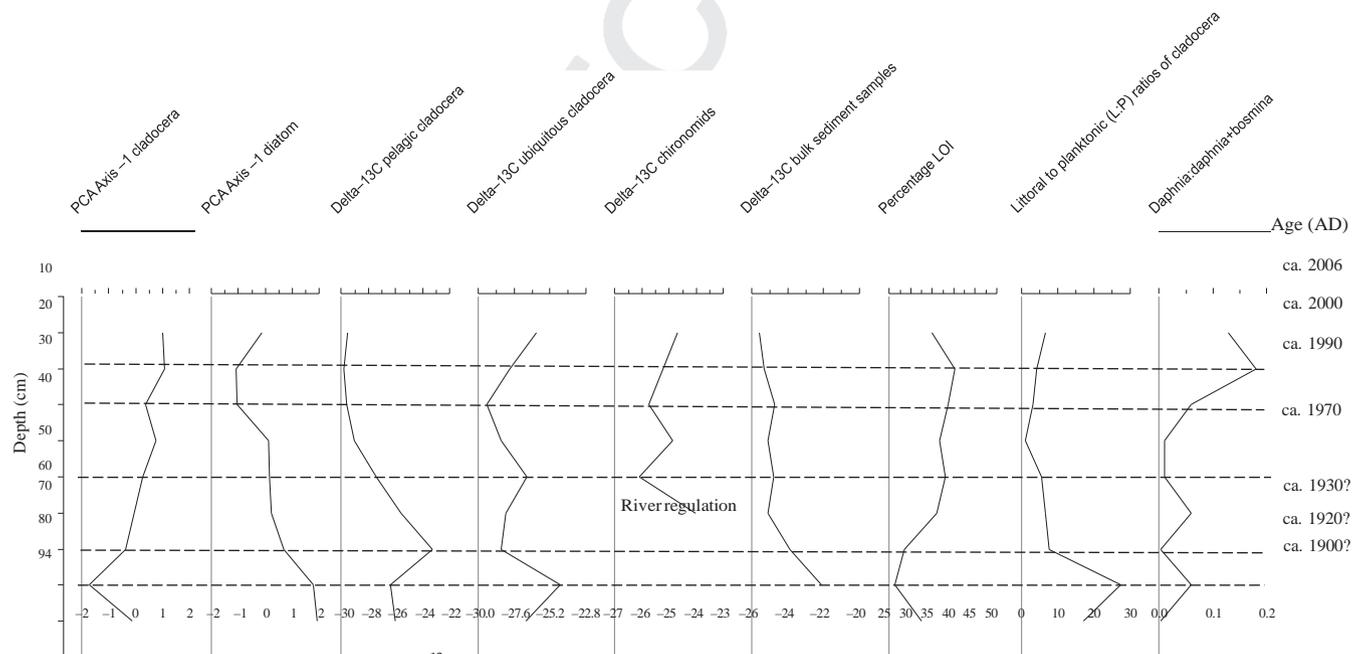

Fig. 4 The stable isotope values of carbon (d^{13}C) in subfossil pelagic *Daphnia*, ubiquitous *Bosmina* and *Alona* sp., and chironomids, and the bulk sediment samples are compared to changes in the PCA axis 1 of the cladoceran and diatom assemblages and the percentage LOI of the sediments samples collected from Kings Billabong. The transition of the ecosystem from pre- to post-human impacts is reflected in the littoral:planktonic ratio of cladocerans during the late 1920s, and changes in predation pressure in the *Daphnia*:*Daphnia*+*Bosmina* ratio in 1990s and 2000s. The stable isotope values for carbon in subfossil cladocerans and chironomids were calculated at 10-cm resolution while, for bulk sediment samples, at 2-cm resolution. Age is based on ^{210}Pb dating.

