



Flow event size influences carbon, nutrient and zooplankton dynamics in a highly regulated lowland river

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Abstract River regulation and water extraction has significantly altered flow regimes and reduced flood events in many inland river systems. Environmental flows have been adopted in many systems to mitigate the ecological impacts of river regulation, however a lack of knowledge regarding the interrelationship between flow regimes, carbon transport and instream

productivity make prioritising water management difficult. To address this knowledge gap, we conducted a study on the Namoi River in the Murray-Darling Basin, Australia, monitoring changes in dissolved organic carbon (DOC), nutrient dynamics and planktonic food web structure during a period of variable flows. Nutrient and DOC concentrations were positively correlated with river discharge and zooplankton concentrations were highest post flow events. Planktonic chlorophyll-*a*, increased DOC concentration and higher discharge were the most influential drivers of change in zooplankton communities. Further, our results indicated that flow events increased production through both heterotrophic and autotrophic pathways, significantly boosting zooplankton concentration compared to base flow conditions across all measured flow events. We suggest even small in-channel flow events can be important for increasing basal and zooplankton production in rivers, and therefore should be protected or promoted by environmental flow management, particularly during drought conditions.

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Introduction

The flow regime is an important controlling factor for the health and productivity of river ecosystems (Bunn & Arthington, 2002; Poff & Zimmerman,

2010). The flow regimes in Australian semi-arid and lowland river systems are some of the most variable in the world with huge differences between minimum and maximum flow sizes and interannual average discharge (Puckridge, 1998). Understanding how riverine food webs respond to the changes in basal resources that occur during different flows conditions is crucial for understanding ecosystem function in lowland rivers (Humphries et al., 2014). The extreme variability of flows in Australian dryland rivers leads to “boom and bust” conditions for riverine food webs. “Boom” periods of high flow result in high resource availability and significantly increased food web productivity whereas “bust” periods are characterised by resource limitation and habitat disconnection during low flow or cease to flow conditions (Bunn & Arthington, 2002).

Flow events are important for the productivity of lowland river food webs (Junk et al. 1989; Poff & Zimmerman, 2010). High flow events, such as floods, are large-scale disturbances that often resulting in overbank flows, creating connectivity between the riverine environment and the surrounding floodplain (MDBA, 2018). These increases in connectivity can lead to the mobilisation of allochthonous organic matter and nutrients such as nitrogen and phosphorus from the surrounding terrestrial environment to the aquatic ecosystem (Westhorpe and Mitrovic, 2012). Medium size flow events, sometimes referred to as “freshes”, are increases in river discharge and river height that remain in-channel. These events may also lead to increases in organic carbon and nutrient concentrations via inundation of in-channel banks and benches but often at lower total loads than during high flow events (Hitchcock & Mitrovic 2015a; Woodward et al., 2015).

The alternating dynamics between floodplain-derived organic matter during high flow events and phytoplankton production during low flow can lead to distinctly different groups of producers at the base of the food web and shift rivers from being net autotrophic to net heterotrophic (Gawne et al., 2007; Humphries et al., 2014; Carney et al., 2016). During flow events, bacterial production may dominate the basal food web, using dissolved organic carbon (DOC) transported from the floodplain whilst phytoplankton are suppressed due to dilution and reduced light (Drakare et al., 2002). During low flow conditions autochthonous production

(primarily algal growth in lowland rivers) is the primary source of energy in the system (Bunn et al., 2003). These changes between basal resources may lead to a significant bottom-up effect as different secondary consumers may dominate the community structure as the amount and source of food resources shifts (Hunter & Price, 1992; Balzer et al. 2023).

Mesozooplankton such as copepods, are major consumers of phytoplankton, protists and other microplankton organisms in freshwater systems, with heterogeneous assemblages of different taxa feeding in different niches (Shiel, 1995; Kobayashi, 1996; 1998). Consequently, zooplankton are a crucial link in transferring energy from basal producers to higher trophic levels (Kobayashi & Church, 2003; Ning et al., 2010). Zooplankton groups such as rotifers, copepods and cladocerans are particularly important for the recruitment of Australian native fish, making up a significant part of fish diets during their larval and juvenile stages (Rowland, 1996; Humphries et al., 1999). The importance of flow events in supporting increased food web production is contested (Junk et al 1989; Thorp & Delong, 1994). Some studies have shown increases in zooplankton abundance concomitant with flow events (Ning et al., 2013; Furst et al., 2014). Contrastingly, others have suggested that flow events may not be important as the resulting allochthonous food resources are of poor quality (Thorp & Delong, 2002; Brett et al., 2009). It currently remains unclear what changes in secondary production can be expected following flow events in lowland systems.

The regulation of rivers has significant impacts on the flow regime, nutrient dynamics and biodiversity of rivers and is considered a key threatening process to freshwater biodiversity globally (Poff et al., 1997; Kingsford, 2000; King et al., 2009). These impacts include a reduction in nutrient and organic matter loads associated with high and medium flows events, which may alter primary and secondary production, potentially reducing food for larval and juvenile fish (Baldwin et al. 2016; Humphries et al., 1999; Johnson et al., 2023). To mitigate the effects of regulation, restoring or protecting flow events that inundate floodplains and in-channel benches may be crucial in maintaining the health of rivers (Westhorpe & Mitrovic 2012; Arthington, 2015; Townsend & Douglas, 2017). However, there is still a major knowledge gap in the relationship between flow events, the lower

food web and food resources for higher trophic levels (Poff & Zimmerman, 2010; Rolls et al., 2012).

