PRIMARY RESEARCH PAPER

Zooplankton dynamics in response to the transition from drought to flooding in four Murray–Darling Basin rivers affected by differing levels of flow regulation

**Nathan S. P. Ning · Ben Gawne ·
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Abstract Extreme low and high flow periods associated with droughts and floods regularly influence many river systems, yet little is known regarding their role in shaping riverine zooplankton communities. This study investigated zooplankton dynamics in response to the transition from drought to flooding in four southern Murray–Darling Basin rivers managed by different levels of flow regulation. Results indicated that the onset of flooding was associated with an increase in the taxon richness and total transport (abundance) of zooplankton in the unregulated Ovens and Kiewa Rivers, and an increase in the total transport of zooplankton in the mildly regulated Broken River. In comparison, no significant flood effects on zooplankton taxon richness or transport were detected in the highly regulated Murray River. This suggests that the flooding was beneficial for enhancing zooplankton abundance in the Ovens, Kiewa and Broken Rivers, whereas any potential benefits were comparatively short-term and/or reduced in the Murray River. We hypothesise that the relatively short-term and/or reduced response of the zooplankton community to the flooding in the Murray River was probably largely due to the occurrence of a hypoxic blackwater event in suppressing zooplankton emergence.

Keywords Australia · Disturbance · Hydrology · Productivity · Regulated river

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Introduction

It is well accepted that extreme low and high flow periods associated with droughts and floods play an important role in influencing the ecology of river systems (Humphries & Baldwin, 2003; Lytle & Poff, 2004; Suren & Jowett, 2006). Floods are discrete pulse disturbances, which are often thought to be associated with a boom in productivity by aquatic biota (Kingsford, 2000; Lake, 2000; Shiel et al., 2006). In comparison, droughts are ramp disturbances that are typically associated with low flows and contracted aquatic habitat (Lake, 2000, 2011; Bond et al., 2008). The alternation between these hydrological extremes is believed to be a major force shaping the evolutionary adaptations of riverine biota (Lytle & Poff, 2004).

In many rivers, historic cycles of flooding and drought are being dramatically modified through flow regulation, levee construction and other direct human impacts (Lytle & Poff, 2004; Bunn et al., 2006). Some regulated rivers in temperate regions like southern Australia now experience 'anti-drought' conditions—periods that have higher flows than would be expected naturally (McMahon & Finlayson, 2003). Also, in some periods, high natural flows have been switched for periods of lower flows due to flow regulation or water extraction (McMahon & Finlayson, 2003). This has typically led to an overall reduction in natural flow variability, and an associated decline in the ecological integrity of regulated systems (Gehrke & Harris, 2001; Robinson & Uehlinger, 2008).

Despite the importance of flooding and drought cycles for the ecology of riverine biota, along with the impacts of flow regulation and other anthropogenic factors in modifying these cycles, there is currently little empirical data relating to the response of riverine biota to the transition from drought to flood, or vice versa (but see exceptions such as Suren & Jowett, 2006). Most riverine studies undertaken thus far have focused on the impacts of hydrological alterations on biotic groups such as macroinvertebrates (Boulton, 2003; Covich et al., 2003) or fish (Cowx et al., 1984; Bêche et al., 2009). In comparison, very little is known for riverine zooplankton (Shiel et al., 2006), most likely because few riverine microinvertebrate studies have been undertaken for sufficiently long enough periods to identify any changes in response to the transition between drought and flood. Nevertheless, the zooplankton are a ubiquitous and diverse group that play a crucial role in riverine foodwebs by transferring energy from algae, bacteria and fungi to a range of secondary consumers including macroinvertebrates, amphibians, waterbirds and fish (Boulton & Lloyd, 1992; Schmid-Araya & Schmid, 2000; Ning et al., 2010a).

Studies relating to the influence of hydrology on zooplankton indicate that zooplankton abundance is typically positively related to water residence time (Basu & Pick, 1996; Baranyi et al., 2002) and negatively related to current velocity (Saunders & Lewis, 1989; Vranovský, 1995; Ning et al., 2010b). Also, flooding has been shown to be the critical driver for triggering the emergence of floodplain zooplankton communities from dormant egg banks following extensive periods of drought (Boulton & Lloyd, 1992;

Jenkins & Boulton, 2007), and the Flood Pulse Concept predicts that much of this newly emerged animal biomass gets transported back into the main channel upon flood recession (Junk et al., 1989). However, alterations to the frequency and timing of flooding events associated with flow regulation are thought to have reduced the viability and emergence of the floodplain egg bank communities in many river systems such that when floodplain inundation events do occur, the blooms of emerging zooplankton are vastly reduced compared to those occurring under unregulated conditions (Boulton & Lloyd, 1992; Jenkins & Boulton, 2007; Watkins et al., 2011). For example, Watkins et al. (2011) found that hypoxic blackwater conditions caused by the co-occurrence of summer inundation with peak leaf litter fall from river red gum forests (*Eucalyptus camaldulensis* Dehn.) inhibited the emergence of zooplankton from Murray River wetland sediments.

Between 1997 and 2010, south-eastern Australia was subjected to the most persistent drought conditions and associated low flows, since the beginning of the twentieth century (CSIRO, 2011; Lake, 2011). Annual rainfall during this period was 73 mm, or 12.4%, below the twentieth century average for the years 1997–2009 inclusive (CSIRO, 2011). Approximately, two-thirds of the rainfall deficit occurred during autumn each year, with smaller reductions during the other seasons (Chiew et al., 2011; CSIRO, 2011). The drought was broken by a period of above-average rainfall in 2010, which peaked in the summer of 2010–2011 and caused widespread flooding events in the southern Murray–Darling Basin (MDB) (Whitworth et al., 2012).

This study took advantage of long-term data for zooplankton collected from November 2006 to February 2011 to assess zooplankton dynamics in response to the transition from drought to flooding in four southern MDB rivers managed by differing levels of flow regulation. The four rivers included the unregulated Ovens and Kiewa Rivers, the mildly regulated Broken River and the highly regulated Murray River. Both the Broken and Murray Rivers experience augmented summer irrigation flows and reduced overall flow variability (Walker & Thoms, 1993; Cottingham et al., 2001). The specific aim of the study was to investigate changes in the taxon richness, density and mean daily transport (i.e. overall abundance of animals moving downstream each day—

Saunders & Lewis, 1988, 1989) of the zooplankton communities in each river during the transition from drought to flooding.

Materials and methods

Study sites

Ovens River

The Ovens River is a tributary of the Murray River. It rises in the Great Dividing Range in the Alpine National Park and drains into the Murray River at Lake Mulwala (King, 2002). The river's flow regime remains essentially unregulated with only approximately 1.5% of it's annual flow being diverted for irrigation (King, 2002). The study reach was located in the lower section of the river near the township of Peechelba (lat. 36°09′29.90″S, long. 146°14′17.96″E) (Table 1).

Kiewa River

The Kiewa River is also a tributary of the Murray River. It originates in the Great Dividing Range in the Alpine National Park as east and west branches, which unite on the narrow floodplain at Mount Beauty township, and eventually discharges into the Murray River near Albury. There is a small storage reservoir (Rocky Valley storage) located at the upper end of the east branch that releases water for hydroelectric power generation. Short-term alterations to flow in the east branch of the river caused by the storage releases can be large and rapid, with fluctuations of up to 95 Ml h^{-1} occurring up to four times a day (Newall et al., 2006). Nevertheless, the river's overall flow

regime remains essentially unregulated (Schreider et al., 1997; Reid & Ogden, 2009). Peak river flows still occur during August to October and only 7% of annual flow occurs during January to March (Schreider et al., 1997). The reach sampled in this study was located in the lower section of the river near Wodonga (lat. 36°8′18.23″S, long. 146°57′23.15″E) (Table 1).