France, 1996; Grey & Deines, 2005). Depositional and diagenetic processes only slightly affect the carbon isotope composition of cladoceran subfossil remains (changes by <1‰; Perga, 2011) and may not account for observed patterns. However, overall, the $d^{13}C$ of *Daphnia* followed the same trend as bulk sediment $d^{13}C$ and such a common trend mirrored temporal changes of $d^{13}C$ of the autochthonous primary producers. Prior to about 1920 (below 80 cm), Kings Billabong was dominated by littoral-submerged vegetation, as indicated by PCA axes 1 for cladocerans and diatoms and the littoral:planktonic ratios (Fig. 4). Both ubiquitous and pelagic consumers showed relatively enriched $d^{13}C$ values, with differences of about 1–1.5‰ in between them. However, during the time of river regulation in *c.* 1927, and immediately after this period (80–70 cm), the $d^{13}C$ values of pelagic *Daphnia* became as high as -23‰, while the $d^{13}C$ values of ubiquitous cladocerans depleted steadily (Fig. 4). This period was also reflected in PCA axis 1 scores for cladocerans. The strong differences in $d^{13}C$ values between the two cladoceran groups, and for PCA axis 1 scores at the initial transition phase from pre- to post-river regulation, indicate a clear separation in their trophic niche/ micro-habitat preference. By 1970, as the system became more productive, with planktonic flora and fauna being dominant (see Figs. 3 & 4), the $d^{13}C$ values of both ubiquitous and pelagic cladocerans began to converge, showing the uptake of similar carbon sources (Fig. 4). However, by 1990 and subsequently, the $d^{13}C$ values of ubiquitous and pelagic cladocerans diverged. *Daphnia* $d^{13}C$ remained at similar low values, but those of ubiquitous cladocerans increased by more than 3.5‰ and the *Daphnia; Daphnia+Bosmina* ratio increased (Fig. 4). These patterns were opposite to those observed immediately around the time of, and after, river regulation (80 cm) as the $d^{13}C$ values for *Daphnia* were enriched compared with the depleted $d^{13}C$ values of ubiquitous cladocerans (Fig. 4).

Discussion

Our study, based on analyses of sediment accumulation, subfossil data and stable isotopes, revealed a significant transition in the Kings Billabong ecosystem following river regulation. Within the past 50-year time span, the sediment accumulation rates increased. By 2006, the rate was high (*c.* 1 g cm^{-2} year^{-1}) and similar to other billabongs in the region, suggesting widespread disturbances of catchments by humans (e.g. Gell *et al.*, 2009). Previous studies in upstream River Murray billabongs suggest that the period of catchment disturbance, ero-

sion and input of allogenic minerals to lakes coincided with the loss of submerged vegetation (e.g. Reid *et al.*, 2007). Our findings give further evidence of this. Except for a brief peak in planktonic and facultatively planktonic diatoms (possibly due to the 1906 flood), the subfossil assemblages of cladocerans and diatoms, and their littoral to planktonic ratios, clearly indicate that the wetland was densely covered by submerged macrophytes pre- *c.* 1930 AD (below 70 cm) when human disturbance was low. In the absence of river regulation, submerged macrophyte beds are most likely to have played a key role in maintaining a clear-water littoral–benthic dominated system, stabilising sediments, reducing nutrient recycling for phytoplankton and, ultimately, enhancing zooplankton (e.g. *Daphnia*) grazing on phytoplankton, as seen in shallow lakes elsewhere (e.g. Moss, 1990; Scheffer *et al.*, 1993; Jeppesen *et al.*, 1998). However, following human-induced disturbance, including deforestation, agriculture and river regulation (Kingsford, 2000), the littoral and benthic assemblages of subfossil cladocerans (*Dunhevedia crassa*) and diatoms (*Epithemia adnata, Cocconeis placentula*) declined substantially, with a reciprocal increase in ubiquitous cladocerans (*Bosmina meridionalis, Alona guttata, Biapertura longispina*) and facultatively planktonic diatoms, including *Staurosira construens* f. *construens Staurosira construens* f. *venter* (above 75– 70 cm). These opportunistic diatom species are now common in the shallow floodplain lakes of the southeast Australian region (Gell, Sluiter & Fluin, 2002; Gell *et al.*, 2007; Fluin, Tibby & Gell, 2010; Grundell *et al.*, 2012) and reflect turbid conditions and simplified habitat. The changes in littoral–benthic floral and faunal communities suggest a gradual, rather than an abrupt, loss of submerged plants.