The effects of high flows such as large overbank flood events on riverine food webs have been studied extensively on inland Australian rivers (Ning et al., 2013; Nielsen et al., 2016; Cook et al., 2020), however fewer studies have examined the effects of a range of flow sizes on the lower food web. The aim of this study was to understand how organic carbon and nutrient concentrations, phytoplankton and zooplankton respond to flow events of different magnitudes in a lowland river system. To achieve this, we conducted a two-year observational study on the Namoi River, NSW, Australia, during which a range of flow events occurred. We hypothesized that: (i) concentrations of inorganic nutrients and DOC would be predicted by discharge (ii) during and immediately (days to weeks) after flow events, phytoplankton concentrations would decline compared to base flow conditions and, (iii) zooplankton concentration and community assemblage would be significantly different between high, medium and low flow conditions.

Methods

Study area and sites

The Namoi River is a highly regulated system with a significantly altered flow regime due to regulation and extensive water extraction. The major dams on the system include Keepit Dam (425,510 ML); Chaffey Dam (61,830 ML); and Split Rock Dam (397,370 ML). Situated in north central NSW the Namoi catchment receives an average rainfall of 400 mm annually with two-thirds of the catchment running through the semi-arid zone. The average annual discharge for the system at Gunnedah (downstream of dams) is 669 GL. The Namoi sustainable diversion limit (the amount that can be extracted for use in an average year) is 490 GL. Large scale water extraction is common on the mid to lower reaches for cotton irrigation which is a major industry in the region. The Namoi River flows into the Barwon-Darling system.

Two study sites were monitored on the main channel of the Namoi River. The two sites were Site 1, near the Australian Cotton Research Institute “30° 12' 46.8" S 149° 35' 56.4" E” and Site 2, at Redbank farm 50 km downstream of Site 1, “30° 17' 06.6”

S 149° 20' 14.8" E”. Both sites were located in the middle to lower section of the river. Discharge was obtained from two gauging stations operated by the NSW Department of Primary Industries (waterinfo.nsw.gov.au), Namoi River at Mollee (419039), located 12 km upstream of Site 1 and Namoi River Weeta Weir (419068), located directly at Site 2.

Sampling procedures

Samples were taken monthly from September 2016 to February 2018 at each study site ($n = 18$ for both sites). At each site, water samples were collected for the determination of water quality and concentrations of phytoplankton and zooplankton. All instruments and sample bottles were rinsed three times with in situ river water to minimize contamination. Samples were taken using buckets and sub-sampled for nutrients, DOC and chlorophyll-*a* (Chl-*a*). Each bucket sample was taken 20 to 30 m apart and any stream sediment or detritus was avoided. All samples were taken in polyethylene containers, placed in a portable Engel fridge/freezer and frozen. Dissolved oxygen, water temperature, electrical conductivity and pH were measured in situ using a Hydrolab field hand-metre Surveyor and MS5 minisonde probe.

Samples for DOC, oxidised nitrogen (NO_x) and filterable reactive phosphorus (FRP) were filtered using 0.45 µm pore-sized cellulose acetate membrane syringe filters. Samples for total nitrogen (TN) and total phosphorus (TP) were unfiltered. Duplicates were taken of each nutrient and DOC sample. DOC samples were analysed using the High Temperature Combustion Method (APHA, 2005) and all N and P samples were analysed using a segmented flow analyser (OI Analytical Model FS3100, Xylem USA) according to standard methods (APHA, 2005).

Phytoplankton biomass (3 replicates) was measured by Chl-*a* analysis using a 500 mL volume of water for each sample, filtered through a 0.7 µm pore-sized glass fibre filter using a Mitivac vacuum hand pump. Filters were wrapped in aluminium foil and frozen until analysis using the boiling ethanol extraction method (International Standards Organisation, 1994).

Zooplankton samples (3 replicates each site) were collected from the pelagic zone at a depth of 30 cm, with each replicate taken 20 to 30 m apart. River water samples (70 L) were bucket poured through a

35 µm plankton net, concentrated into a sample bottle and preserved with 70% ethanol. For this study all copepods (adults and late stage copepodites) and cladocerans were classified as mesozooplankton. Mesozooplankton were counted and identified to order level for copepods and family level for cladocerans using Bogorov counting chambers and a dissecting microscope at a magnification of $\times 40$ – $\times 100$. Nauplii and rotifers were counted using a Sedgewick-Rafter counting cell on a compound microscope at a magnification of $\times 2000$. Rotifers were identified to family level. The taxonomic key of Shiel (1995) was used for identification of mesozooplankton and rotifers.

Graphical plots and statistical analyses

Graphical plots of data were made using Sigma Plot software. Regression analyses were run to examine relationships between discharge and environmental factors of DOC, Chlorophyll *a*, TN and TP, FRP and NO_x. Quadratic regressions were chosen when considering the potential for a curvilinear relationship in the context of within channel flows and flow size vs flow frequency (Atkinson et al. 2019). Linear regressions were also run when the quadratic term in the regressions were found to be insignificant ($\alpha=0.05$). Before regressions were run data was tested for normality using Shapiro-Wilks test and Ln transformed when required.

To compare different hydrological conditions we categorised flow periods as high, medium and low flows. High flow periods represented bank-full and overbank flows and consisted of any flows greater than 500 ML d⁻¹ and lasting 2 months from start of flow, medium flow periods reflected inundation of benches and consisted of any flows between 200 and 500 ML d⁻¹, and low flow periods reflected basal flow conditions which were characterised as any period of <200 ML d⁻¹ not within two months of a flow event. Permutational analysis of variance with pairwise comparisons (PRIMER 6.0+PERMANOVA; Anderson et al., 2008) was used to analyse the differences in environmental variables (DOC, TN, TP, Chl-*a*), zooplankton and rotifer community structure during high, medium and low flow periods across both sites. Environmental data was based on Euclidean similarity matrices and $\ln(x+1)$ transformed to account for skewed data. Zooplankton data was based on Bray–Curtis

similarity matrices, and all zooplankton data sets were transformed using square-root transformations before analysis to account for skewness whilst allowing for values of zero. All data was subject to PERMDISP analysis and visual inspection using draftman's plots to test for normality before statistical tests were performed. Similarity percentage analysis (SIMPER) was used to analyse changes within zooplankton assemblage during these flow groups using a 90% threshold of species contribution (Clarke & Warwick, 2001). Non-metric Multidimensional scaling (nMDS) plots were used to visualise changes between the flow groups in mesozooplankton, rotifers and environmental variables (Clarke & Warwick, 2001).