Broken River

The Broken River is a tributary of the Goulburn River, which itself is a tributary of the Murray River. It rises on the northern-facing slopes of the Great Dividing Range and discharges into the Goulburn River near Shepparton. The river's flow regime is mildly regulated such that summer/autumn flows have been slightly enhanced and winter/spring flows have been slightly reduced (Cottingham et al., 2001). The study reach was located in the lower section of the river near Shepparton (lat. 36°25′29.10″S, long. 145°37′50.58″E) (Table 1).

Murray River

The Murray River is one of Australia's largest rivers with a discharge of approximately 10.5 Gl year^{-1} (Walker, 1985). It starts in the Snowy Mountains, and meanders north-west forming the border between New South Wales and Victoria, before turning south for its final stretch into South Australia and draining into the ocean at Lake Alexandrina. The river's flow regime is highly regulated such that in the reach between Lake Hume and Barmah, peak flows now occur in summer as opposed to late winter/early spring (Walker, 1985). The reach sampled in this study was located in the mid to lower section of the river near the township of Barmah (lat. 35°59′44.58″S, long. 144°55′57.66″E) (Table 1).

Table 1 Geomorphological and hydrological characteristics of each of the four rivers

River	Main channel length (km)	Basin area (km^2)	Mean annual discharge (Ml)	Percentage of annual flows diverted	Flow regulation status
Ovens	150[b]	7,850[a]	1,620,000[a]	1.5[b]	Unregulated[e]
Kiewa	100[h]	2,050[a]	705,000[a]	1.9[f]	Unregulated[e]
Broken	180[i]	7,330[a]	236,000[b]	10[b]	Mildly regulated[b]
Murray	2,560[c]	1,061,469[a]	10,035,000[g]	44[g]	Highly regulated[d]

[a] Crabb (1997); [b] King (2002); [c] Walker (1985); [d] Nielsen et al. (2005); [e] Reid & Ogden (2009); [f] Schreider et al. (1997); [g] Walker & Thoms (1993); [h] Rowe (1972); [i] Ning et al. (2010a)

Study design

Zooplankters were sampled four times at haphazard intervals of 4–5 weeks over the peak growing period (November–February; Geddes, 1984; Ning et al., 2010b) every year between 2006 and 2010 inclusive. Sampling was undertaken in the pelagic zone of the mid-channel of each river by taking eight 5 l grab samples with a 5 l bucket from the mid-to-upper region of the water column, and pooling them to form a 40 l composite sample. Each 40 l composite sample was then filtered through 50 μm mesh and preserved in 70% ethanol.

Zooplankton samples were subsampled prior to processing. Individual subsamples were counted until a minimum of 300 individuals had been identified or 10% of the sample had been processed. All samples were counted in a Sedgewick-Rafter counting chamber and identified using darkfield microscopy. Zooplankters were identified to the level of Family or Genus, with the exception of ostracods which were identified to Class (Shiel, 1995).

Water quality, nutrients and chlorophyll *a*

Water quality and nutrient concentrations were both assessed in association with the zooplankton communities in each river on every trip. Water temperature, dissolved oxygen (DO), turbidity, electrical conductivity (EC) and pH were measured once in each river using a Hydrolab Quanta multiprobe metre (Hach Environmental, Loveland, CO, USA). Total nitrogen and total phosphorus concentrations were assessed in each river by collecting a 150 ml sample of unfiltered water in a pre-rinsed 200 ml PET jar. Their concentrations were then measured using standard methods (American Public Health Association, 1998) in the Murray–Darling Freshwater Research Centre (MDFRC) analytical laboratory (Wodonga, Victoria), which operates to national guidelines of quality control and quality assurance (National Association of Testing Authorities, Australia).

Water column chlorophyll *a* was also assessed as an indicator of algal biomass, and thus, a surrogate for food availability for the zooplankton. Three replicate water samples were collected at each site on each trip using 1 l opaque plastic jars, put on ice and sheltered from light. Chlorophyll *a* analysis was then undertaken back in the MDFRC analytical laboratory using

the 90% boiling ethanol method (International Standards Organisation, 1994).

Hydrology

Mean daily discharge records for the study period were obtained from gauging stations located near the study reach on each river [Murray—Barmah, Broken—Gowangardie Weir, Kiewa—Bandiana, Ovens—Wangaratta (Theiss Engineering)]. The River Analysis Package (Marsh et al., 2003) was used to establish mean, maximum and minimum discharge, coefficient of variation (CV) and the number of continuous periods of rises/falls all for the 7-day period prior to including each sampling date (as per Basu & Pick, 1996). In addition, the mean daily discharge on each sampling date (Q_{sample}) was obtained from the daily discharge records, and water residence time (an estimate of the time the water has been in the river system) was calculated using the equation:

$$R = 0.08A_d^{0.6}/Q^{0.1}$$

where R is the water residence time at the sampling site (*d*), A_d is the the catchment area upstream of the sampling site (km^2), and Q is the mean daily river discharge for the 7-day period prior to and including each sampling date (m^3 s^{-1}) (Søballe & Kimmel, 1987).

Data analysis

Analyses were undertaken on each river separately because of their distinct zooplankton communities (D. Nielsen unpublished data). Count data were converted to densities (animals l^{-1}) and mean daily transport (animals day^{-1}) prior to undertaking any analyses. Density was used to provide an indication of animal abundance per unit volume of habitat with the acknowledgement that it was influenced by dilution effects (Twombly & Lewis, 1987), whilst transport was used to provide an indication of the overall number of animals moving downstream each day with the acknowledgement that it was influenced by river discharge (Saunders & Lewis, 1988, 1989). This widely applied approach of using these two variables provides a more complete indication of changes in zooplankton abundance (e.g. Saunders & Lewis, 1988, 1989; Scherwass et al., 2010).

Variation in zooplankton univariate characteristics were analysed using Permanova + for Primer (Anderson et al., 2008). One-way Permanova, with 'year' (2006 vs. 2007 vs. 2008 vs. 2009 vs. 2010) as a fixed factor, was undertaken to examine inter-year variation in the taxon richness of total zooplankton, rotifer and microcrustacean communities, as well as the density and transport of the total zooplankton, rotifer, cladoceran, copepod and ostracod communities. All analyses were derived from Euclidean distance matrices, and performed on $\log_{10}(x + 1)$ transformed data to reduce the influence of outliers (Anderson et al., 2008). Where significant main effects were detected, pairwise comparisons were undertaken to determine which treatment groups differed.

Inter-year differences in zooplankton community structure were also examined using Non-metric Multidimensional Scaling (NMDS in Primer v6.0 (Clarke & Warwick, 2001)) in conjunction with the same one-way Permanova model used for the univariate analysis. All multivariate zooplankton analyses were derived from Bray-Curtis similarity matrices, and performed on square-root transformed density data. Taxa contributing most to within-year group similarity were assessed using the similarity percentages procedure [SIMPER in Primer v6 (Clarke & Warwick, 2001)] on square-root transformed density data to complement the community structure analysis.

Inter-year variation in environmental conditions (hydrology, water quality, nutrients, chlorophyll a) was examined using Principle Components Analysis [PCA in Primer v6.0 (Clarke & Warwick, 2001)], and one-way Permanova derived from Euclidean distance matrices [Permanova + for Primer (Anderson et al., 2008)]. Zooplankton–environment relationships were also investigated to elucidate which environmental attributes were most strongly related to the zooplankton communities in each river using the distance-based linear models procedure [DISTLM in Permanova + for Primer (Anderson et al., 2008)]. All DISTLM analyses were based on Bray-Curtis similarity matrices and undertaken on square-root transformed zooplankton density data (Anderson et al., 2008). Prior to undertaking any PCA, Permanova or DISTLM analyses, environmental variables were $\log_{10}(x + 1)$ transformed (except pH), normalised and draftsman plots were examined to determine whether any environmental variables were highly correlated (95% or greater, Bob Clarke, Plymouth Marine Laboratory, UK, pers. comm.). The following variables were found to be highly correlated with water residence time and thus, were removed: 7-day mean discharge, 7-day maximum discharge and sampling date discharge (Q_{sample}) in the Murray and Ovens Rivers; and 7-day mean discharge and 7-day maximum discharge in the Broken and Kiewa Rivers.