The $d^{13}C$ signatures of key primary consumers (chironomids, pelagic *Daphnia* and ubiquitous cladocerans), as well as in sediment organic matter, provide further evidence of a shift in tropic structure in the billabong. It is well established that $d^{13}C$ values at the base of littoral–benthic food webs are usually enriched in ^{13}C (less negative $d^{13}C$) than those at the base of pelagic food webs (Post, 2002), due to differential fractionation of inorganic carbon taken up by primary producers (France, 1995). Local dissolved inorganic carbon (DIC) availability is controlled by a combination of boundary layer thickness and the uptake rate of primary producers relative to the DIC diffusion rate into the boundary layer (Post, 2002). Normally, littoral producers may experience less turbulence and have a thicker boundary layer than pelagic producers (France, 1995); they are therefore more CO_2 limited, fractionate less DIC during

uptake and are enriched in ^{13}C compared to pelagic zone producers. Moreover, and accordingly, percentage LOI, bulk sediment ^{13}C, and ubiquitous cladoceran and chironomid ^{13}C were all enriched immediately after the wetland was inundated in the 1930s (Fig. 4). Temporal changes in phytoplankton with depleted ^{13}C were apparent as suggested by the declining d^{13}C values in *Daphnia* and sediment bulk organic matter (Fig. 4).

Prior to river regulation (1900–1930), there was only a small difference (about 1&) in d^{13}C values between pelagic *Daphnia* and ubiquitous cladocerans, indicating the predominant reliance of both consumer groups on littoral–benthic derived carbon sources, probably reflecting the widespread distribution of submerged macrophytes in the billabongs. However, around the time of river regulation (after 1927 AD), the d^{13}C values in pelagic *Daphnia* became enriched to -23.2 &, while in ubiquitous cladocerans, the d^{13}C values depleted to -28.4& (Fig. 4). This coincided with low littoral:planktonic ratios and high PCA axis 1 sample scores for cladocerans, suggesting expansion of the pelagic habitat (Fig. 4). Although this is based on a single data-point, results suggest that the contribution of littoral-benthic-derived carbon sources to the food web became substantially lower during this period, except for *Daphnia* being 7& more enriched than the ubiquitous cladocerans. Jones & Waldron (2003) suggested that an increased density of predatory fish in shallow U.K. lakes can affect the invertebrate prey communities via two different mechanisms: zooplankton (*Daphnia*) would spend more time among the plants with potential access to periphyton during the day, whilst other invertebrates would take refuge in the benthos during the day by leaving the periphyton. Such a behavioural phenomenon in invertebrate migrations is significant in the context of ^{13}C enrichment. Periphyton can have a substantially thicker boundary layer and a correspondingly reduced supply of CO_2, with possible enriched ^{13}C, than the free floating phytoplankton (Hecky & Hesslein, 1995). In Kings Billabong, the large-bodied cladocerans (*Daphnia*) may have sought refuge in the periphyton-dominated littoral vegetation during the day, due to a high risk of fish predation in the pelagic zone, leading to this ^{13}C enrichment. Such a behavioural shift is also well known from other northern temperate lakes (Lauridsen *et al.*, 1996; Jeppesen *et al.*, 1998).