To test which environmental factors explained variances in zooplankton taxa concentration and assemblages, a redundancy analysis was performed using CANOCO 4.5 (Braak and Smilauer, 2002). Separate analyses were performed for Site 1 and Site 2. At both sites, copepods, cladocerans and rotifers were combined (all in indi. m⁻³) to account for factors such as competition and predation, zooplankton data was also square-root transformed to generate even distributions for analysis. All samples and variables were subject to Shapiro-Wilks test for normality. To account for large variation and inflation factors all environmental variables were standardized using z-scores which describe the position of the raw score in comparison to the mean based off the standard deviation. The explanatory environmental variables were selected using automatic forward selection. The variables used in all analyses included discharge on day, mean 7- and 14-day antecedent discharge, 7- and 14-day max discharge, days since flow event, days pre flow event, DOC, TN, TP and Chl-*a*. Factors such as FRP, NO_x and dissolved oxygen were not included in the final analysis due to high covariance with TP, TN and Chl-*a*, respectively. At Site 2 additional flow variables (Site 1 discharge on day, Site 1 thirty-day max) were added to the analysis to account for any upstream influences on downstream zooplankton communities. Monte-Carlo permutation (999 permutations without restriction) was used to test the significance of canonical axis and environmental variables on zooplankton communities. Other variables measured but not shown were temperature, pH, turbidity and conductivity; these variables either showed very high covariance with other factors or were strongly insignificant.

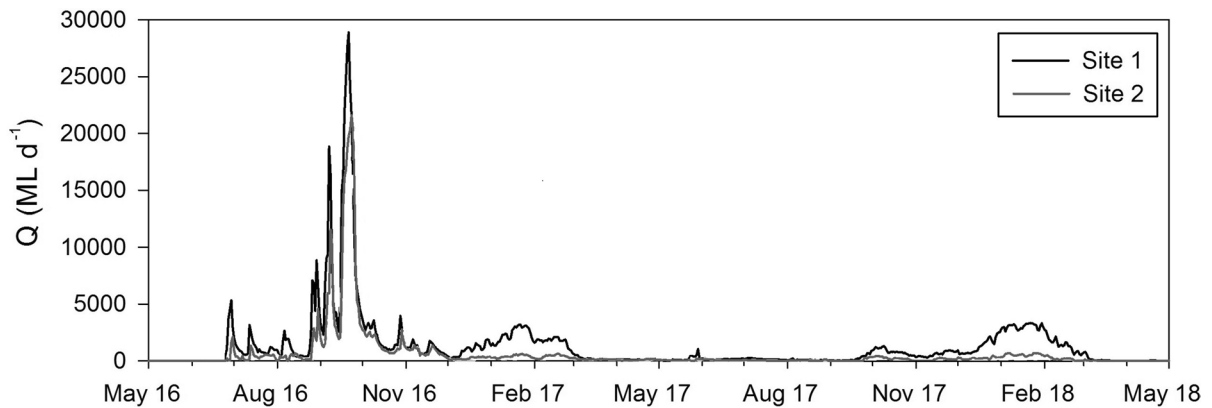


Fig. 1 Hydrographs showing daily average discharge (ML d^{-1}) for the 2 sampling sites on the Namoi River across the sampling period June 2016 to February 2018. Site 1 is in black, Site 2 grey

Flow conditions

Flow conditions were highly variable during the study period, which is common for the Namoi River. The first half of 2016 was very dry within the catchment with several cease-to-flow periods (Fig. 1). A high rainfall period during winter 2016 across central Northern NSW led to several flow events from June onwards and a large flood event in late September 2016 peaking at $28,899 \text{ ML d}^{-1}$ at Site 1. From March 2017, river discharge levels were consistently low ($50\text{--}200 \text{ ML d}^{-1}$) until October 2017 where a small flow occurred at Site 1 (1294 ML d^{-1}) which was followed by 3 months of flows $>1000 \text{ ML d}^{-1}$. Typically flow magnitude was much higher at Site 1 (the most upstream site) than at Site 2 (Fig. 1) as water is extracted or diverted for irrigation purposes between these two sites (mean discharge range at Site 2 was 33–44% less than mean discharge at Site 1).

Results

DOC, nutrient and chlorophyll-a concentrations

Dissolved organic carbon generally increased with discharge, with both sites displaying a similar temporal trend across the sampling period (Fig. 2A, B). DOC concentrations peaked during September 2016, January 2017 and from October 2017 to February 2018 which coincided with high and medium sized flow events. DOC concentrations remained

similar across sites despite reduced discharge (Q) at Site 2 compared to Site 1. Quadratic regressions (Table 1) showed that DOC at Site 1 was significantly related to discharge ($P=0.0255$, $R^2=0.35$, $y=13.56 - 3.29 + 0.35^2$). DOC at Site 2 was not related to discharge at Site 2 but was significantly related to upstream discharge at Site 1 ($P=0.039$, $R^2=0.23$).