Results

Environmental conditions

All four rivers experienced relatively low flows during the drought years of 2006, 2007, 2008 and 2009 (Fig. 1). Nevertheless, summer flows in the highly regulated Murray River were somewhat augmented by irrigation releases during these years (Fig. 1). Consequently, flows in the Murray were much less variable than those in the other three rivers at a seasonal scale, even though annual flows were still reduced overall by the drought conditions (Fig. 1).

High flows in 2010 resulted in the main channel and floodplain becoming connected and disconnected on multiple occasions in the Ovens, Kiewa and Broken Rivers (Fig. 1). The high flows also resulted in flooding in the Murray River, although unlike at the other three rivers, the floodplain at the Murray River site, Barmah, was essentially continuously connected to the main channel from September 2010 to February 2011.

For the Ovens River, PCA indicated that 2010 and 2006 both separated from the other years (Fig. 2). 2010 was distinguished by relatively short water residence times, high minimum discharges, high turbidity and relatively high total nitrogen and phosphorus concentrations (Fig. 2). In comparison, 2006 was characterised by relatively long water residence times, warm water temperatures, high pH, EC and chlorophyll a concentrations, and a high number of falls in flow (Fig. 2). Permanova confirmed that environmental conditions differed significantly between 2010 and all other years (except 2007 and 2009) (2010–2008 and 2010–2006 both $P < 0.05$), and between 2006 and all other years (2006–2010 $P < 0.05$; 2006–2009 $P < 0.05$; 2006–2008 $P < 0.01$; 2006–2007 $P < 0.01$) (Table 2).

For the Kiewa River, 2010 separated from the other years because it was distinguished by relatively short water residence times, high sampling date and minimum discharges, high turbidity and relatively high total nitrogen and phosphorus concentrations (Fig. 2).
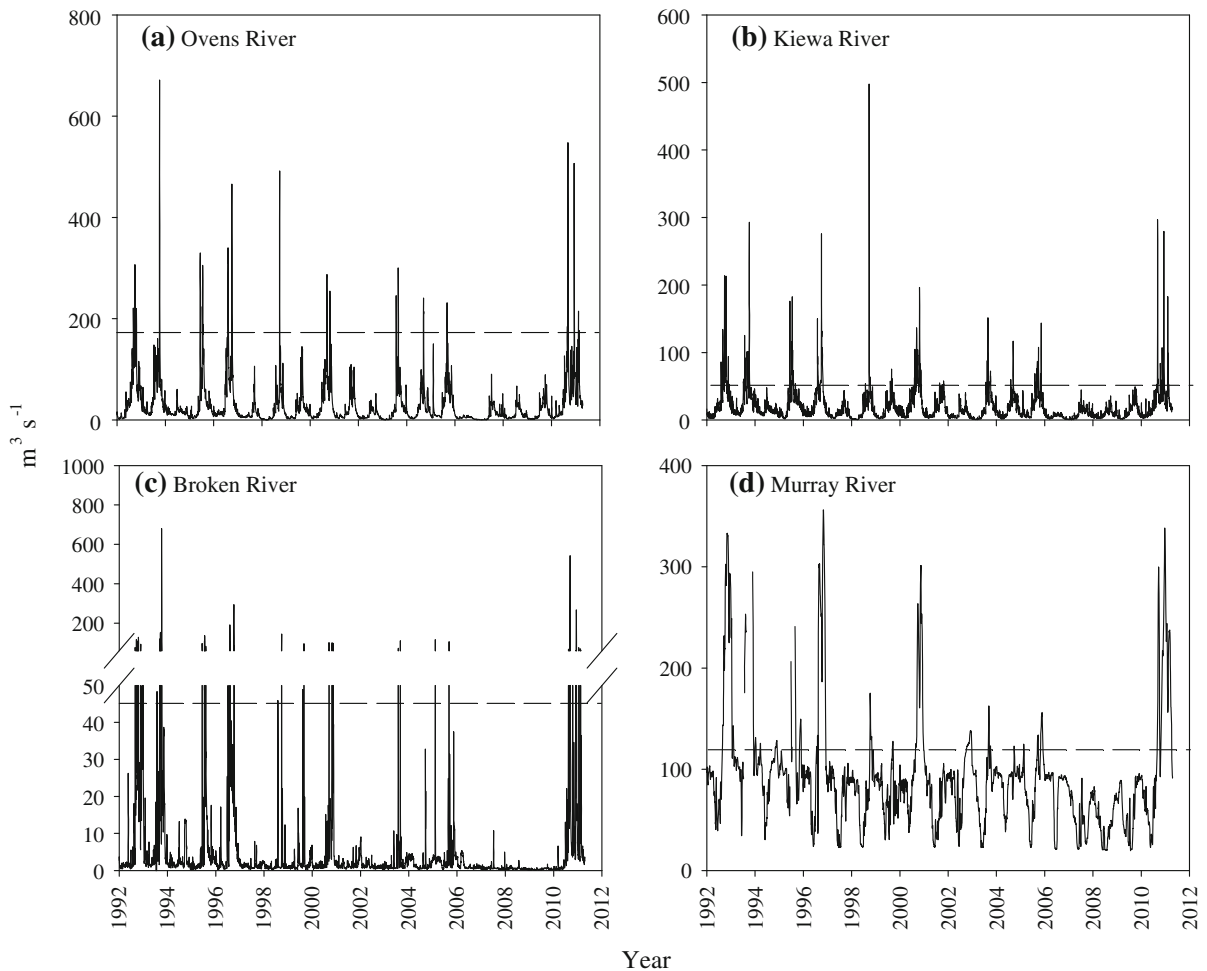
Fig. 1 Discharge patterns in each river. *Dotted lines* indicate approximate thresholds of floodplain inundation for the reach examined in each respective river (Murray River— 10,200 Ml day^{-1}—K. Ward pers. com.; Broken River— 4,000 Ml day^{-1}—G. Vietz pers. com.; Ovens River— 15,000 Ml day^{-1}—T. Hillman pers. com.; Kiewa River— 3,800 Ml day^{-1}—Bureau of Meteorology minor flood level)

Permanova confirmed that environmental conditions during 2010 differed significantly from those during 2008 and 2006 (2010–2008 and 2010–2006 both $P < 0.05$) (Table 2).

For the mildly regulated Broken River, PCA indicated that 2010 separated from the other years because it was distinguished by relatively short water residence times, high sampling date and minimum discharges, and high variability in discharge (Fig. 2). Permanova confirmed that environmental conditions varied significantly between 2010 and all other years (2010–2009 $P < 0.05$; 2010–2008 $P < 0.01$; 2010–2007 $P < 0.05$; 2010–2006 $P < 0.05$) (Table 2).

For the highly regulated Murray River, 2010 separated from the other years because it was

distinguished by relatively short water residence times, relatively high total nitrogen and phosphorus concentrations, high chlorophyll *a*, and low DO concentrations (Fig. 2). Permanova confirmed that environmental conditions varied significantly between 2010 and all other years (2010–2009 $P < 0.01$; 2010–2008 $P < 0.01$; 2010–2007 $P < 0.05$; 2010–2006 $P < 0.05$) (Table 2).