Since the 1970s until the 1990s, however, the d^{13}C values in both pelagic *Daphnia* and ubiquitous cladocerans depleted substantially and converged, indicating exploitation of the same food, presumably following a further reduction in the littoral area and the loss of refuge areas for *Daphnia*. Increased turbidity also reduces the hunting ability of fish (Vinyard & O'Brien, 1976). Depletion of ^{13}C in pelagic *Daphnia* during 1990–2006, and reciprocal enrichment in ubiquitous cladocerans, indicates some major changes in the feeding patterns of these consumers (*Daphnia* being more pelagic and ubiquitous cladocerans more littoral-benthic) and subsequent changes in trophic pathways at the base of the food web in Kings Billabong in recent decades. Moreover, the *Daphnia*: *Daphnia* + *Bosmina* ratio suggests reduced fish predation (e.g. Jeppesen *et al.*, 2003). Apparently, fish predation became less strong during this period, allowing *Daphnia* to stay more in the pelagic zone and thereby forcing ubiquitous cladocerans to be more littoral-benthic. The prolonged drought during the 2000s in north-west Victoria could have altered the effect of fish predation on *Daphnia* (e.g. Matthews & Matthews, 2003). However, it must be emphasised that that the depletion of ^{13}C in pelagic *Daphnia* at the top of the core is based on only one sample and therefore should be interpreted with caution. A lower water volume due to drought may also have resulted in slightly increased submerged macrophyte abundance, as indicated by the increased density of epiphytic diatoms (*Achnanthidium minutissimum*) in the Billabong (Fig. 2).

Chironomid head capsules gradually became more depleted in ^{13}C at the time of river regulation but were less affected by the regime shift than the cladocerans. This may reflect the fact that the remains of cladocerans in lake sediment are from individuals, feeding in the pelagic or in the littoral zone, having contrasting d^{13}C values, and that the d^{13}C also varies seasonally, while most chironomids feed on a mixture of food in the sediment, showing less seasonality and living longer (Van Hardenbroek *et al.*, 2010). Accordingly, the d^{13}C values in chironomid head capsules followed those of the bulk sediment samples (Fig. 4). Chironomid head capsules were enriched by about 6& compared to pelagic *Daphnia* and were about 4& higher than that of the ubiquitous cladocerans. As for cladocerans, isotopic fractionation between chironomid exuvia and their food sources are small (0–1&) and cannot be responsible for observed isotope differences between the two taxa (Frossard *et al.*, 2013). In the River Murray system, depleted d^{13}C (as low as d^{13}C = -54.7&) values have been measured in riparian leaf litter (Bunn *et al.*, 2003) and d^{13}C values as low as -64& have been measured in chironomids elsewhere (Jones *et al.*, 2008). In deeper lakes in Europe, methane oxidising bacteria in the sediment–water interface have substantially depleted ^{13}C carbon values (Segers, 1998). However, the d^{13}C values of head capsules in Kings Billabong are greatly enriched relative

to those of the riparian leaf litter, more enriched than the algae as judged from the cladoceran $d^{13}C$ data but rather similar to the values of the biota measured prior to river regulation. Apparently the carbon sources for chironomids are still, to some extent, derived from benthic algae and macrophyte debris may have accumulated prior to river regulation or wetland plant remains may have been washed into the billabong. In the Mississippi River system (U.S.A.), the $d^{13}C$ values in decaying aquatic vegetation were found to be higher (-27& to -20&) than those of terrestrial plants (-32& to 22&) in the river (Kendall, Silva & Kelly, 2001).

In conclusion, the integration of palaeoecology and stable isotope analyses of selected subfossils in Kings Billabong has offered a better understanding of ecological succession over temporal scales in a regulated floodplain wetland in south-east Australia. The succession of pelagic-benthic primary producers (e.g. diatoms) and consumers (chironomids and cladocerans) over the past century provides evidence of an ecological transition caused by human-induced disturbance, while the $d^{13}C$ signatures of subfossil consumers reflect the disturbance through the carbon energy flow. The collapse of the benthic-littoral food web following river regulation and the depleted ^{13}C values in pelagic *Daphnia,* reflect a possible shift in trophic pathways and in ecosystem structure.

Our results demonstrate that high-resolution sediment samples show long-term changes in carbon flows in subfossil pelagic and benthic consumers and ecosystem regime shifts. Replication of such studies in other wetlands would be valuable in providing landscape level information about trophic dynamics, regime shifts and wetland resilience in response to varying disturbance regimes, including river regulation, nutrient loading, species invasion and climate change.

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