Similarly to DOC, nitrogen and phosphorus increased with discharge (Fig. 2C–F). Total nitrogen (TN) and total phosphorus (TP) concentrations showed high variability across the sampling period with a similar range at both sites. TN and TP concentrations peaked at both sites during the September 2016 high flow event and were lowest during the low flow period from June to August 2017. Both TN and TP also increased at both sites during the medium-sized flow events in January and October 2017. TN was significantly related to flow at Site 1 ($P=0.0019$, $R^2=0.52$, $1.58 - 0.47 + 0.05^2$) and Site 2 ($P=0.0023$, $R^2=0.56$). TP was strongly related to flow at Site 2 ($P=0.0001$, $R^2=0.89$) but weakly related at Site 1 ($P=0.009$, $R^2=0.32$). Filtered nutrients (NO_x and FRP) showed weaker relationships to discharge than total nutrients. At Site 1 NO_x was significantly related to discharge ($P=0.032$, $R^2=0.23$); as was FRP ($P=0.036$, $R^2=0.22$). Filtered nutrients at Site 2 were both significantly related to discharge (NO_x: $P=0.0006$, FRP $P=0.0001$) with FRP showing a strong correlation to discharge ($R^2=0.75$). TN ($R^2=0.4$), TP

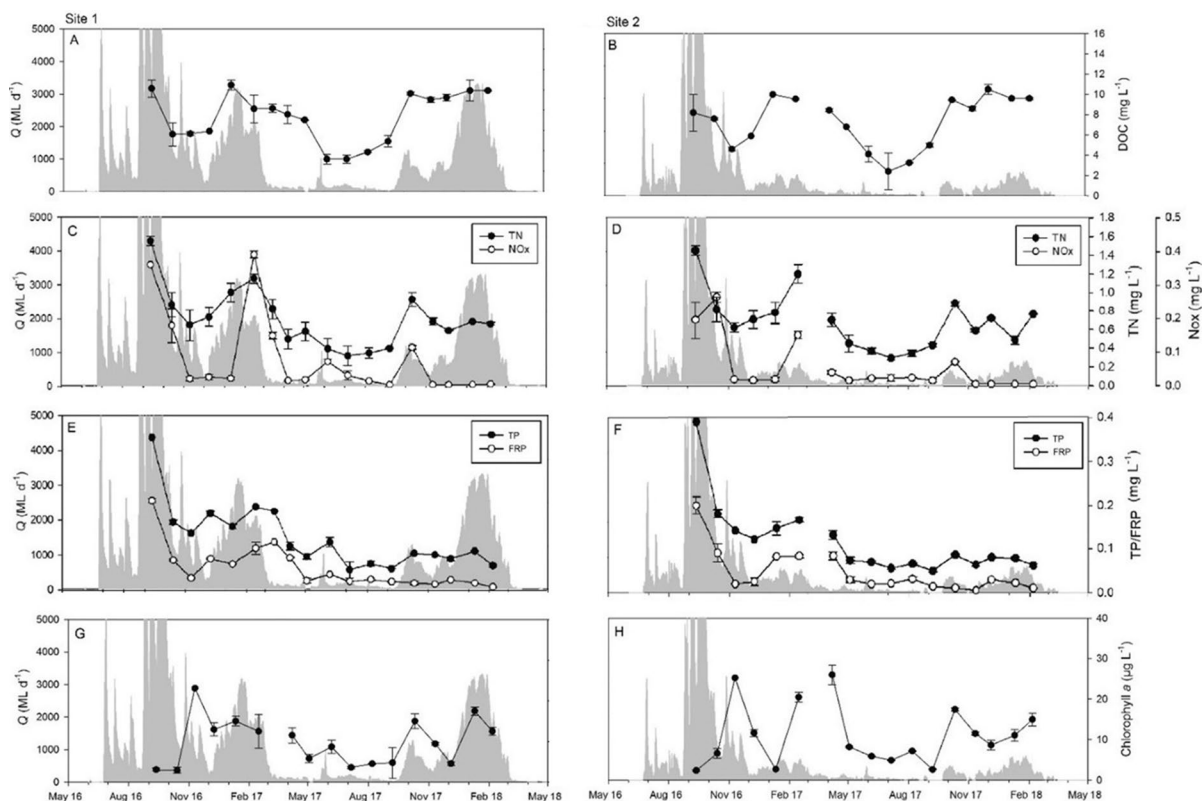


Fig. 2 Monitoring data from the Namoi River for the sampling period June 2016 to February 2018. Discharge is shown in grey. Site 1 data is shown in the left column, Site 2 on the

right. Mean concentrations of DOC (mg l^{-1} , **A–B**), TN and NOx (**C–D**, mg l^{-1}), TP and FRP (**E–F** mg l^{-1}) and Chl-a (**G–H**, $\mu\text{g l}^{-1}$) are all shown with standard error of the mean

($R^2=0.44$) and FRP ($R^2=0.38$) at site 2 were all significantly related to discharge at site 1 ($P<0.05$).

Chlorophyll-a concentrations were highly variable over the sampling period (Fig. 2G, H). At both sites Chl-a concentrations were highest in November 2016 following the September flows. Chl-a was also high in February and April 2017 at Site 2. During the flow event in October 2017, Chl-a concentrations more than tripled from the previous month, 23 days after the start of the flow (4.75 to $15 \mu\text{g L}^{-1}$ at Site 1 and 2.65 to $17.5 \mu\text{g L}^{-1}$ for Site 2). Regression analysis demonstrated there was no significant relationship between Chl-a concentrations and discharge at either site (Table 1).

Non-metric MDS showed high and medium flow groups separated moderately from the low flow group (Fig. 3). Permutational Analysis of Variance (Table 2) supported this, finding DOC, TN, TP and Chl-a concentrations were significantly different between flow groups ($P=0.001$) but not between sites ($P>0.05$).

At Site 1, pairwise comparisons showed high and medium flow groups were significantly different from the low flow group ($P=0.016$ and $P=0.03$, respectively). At Site 2 environmental factors were only significantly different between medium and low flow groups ($P=0.042$), with high and medium flow periods not significantly different from each other at either site.