Correlations between the zooplankton and environmental conditions

Variation in zooplankton community structure in the Ovens River was best explained by EC ($r^2 = 0.22$; $P = 0.001$), chlorophyll *a* concentration ($r^2 = 0.19$;
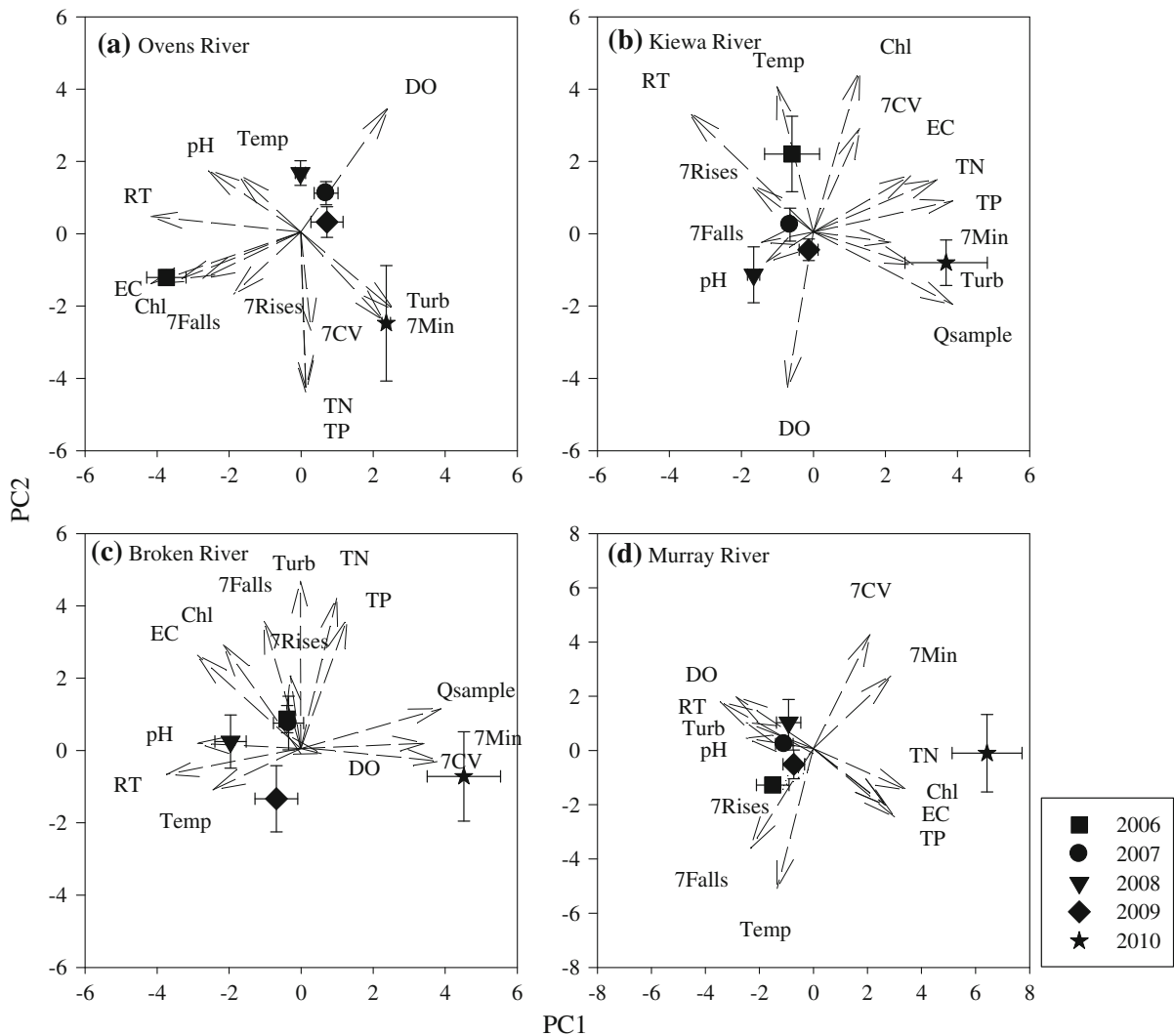
Fig. 2 PCA of environmental conditions in each of the four rivers between 2006 and 2010 (error bars represent 1 SE of the PC1 and PC2 means of the centroid). *Note* 2006, 2007, 2008 and 2009 were drought years, whilst 2010 was characterised by high flows and flooding. *Temp* water temperature, *DO* dissolved oxygen, *Turb* turbidity, *EC* electrical conductivity, *TN* total nitrogen, *TP* total phosphorus, *Chl* chlorophyll-*a*, *Qsample* mean daily discharge on each sampling date, *RT* water residence time, *7Min* minimum discharge, *7CV* coefficient of variation, *7Rises* number of rises, *7Falls* number of falls all for the 7-day period prior to and including each sampling date)

$P = 0.004$) and water residence time ($r^2 = 0.15$; $P = 0.014$) (Table 3).

Zooplankton community structure in the Kiewa River was best related to sampling date discharge ($r^2 = 0.14$; $P = 0.010$), followed by water residence time ($r^2 = 0.13$; $P = 0.010$); although these two explanatory variables were negatively correlated (Pearson correlation $= -0.92$) (Table 3).

Variation in zooplankton community structure in the Broken River was best explained by DO, total nitrogen and total phosphorus concentrations, although none of these variables were significant (all $P > 0.05$) (Table 3).

Zooplankton community structure in the Murray River was best explained by DO ($r^2 = 0.34$; $P = 0.001$), closely followed by total phosphorus

Table 2 Pseudo-*F* ratios and significance levels for Permanova investigating inter-year variation in environmental and biotic response variables for each river

Analysis subject	Variable type	Response variable	Pseudo-*F* ratio			
			Ovens	Kiewa	Broken	Murray
Environmental variables	Multivariate	Environmental conditions	3.943**	2.596**	3.376**	4.630**
Total zooplankton	Univariate	Richness	10.801**	7.700**	1.684	1.638
Rotifera	Univariate	Richness	21.344**	6.518**	1.090	2.466
Microcrustacea	Univariate	Richness	2.107	0.906	2.318	0.510
Total zooplankton	Univariate	Density	7.822**	5.719**	0.688	3.391
Rotifera	Univariate	Density	7.427**	4.346*	0.716	3.663*
Cladocera	Univariate	Density	42.250**	0.506	4.249*	1.129
Copepoda	Univariate	Density	25.536**	7.693**	0.735	0.645
Ostracoda	Univariate	Density	1.145	0.575	1.122	0.843
Total zooplankton	Univariate	Transport	7.299**	8.972**	5.657**	1.085
Rotifera	Univariate	Transport	7.660**	8.054**	5.415*	1.097
Cladocera	Univariate	Transport	0.816	0.53	1.186	0.335
Copepoda	Univariate	Transport	6.275**	8.690**	8.488**	0.997
Ostracoda	Univariate	Transport	0.935	0.558	2.882	0.843
Total zooplankton	Multivariate	Community structure	2.556**	1.959**	1.444*	1.973**

* *P* < 0.05; ** *P* < 0.01

Table 3 Percentage of variation in zooplankton community structure (square-root transformed density data) explained by environmental variables assessed in each river

Variable	Ovens		Kiewa		Broken		Murray	
	Variation	*P*	Variation	*P*	Variation	*P*	Variation	*P*
pH	9.43	0.154	7.06	0.276	4.22	0.720	**15.44**	**0.045**
EC	**21.61**	**0.001**	6.49	0.348	3.08	0.925	**23.48**	**0.006**
Turb	5.85	0.552	10.06	0.059	5.71	0.408	**27.99**	**0.008**
DO	**13.64**	**0.038**	3.49	0.770	9.16	0.055	**33.85**	**0.001**
Temp	6.36	0.459	6.34	0.374	3.57	0.855	6.13	0.523
TN	**14.84**	**0.010**	9.97	0.064	7.41	0.151	**25.21**	**0.006**
TP	10.18	0.122	9.77	0.064	7.40	0.153	**31.98**	**0.001**
Chl	**19.28**	**0.004**	5.17	0.540	5.95	0.365	**18.12**	**0.022**
Qsample	–	–	**13.55**	**0.010**	5.20	0.502	–	–
7CV	5.44	0.619	4.47	0.640	5.84	0.369	7.33	0.378
7Min	5.22	0.655	4.42	0.648	6.09	0.313	13.68	0.067
7Falls	12.44	0.050	10.05	0.058	3.07	0.938	**14.72**	**0.040**
7Rises	7.90	0.285	5.34	0.506	4.56	0.679	10.68	0.133
RT	**15.05**	**0.014**	**12.77**	**0.013**	5.60	0.401	**30.94**	**0.001**

Significant environmental variables (*P* < 0.05) are in bold. Qsample was excluded for the Ovens and Murray Rivers because it was highly (≥95%) correlated with other variables. See Fig. 2 caption for an explanation of environmental variable codes

$(r^2 = 0.32; P = 0.001)$ and water residence time $(r^2 = 0.31; P = 0.001)$ (Table 3).

Zooplankton results

Taxon richness, density and transport

In the unregulated Ovens and Kiewa Rivers, total zooplankton and rotifer richness, and total zooplankton, rotifer and copepod transport were all significantly greater in 2010 than in the preceding years (except for total and rotifer transport in the Ovens River in 2007) (Table 2; Figs. 3, 5). Likewise, total zooplankton, rotifer and copepod density in the Kiewa River were all significantly greater in 2010 compared with all other years (except for total density in 2007, and rotifer density in 2006 and 2007) (Table 2; Fig. 4). By contrast, total zooplankton, rotifer, cladoceran and copepod density in the Ovens River were

all significantly greater in 2006 than in any other year (Table 2; Fig. 4).

In the mildly regulated Broken River, total zooplankton, rotifer and copepod transport were all significantly greater in 2010 than in the previous years (except for total and rotifer transport in 2007); however, their densities did not vary significantly amongst peak growing periods (except for cladoceran density) (Table 2; Figs. 4, 5). Also, the mean taxon richness of total zooplankton, rotifer and microcrustacean communities did not vary significantly amongst years (Table 2; Fig. 3), although overall taxon richness was greatest in 2010 (2010: 36 taxa; 2009: 30 taxa; 2008: 34 taxa; 2007: 31 taxa; 2006: 28 taxa).

For the highly regulated Murray River, neither total, rotifer nor microcrustacean richness varied significantly amongst years (Table 2; Fig. 3). Copepod transport was greatest in 2010 coinciding with the flooding, whilst rotifer density was greatest in 2007
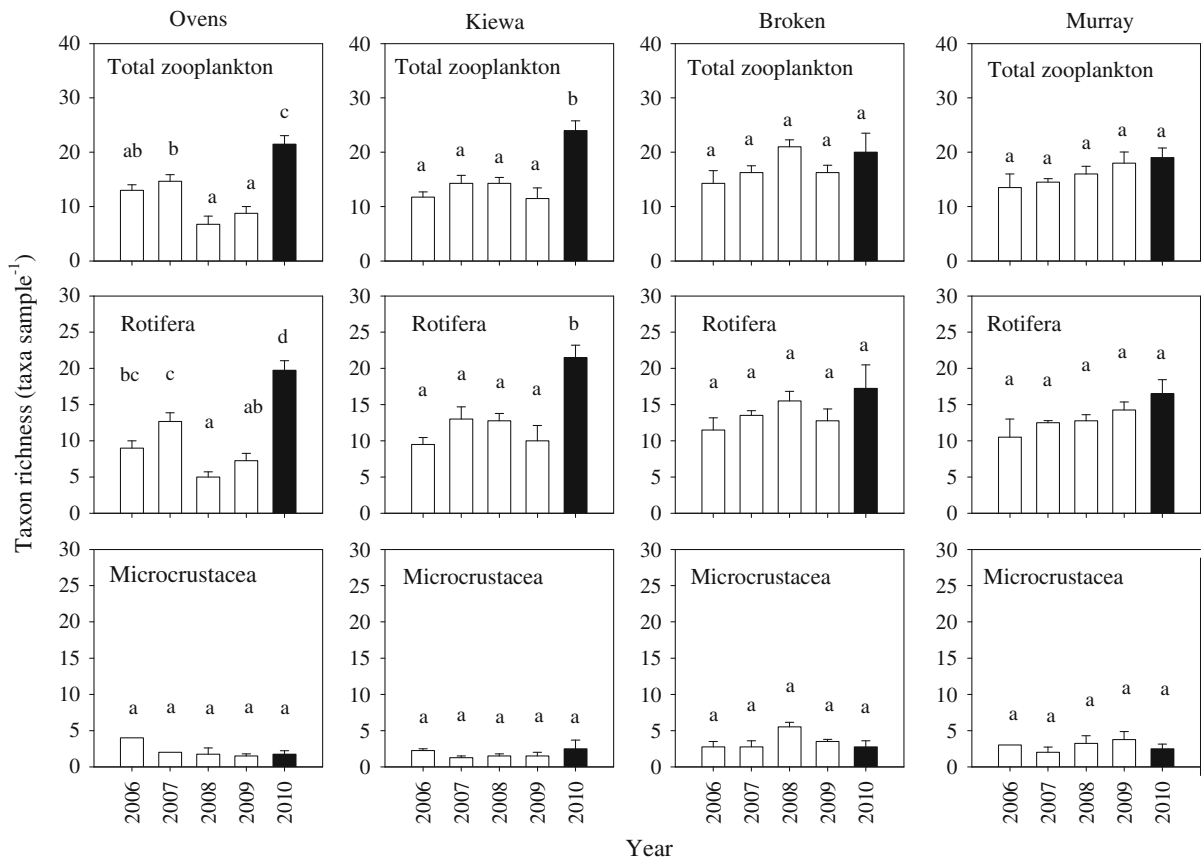

Fig. 3 Mean (+1 SE) taxon richness in each river between 2006 and 2010. *Note* 2006, 2007, 2008 and 2009 (the *white bars*) were drought years, whilst 2010 (the *black bar*) was