Zooplankton

The concentration of all measured zooplankton groups increased during or after flow events (Fig. 4). A total of 17 rotifer families were identified during this study. *Brachionus* spp. was the most common, occurring in 100% of samples at both sites. Rotifers were overwhelmingly the most abundant zooplankton group, typically two orders of magnitude higher in concentration than nauplii and mesozooplankton (Fig. 4A, B). High variation in rotifer concentration

Table 1 Regression results of flow (X) vs DOC, TN and TP (y). Results in bold indicate quadratic regressions were the most significant model, 'n.s.' indicates that neither quadratic

nor linear regressions are significant at $\alpha=0.05$, whilst * indicates both quadratic and linear regressions were significant

Response variable	Site 1	Site 2	Site 2 vs Q at Site 1
DOC	$y = 13.56 - 3.29X + 0.35X^2$ $R^2 = 0.35, P = 0.0255^*$	n.s	$y = 6.37X + 0.001$ $R^2 = 0.23, P = 0.039$
Chl-a	n.s	n.s	n.s
TN	$y = 1.58 - 0.47X + 0.05X^2$ $R^2 = 0.52, P = 0.0019^*$	$y = 0.549X + 0.0003$ $R^2 = 0.56, P = 0.00023^*$	$y = 0.518X + 0.00017$ $R^2 = 0.40, P = 0.0032$
TP	$y = 0.08X + 0.00038$ $R^2 = 0.32, P = 0.009^*$	$y = 0.061X + 0.00012$ $R^2 = 0.89, P = 0.0001^*$	$y = 0.06X + 0.00049$ $R^2 = 0.44, P = 0.0021$
NOx	$y = 0.032X + 0.00052$ $R^2 = 0.23, P = 0.032$	$y = 0.017X + 0.00081$ $R^2 = 0.51, P = 0.0006^*$	n.s
FRP	$y = 0.027X + 0.00022$ $R^2 = 0.22, P = 0.036$	$y = 0.016X + 0.00064$ $R^2 = 0.75, P = 0.0001^*$	$y = 0.015X + 0.00027$ $R^2 = 0.38, P = 0.005$

Downstream (Site 2) nutrient concentrations were also compared to upstream (Site 2 vs Q at Site 1) discharge levels to account for irrigation extraction

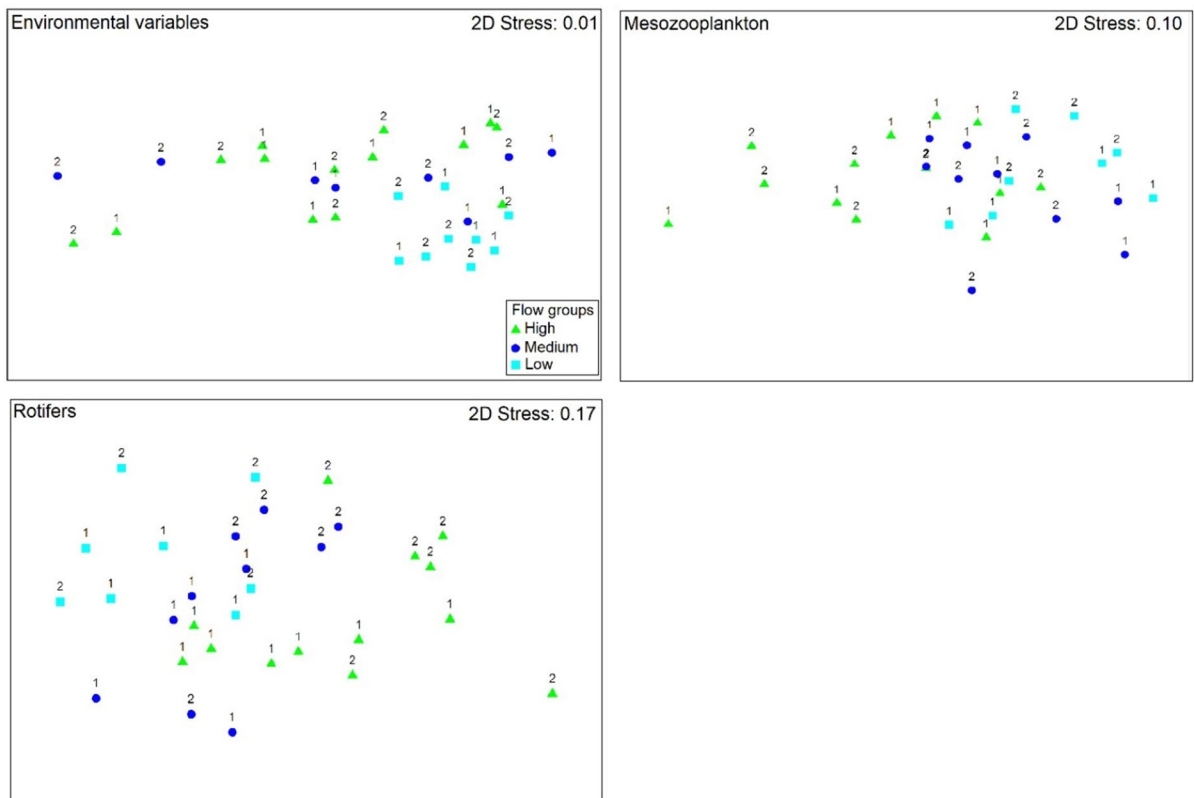


Fig. 3 nMDS plots of environmental variables (DOC, TN, TP and Chl-a), rotifer community assemblage and mesozooplankton assemblage and at high (green triangles), medium (dark

blue circles) and low (light blue squares) flow periods. The numbers above each point represent Sites 1 and 2

Table 2 PERMANOVA with pairwise comparisons for environmental (Chl-a, DOC, TN, TP) concentrations, mesozooplankton assemblage and concentration and rotifer assemblage and concentration