characterised by high flows and flooding. There was no significant difference ($P > 0.05$) amongst years sharing the *same letter*
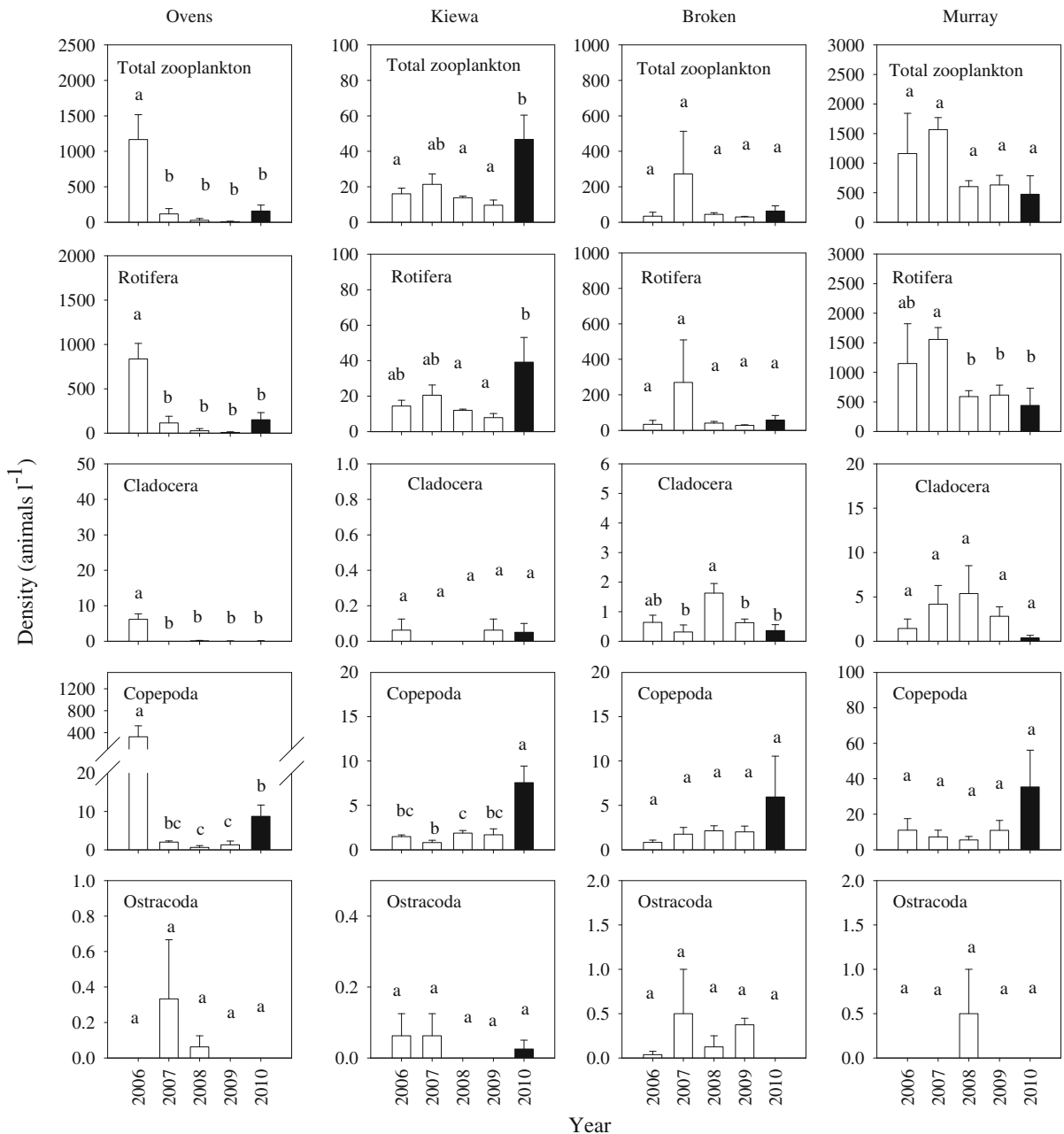
Fig. 4 Mean (+1 SE) zooplankton density in each river between 2006 and 2010. *Note* 2006, 2007, 2008 and 2009 (the *white bars*) were drought years, whilst 2010 (the *black bar*) was characterised by high flows and flooding. There was no significant difference ($P > 0.05$) amongst years sharing the *same letter*

(Figs. 4, 5). However, Permanova indicated that, of the two variables, only rotifer density varied significantly according to year, and that it was significantly greater in 2007 than in all other years except for 2006 (Table 2; Fig. 4).

Community structure

In the Kiewa River, community structure differed significantly between 2010 and all previous years (except 2006 and 2008) (all pairwise comparisons
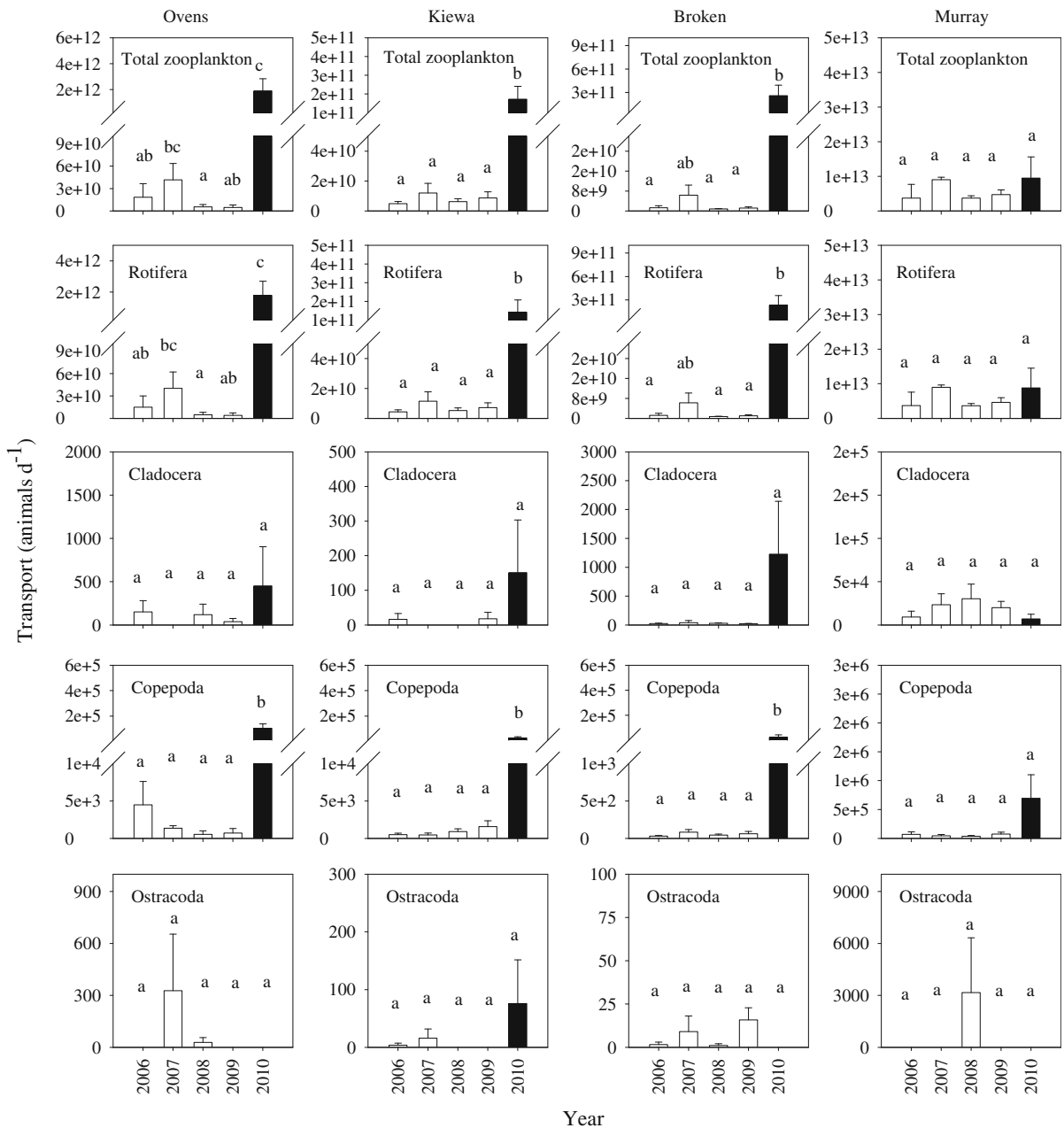
Fig. 5 Mean (+1 SE) zooplankton transport in each river between 2006 and 2010. *Note* 2006, 2007, 2008 and 2009 (the *white bars*) were drought years, whilst 2010 (the *black bar*) was characterised by high flows and flooding. There was no significant difference ($P > 0.05$) amongst years sharing the *same letter*

$P < 0.05$) (Table 2; Fig. 6). SIMPER indicated that the 2010 community was characterised by relatively high densities of copepod nauplii and the rotifer, *Keratella* (Table 4).

By contrast, in the Ovens River, community structure differed significantly between 2006 and the

other years except 2010 (all pairwise comparisons $P < 0.05$) (Table 2; Fig. 6), as well as between 2010 and 2008. SIMPER indicated that both 2006 and 2010 were characterised by the occurrence of *Keratella*, *Polyarthra* and copepod nauplii, but in differing proportions (Table 4).