PERMANOVA	TEST	Environmental		Mesozooplankton		Rotifers	
		f/t	<i>P</i>	f/t	<i>P</i>	f/t	<i>P</i>
Main test	SITES	0.068	0.914	1.118	0.346	8.715	0.001
	FLOW	6.288	0.001	12.851	0.001	11.542	0.001
	Site × flow	0.035	0.905	2.881	0.004	2.715	0.001
Site 1	H-M	0.556	0.682	2.413	0.001	1.778	0.010
	H-L	2.421	0.016	2.620	0.001	2.421	0.001
	M-L	2.394	0.034	1.466	0.064	1.973	0.001
Site 2	H-M	1.088	0.313	2.917	0.001	2.781	0.001
	H-L	1.652	0.107	4.614	0.001	3.872	0.001
	M-L	1.958	0.042	2.048	0.005	2.925	0.001

Main test results use pseudo-f statistic whereas pairwise tests between flow groups use *t*-statistic

Flow categories: *H* high, *M* medium, *L* low

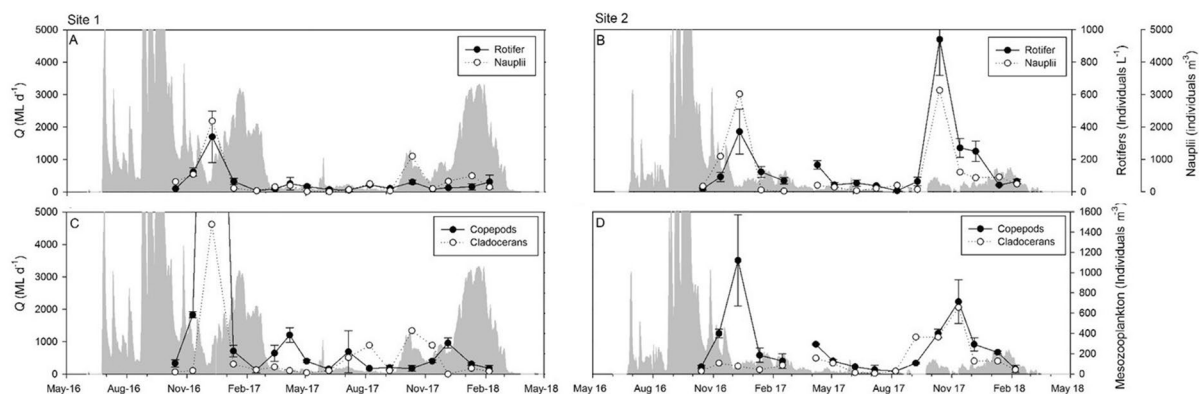


Fig. 4 Monitoring data for zooplankton concentrations on the Namoi River from June 2016 to February 2018. **A–B** shows mean rotifer (individuals L^{-1}) and Nauplii (individuals m^{-3}) concentrations with standard error of the mean. Rotifers are in black whilst nauplii are on a secondary axis in white. **C–D**

shows mean mesozooplankton concentrations (individuals m^{-3}) with standard error of the mean. Copepods are in black whilst cladocerans are in white. Zooplankton concentration peaks were not included to allow visibility of low concentration periods. Site 1 is the left column, Site 2 on the right

was seen across the study period with a peak (939 ind. L^{-1}) in December 2016 for Site 1 and 2 and November 2017 for Site 2 more than 100 times higher than the lowest concentration (6 ind. L^{-1}). At both sites, rotifer concentrations increased after the September 2016 flood. The mean concentrations of total rotifers at Site 1 peaked post flood in December 2016 (339 ind. L^{-1}). At Site 2 concentrations were similar (372 ind. d^{-1}) during December 2016 but peaked during the October 2017 flow event (939 ind. L^{-1}) with rotifer concentrations remaining above 200 ind. L^{-1} until January 2018. Non-metric MDS showed that high

and low flow groups separated strongly in zooplankton community structure (Fig. 3). PERMANOVA with pairwise comparisons (Table 2) supported this, identifying significant differences between the rotifer community and flow groupings ($P=0.001$, $f=11.542$), and sites ($P=0.001$, $f=8.715$). The rotifer communities were significantly different across all flow groups ($P\leq 0.010$) at both sites. Similarity percentage analysis (Fig. 5) found an average dissimilarity of 81% in rotifer community structure between high and low flow periods. At high flow *Keratella* (32%), *Brachionus* (23%) and *Filinia* (15%) were the

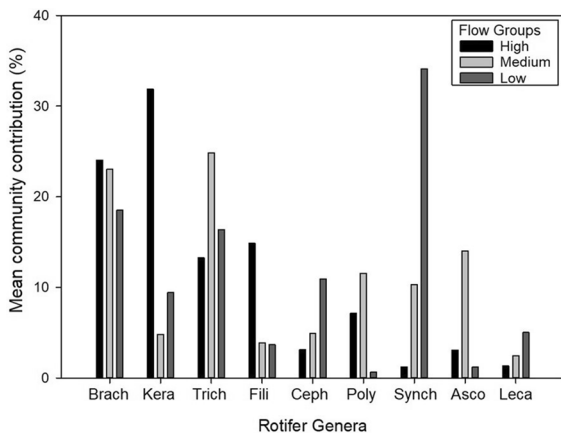


Fig. 5 SIMPER analysis of rotifer communities at high, medium and low flow periods. *Brach*, *Brachionus*; *Kera*, *Keratella*; *Trich*, *Trichocerca*; *Fili*, *Filinia*; *Ceph*, *Cephalodella*; *Poly*, *Polyarthra*; *Synch*, *Synchaeta*; *Asco*, *Ascomorpha*; and *Leca*, *Lecane*

most dominant genera whereas at low flow *Synchaeta* (34%), *Brachionus* (18%) and *Trichocerca* (17%) were the most dominant (Fig. 5).