Fig. 6 Two-dimensional NMDS solutions for the mean density of all zooplankton taxa in the four rivers (error bars represent 1 SE of the *x* and *y* means of the centroid). *Note* 2006, 2007, 2008 and 2009 were drought years, whilst 2010 was characterised by high flows and flooding
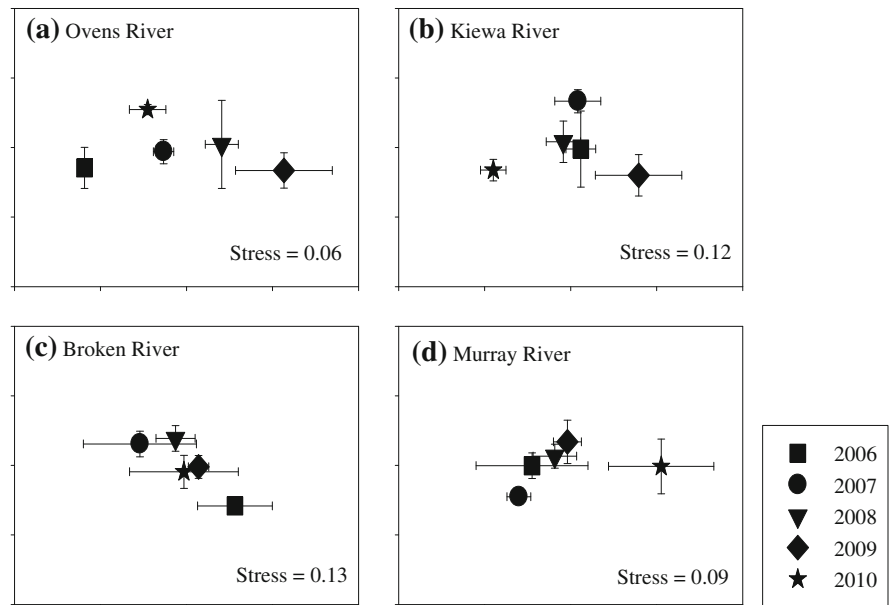
Temporal differences in community structure were less apparent in the mildly regulated Broken River and highly regulated Murray River (Fig. 6). In the Broken River, there were no significant differences in community structure amongst peak growing periods (Table 2; Fig. 6), although SIMPER indicated that within-group similarity was greater in 2009 than in 2007 (Table 4). In the Murray River, community structure differed significantly between 2007 and 2009 ($P < 0.05$) (Table 2; Fig. 6). SIMPER indicated that the 2007 community was mainly characterised by the rotifer, *Filinia*; whereas the 2009 community was mainly characterised by the rotifer, *Trichocerca* (Table 4).

Discussion

The 2010–2011 drought-breaking flooding significantly increased both the taxon richness and total transport (abundance) of zooplankters in the unregulated Ovens and Kiewa Rivers, as well as the total transport of zooplankters in the mildly regulated Broken River. In comparison, no significant flood effects on zooplankton taxon richness or transport were detected in the highly regulated Murray River during this study. This suggests that the flooding was beneficial for enhancing overall zooplankton abundance in the Ovens, Kiewa and Broken Rivers, whereas any potential benefits were comparatively short-term and/or reduced in the Murray River. We hypothesise that the relatively short-term and/or reduced response of the zooplankton community to the 2010 flooding in the Murray River was probably largely due to the occurrence of a hypoxic blackwater event in suppressing zooplankton emergence.

Environmental conditions

All four rivers experienced relatively low flows during the drought years of 2006, 2007, 2008 and 2009. Nevertheless, summer flows in the highly regulated Murray River were somewhat augmented by irrigation releases and thus never became extremely low like in the other three rivers. High rainfall and resultant runoff during spring 2010 and summer 2010–2011 resulted in widespread flooding events occurring across the southern MDB and mean water residence times were particularly low during the 2010 peak growing period [November–February (Geddes, 1984; Swan & Palmer, 2000; Ning et al., 2010b)]. PCA and Permanova both confirmed that the environmental conditions during the 2010 peak growing period clearly differed from those during the rest of the study period for all four rivers, largely due to the particularly

Table 4 SIMPER analysis (square-root transformed density data) showing the three main taxa contributing to within-year similarity in zooplankton communities for each river (density values are untransformed)

River	Ave. sim.	Taxon	Density	Contrib%
Density-based community structure			
Ovens				
2006		*Polyarthra*	408.44	33.23
	53.18	Nauplii	226.50	19.9
		Keratella	126.79	15.88
2007		*Trichocerca*	61.47	25.58
	57.59	*Keratella*	2.72	10.27
		Brachionus	2.89	10.2
2008		Bdelloid	0.86	49.32
	23.83	*Trichocerca*	8.70	24.89
		Nauplii	0.31	12.45
2009		*Trichocerca*	2.62	29.85
	18.05	Bdelloid	0.29	23.46
		Nauplii	0.58	20.67
2010		*Keratella*	18.32	14.35
	46.27	Nauplii	7.84	12.75
		Polyarthra	24.60	10.78
Broken				
2006		*Trichocerca*	2.28	17.78
	47.61	*Cephalodella*	1.90	13.29
		Keratella	1.17	12.85
2007		*Trichocerca*	63.20	17.59
	42.59	*Cephalodella*	3.20	13.23
		Lecane	2.82	12.58
2008		*Trichocerca*	7.78	15.23
	56.34	*Keratella*	5.57	11.26
		Polyarthra	3.69	10.18
2009		*Trichocerca*	10.63	26.7
	64.15	*Keratella*	4.67	13.2
		Nauplii	1.77	9.12
2010		*Keratella*	9.99	18.82
	44.66	*Polyarthra*	6.60	9.9
		Trichocerca	2.56	8.35
Kiewa				
2006		Nauplii	1.12	16.65
	46.44	*Trichocerca*	2.66	14.2
		Keratella	1.00	13
2007		Bdelloid	6.15	28
	61.12	*Lecane*	4.24	16.78
		Cephalodella	1.25	11.5
2008		Bdelloid	1.82	16.21
	58.17	Nauplii	1.72	15.87

Table 4 continued

River	Ave. sim.	Taxon	Density	Contrib%
Density-based community structure			
		Lecane	1.66	13.61
2009		Bdelloid	1.25	19.01
	45.42	*Keratella*	0.94	16.77
		Trichocerca	1.02	16.33
2010		Nauplii	6.81	13.03
	62.52	*Keratella*	4.24	8.65
		Bdelloid	1.90	7.65
Murray				
2006		*Filinia*	177.69	27.47
	54.75	*Polyarthra*	269.62	23.63
		Keratella	89.68	18.65
2007		*Filinia*	500.42	23.39
	74.55	*Polyarthra*	373.26	20.71
		Trichocerca	242.11	15.56
2008		*Polyarthra*	123.65	20.53
	63.22	*Trichocerca*	157.50	19.88
		Filinia	97.61	16.4
2009		*Trichocerca*	225.90	22.6
	60.3	*Polyarthra*	79.03	17.79
		Keratella	64.00	14.22
2010		*Polyarthra*	34.46	11.7
	46.72	Bdelloid	19.18	10.56
		Brachionus	27.46	10.48

Note 2006, 2007, 2008 and 2009 were drought years, whilst 2010 was characterised by high flows and flooding

high flows and short water residence times occurring during that period.

Dissolved oxygen concentrations became markedly suppressed (<4 mg l⁻¹) in the Murray River during summer 2010–2011 due to the occurrence of a hypoxic blackwater event (Whitworth et al., 2012). According to Whitworth et al. (2012), the blackwater event in this region of the MDB was invariably related to the inundation of forested floodplains. The dominant tree species on lowland river floodplains of the MDB, the river red gum (*E. camaldulensis* Dehn.), provides the main source of dissolved organic carbon (DOC) to the water column (Hladyz et al., 2011) and has its maximum leaf fall in summer (Watkins et al. 2011; Whitworth et al., 2012). Consequently, summer inundation of the floodplain is most likely to result in high concentrations of DOC (Whitworth et al., 2012). Higher net litter accumulation may also occur as a

consequence of less frequent inundation in response to flow regulation, higher tree productivity, drought and tree stress (Whitworth et al., 2012). The Murray River site sampled in this study, the Barmah-Millewa Forest, had not experienced floodplain inundation for an extended period of time prior to 2010 and presumably had particularly high leaf litter accumulation on its floodplain. Furthermore, the 2010 high flows resulted in the Barmah floodplain being nearly continuously connected to the main channel from September 2010 to February 2011. In comparison, the 2010 high flows resulted in the main channel and floodplain of the other three rivers being connected and disconnected on multiple occasions, thus providing more of a physical flushing effect on floodplain material back into the main channel.