Concentrations of nauplii showed a similar pattern to rotifers and increased by a factor of three at Site 1 (2185 ± 71 ind. m^{-3}) and Site 2 (3014 ± 450 ind. m^{-3}) in the two months after the September 2016 high flow flood event (Fig. 4A, B). At both sites nauplii concentrations also increased during the October 2017 medium flow event leading to the highest concentrations for the sampling period at Site 2 (3128 ± 314 ind. m^{-3}). The copepod community consisted of four taxonomic groups (Cyclopoids: *Mesocyclops* spp., *Thermocyclops* spp.; Calanoids: *Boeckella* spp., *Calamoecia* spp.) which were heavily dominated by cyclopoids, occurring in 100% of samples at both sites. Calanoids were present in 47% of samples, occurring from October 2016 to January 2017 and again from September 2017 to December 2017 at both sites. The average ratio of cyclopoids to calanoids was $12(\pm 3):1$ across both sites. Total copepods showed high variation in concentration throughout the sampling period peaking at $6614 (\pm 770)$ ind. m^{-3} in December 2016 and lowest at $29 (\pm 2)$ ind. m^{-3} in August 2017. Copepod concentrations increased in the two months following the September 2016 flood event leading to very high concentrations at Site 1 (6614 ± 770 ind. m^{-3}) and Site 2 (1121 ± 289 ind. m^{-3}) in December 2016. High concentrations were

also recorded at Site 2 (713 ± 153 ind. m^{-3}) during and after the October 2017 flow event. Cladocerans followed similar trends to copepods, peaking in December 2016 at Site 1 (1478 ± 278 ind. m^{-3}) and in November 2017 at Site 2 (657 ± 173 ind. m^{-3}). Five genera (*Daphnia*, *Ceriodaphnia*, *Chydorus*, *Bosmina*, *Moina*) of cladocerans were identified across the study period, *Chydorus* spp. was the most common at both sites, occurring in 65% (Site 1) and 82% (Site 2) of samples respectively.

Non-metric MDS showed a clear separation of zooplankton samples between high and low flow periods (Fig. 3). PERMANOVA with pairwise comparisons (Table 2) supported this, identifying a significant difference between flow groups ($P=0.001$) and no significant difference between sites ($P=0.346$). At Site 1, zooplankton were significantly different at high flow compared to medium ($P=0.001$) and low ($P=0.001$) but not between medium and low flow groups ($P>0.05$). At Site 2 zooplankton communities were significantly different between all flow groups ($P \leq 0.005$). Redundancy analysis explained a total of 52% of variation in the zooplankton community at Site 1 and 62% at Site 2 (Fig. 6). At Site 1 all rotifers including *Brachionus*, *Filinia* and *Synchaeta* were strongly positively related to Chl-*a* and TN concentrations. *Keratella* showed a positive correlation with TP and a negative relationship to daily discharge whereas *Lecane* and *Ascomorpha* were closely positively correlated to daily discharge. Cyclopoids and nauplii were positively correlated to Chl-*a* concentrations whilst calanoids and cladocerans were positively correlated to TP concentrations and negatively correlated to daily discharge. Similar patterns were seen at Site 2 with the first 2 canonical axes explaining 55% of total variation. Chl-*a* was very similar to Site 1 and explained 36% of total variation, correlating positively to 65% of all rotifer families with *Brachionus*, *Filinia* and *Keratella* most closely related. *Polyarthra*, *Asplanchna* and *Lecane* were positively correlated to both Chl-*a* and DOC which played a much stronger role at Site 2 explaining 11% of total variation. *Synchaeta* and *Lepadella* were closely positively correlated to DOC at site 2 and *Trichocera* was positively correlated to DOC at both sites. Calanoids and nauplii were closely positively related to Chl-*a* concentrations. Cyclopoids and cladocerans were positively correlated to both Chl-*a* and DOC concentrations and negatively related to daily discharge.