Environmental variables related to temporal zooplankton dynamics in each river

Hydrological conditions have been identified as being central to influencing zooplankton population and community dynamics in many rivers (Swan & Palmer, 2000; Lair, 2006). Sufficient hydrological retention, in particular, is thought to be fundamental to sustaining zooplankton production in the main channel (Reckendorfer et al., 1999; Nielsen et al., 2005; Ning et al., 2010b), since high current velocities (or short water residence times) constrain the distribution and abundance of riverine zooplankters by dispersing them into inhospitable environments (Swan & Palmer, 2000), reducing their fecundity or fitness, and/or affecting their food supply or feeding (Casper & Thorp, 2007). The results for the Ovens, Kiewa and Murray Rivers support this view and indicate that zooplankton community structure in these rivers was significantly related to water residence time. Zooplankton community structure in the Broken River, on the other hand, was not significantly related to any of the environmental variables assessed during this study, suggesting these specific variables were not directly important, or that our sampling regime was not sensitive enough to detect any relationships.

Zooplankton dynamics during the drought years

Whilst there was no pre-drought data in this study to allow for the elucidation of any potential drought effects, it was evident that zooplankton density was

significantly greatest during the drought year of 2006 in the Ovens River, coinciding with the river's lowest period of discharge during the study. Closer examination of the data, indicated that the 2006 peak growing period was characterised by particularly long water residence times, warm water temperatures and high chlorophyll a concentrations, suggesting that the mid-channel of the lower Ovens River was essentially functioning more like a large slackwater during this period (Reckendorfer et al., 1999; Nielsen et al., 2005; Ning et al., 2010b). The importance of main channel slackwater habitats for supporting relatively high densities of zooplankton is well known and is thought to be largely due to their protection from hydrodynamic forces and their relatively long water residence times, warm temperatures and high food availability (Reckendorfer et al., 1999; Ning et al., 2010b). Such habitats are typically located on the periphery of the main channel, where they are away from, but still exchange material with the bulk flow (Lancaster & Hildrew, 1993). This study suggests that extreme drought conditions can transform much of the mid-channel region of the lower Ovens River from flowing into slackwater habitat and thus potentially support high densities of zooplankton in areas where flow would typically inhibit such densities from occurring (Nielsen & Watson, 2008). No such response patterns were observed during the drought in the other three rivers, although these rivers did not experience the same level of flow reduction as the unregulated Ovens River.

Zooplankton dynamics in response to the 2010–2011 floods

Flooding during the 2010 peak growing period enhanced the total transport (abundance) and taxon richness of zooplankton communities in both the unregulated Kiewa and Ovens Rivers. Zooplankton community structure was also altered in 2010 in the Kiewa River, and density was enhanced, suggesting that the increase in abundance exceeded any dilution effects from the floodwaters in this river. High transport at high discharges would not occur if densities were affected by dilution alone (Saunders & Lewis, 1988). The relationship between transport and discharge in these rivers instead shows that overall zooplankton abundance was being enhanced by flooding (as per Saunders & Lewis, 1988). Saunders & Lewis (1988) similarly noted a rise in zooplankton

transport in the Apure River (Venezuela) during periods of floodplain inundation, and argued that the rise was due to animals being exported from the floodplain. Likewise, Shiel et al. (2006) reported that zooplankton diversity was positively associated with flood size in arid zone rivers of the Lake Eyre Basin, Australia. According to the Flood Pulse Concept (Junk et al., 1989), most of a river's productivity originates either directly or indirectly from production within the floodplain and not from downstream transport as suggested by the River Continuum Concept (Vannote, 1980). In this study, the increase in total zooplankton transport and richness in the Kiewa and Ovens Rivers in 2010 was probably due to the combined influence of multiple flooding events in transporting both existing and newly emerged zooplankters from upstream sources and the adjacent floodplain (Saunders & Lewis, 1988; Junk et al., 1989; Boulton & Lloyd, 1992). Instream zooplankton production may have also been stimulated from nutrients and organic matter being transported from the floodplain back into the main channel (Junk et al., 1989; Poff et al., 1997), since there was evidence of total nitrogen and phosphorus concentrations being relatively high during the flooding period in both the Kiewa and Ovens Rivers.

The 2010 flooding also enhanced the overall abundance of animals (i.e. transport) in the mildly regulated Broken River, similarly to the response in the unregulated Ovens and Kiewa Rivers. However, no significant differences in mean density, taxon richness or community structure were detected, although overall taxon richness was greatest in 2010. The lack of concurrence between the abundance and density results suggest that the overall increase in abundance was masked by dilution in this river (Saunders & Lewis, 1988; Tan & Shiel, 1993). Tan & Shiel (1993) similarly argued that rapid population increases in the rotifer communities of a floodplain wetland were masked by a fourfold dilution from intrusion of river water, whilst Saunders & Lewis (1988) observed a strongly inverse relationship between zooplankton abundance and discharge in the Apure River (Venezuela) and suggested that this was simply reflective of a dilution effect.

The changes associated with the transition from drought to flood were much less obvious for the zooplankton community in the highly regulated Murray River. Flooding in 2010 appeared to slightly enhance microcrustacean transport and alter the structure of the zooplankton community, although these patterns were not statistically significant due to high variability. Furthermore, no statistically significant flood effects on total richness or density were detected. The absence of any detectable response to the 2010 flooding suggests that any potential flood-derived benefits were comparatively short-term and/or reduced in the highly regulated Murray River, probably largely as a consequence of the hypoxic blackwater event suppressing zooplankton emergence (Watkins et al., 2011). Hypoxic conditions have been shown to suppress emergence and/or cause strong reductions in the life expectancy of zooplankton (Invidia et al., 2004; Watkins et al., 2011). Watkins et al. (2011), for example, observed a reduction in the emergence of zooplankton from Murray River wetland sediments in response to hypoxic blackwater conditions caused by the co-occurrence of summer inundation with peak leaf litter fall from river red gum forests (*E. camaldulensis* Dehn.). The hypoxic conditions in this study occurred throughout the 2010 peak growing period from November 2010 until March 2011 (Whitworth et al., 2012) and multivariate multiple regression indicated that variation in zooplankton community structure was best explained by DO concentrations.

Another possible factor contributing to the absence of any detectable effects from the 2010 summer flooding in the Murray River is that that the influence of the flooding was moderated by the artificial augmentation of the river's flows during the summer months of the preceding drought years (McMahon & Finlayson, 2003; Bond et al., 2008). Large irrigation releases would have ensured that the Murray maintained 'anti-drought' conditions whilst the mildly regulated Broken and unregulated Kiewa and Ovens River's all experienced comparatively reduced discharge and contracted aquatic habitat. The length and severity of low flow periods associated with the drought would have been further reduced by the high stream order and associated large catchment area of the Murray River (McMahon & Finlayson, 2003).

Conclusions

Flood and drought events are important factors influencing biotic communities in many river systems, although the influence of these events is highly dependent upon the character of the system (e.g.

forested vs. non-forested floodplain) in association with the direct and indirect effects of any anthropogenic flow modifications (e.g. reduced inundation frequency increasing the potential for hypoxic blackwater events). The results from this study suggest that the 2010 drought-breaking flooding was beneficial for augmenting overall zooplankton abundance in the unregulated Ovens and Kiewa Rivers, and in the mildly regulated Broken River. In comparison, any potential benefits were comparatively short-term and/or reduced in the highly regulated Murray River, most likely due to the occurrence of hypoxic blackwater conditions in that river system.

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