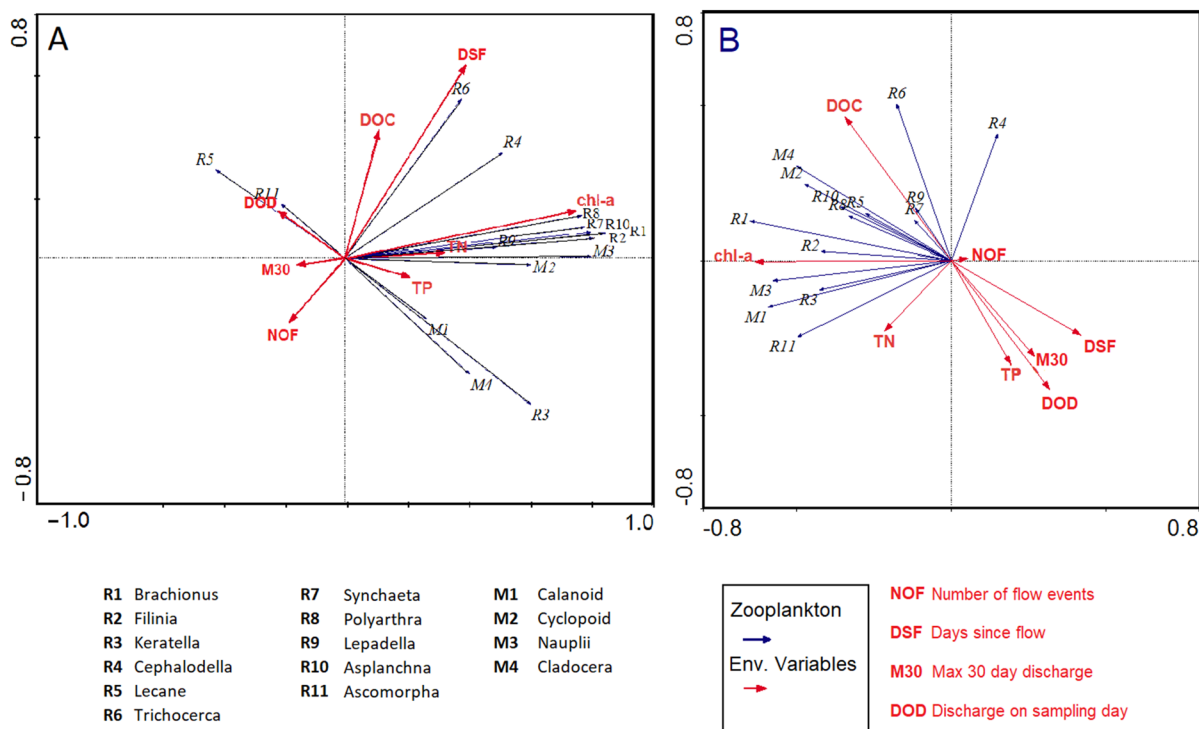


Fig. 6 Redundancy analysis for all major zooplankton groups at Sites 1 (A) and 2 (B)

Discussion

The present study provided some insights into the complex relationship between variable river discharge, nutrients, organic carbon concentrations and their consequent influence on phytoplankton and zooplankton communities. Our results suggest flow events of all sizes were important for the lower food web on the Namoi River, with nutrients positively correlated and DOC showing a curvilinear relationship to discharge and zooplankton increasing during or after flows. Further, during dry periods when water availability is low, protecting in-channel flows may be a critical management tool for providing boosts in productivity.

Basal resources and flow in lowland rivers

Flow events of all sizes appeared important for mobilising nutrients and DOC in the Namoi River, with in-channel flows particularly important sources of nutrients and DOC during low flow conditions. Inputs of organic matter are conceptualised to be the dominant

source of energy for lowland river food webs following high flow periods (Junk et al. 1989). During this study DOC was positively correlated to discharge. Previous research during a period of major flooding on the Namoi found a similar relationship between discharge and DOC mobilisation (Westhorpe and Mitrovic, 2012). Studies on other lowland rivers in Australia (Cook et al., 2015; Nielsen et al., 2016), North America (Dalzell et al., 2005; 2007) and Central Europe (Hein et al., 2003) have also found DOC concentrations increased considerably after large flow pulses. Similarly, nitrogen and phosphorus concentrations were positively correlated with discharge and peaked during the September flood, which is consistent with previous studies on the Namoi River (Westhorpe et al., 2008). These findings support those of the ‘flood pulse concept’ of Junk et al., (1989) and studies on other Australian semi-arid rivers where high flow events have been shown to provide important pulses of energy for connected riverine food webs (Cook et al., 2015; Wallace and Furst, 2016). However, small increases in flow which increased inundation of river channel and benches also appeared

important for mobilising DOC and nutrients, as seen on the Gwydir River, Australia, where in-channel flow pulses were positively correlated with increased nutrient and DOC loads (Woodward et al., 2015).

Our findings suggest flow events may positively influence planktonic food webs either during or after flows. Whilst we found no direct statistical relationship between discharge and Chlorophyll-*a* (Chl-*a*), it is likely the nutrients mobilised during flow events influenced phytoplankton growth in the Namoi River (Hecky & Kilham 1988; Hitchcock and Mitrovic 2015b; Rohlf et al. 2016; Stahl et al., 2013). Chl-*a* was initially suppressed during the September 2016 flood event however, Chl-*a* concentrations increased considerably once flood conditions had subsided, as seen previously following floodplain inundation on the Murray River (Nielsen et al., 2016). Chl-*a* concentrations also increased during several in-channel flow events, which may reflect the increased nutrient concentrations caused by inundation of benches whilst avoiding higher flow velocities and turbidity associated with overbank flows (Irigoiien and Castel, 1997; Townsend and Douglas, 2017). These findings are supported by Westhorpe et al. (2010) who found nitrogen and phosphorus additions to in situ microcosms in the Namoi significantly increased Chl-*a* concentrations, and, when combined with DOC additions significantly boosted bacterial production. Our findings suggest increases in river discharge that raise DOC and nutrient concentrations due to increased connection with riverbanks and floodplains may result in enhanced in-stream primary and/or heterotrophic production (Gawne et al., 2007; Cook et al., 2015). Because DOC is also generated by algal productivity, benthic microbial respiration and the hyporheic zone (Fisher et al. 2005; den Meersche et al. 2009), further studies are warranted to characterise DOC to determine its origins under different flow conditions.

Zooplankton

In this study, rotifers and mesozooplankton concentrations increased following flow events at both sites, but the magnitude of these increases was highly variable. The September 2016 flood event appeared particularly important with all measured components of the zooplankton assemblage increasing significantly following the flood. However, a much smaller flow in October 2017 also significantly increased

zooplankton at site 2, with rotifers and nauplii peaking in concentration. The extreme variability in zooplankton concentrations seen during this study is consistent with the boom-and-bust ecology of semi-arid lowland rivers in Australia (Sternberg et al., 2008; Arthington and Balcombe, 2011). In addition, previous studies have also found both rotifer and mesozooplankton concentration increased considerably after flood events (Shiel et al., 2006; Ning et al., 2013; Furst et al., 2014), at times increasing orders of magnitude compared to base flow conditions (Nielsen et al., 2016; Rees et al., 2020). Inundation of zooplankton egg banks and downstream transport during flow events may account for a large proportion of the observed increases in zooplankton concentration during this study (Jenkins and Boulton, 2003). Emergence from egg banks may take up to two weeks following inundation whereas downstream transport may result in immediate increases of adults to local zooplankton populations (Jenkins and Boulton, 2003). Flow pulses may also increase zooplankton populations indirectly as in situ communities react to increases in food availability caused by flow events (Ning et al., 2013). These flow-pulse booms in zooplankton have been found to also increase the taxonomic richness of local zooplankton communities, the effects of which may last up to a month post-flow (Shiel et al., 2006; James et al., 2008; Ning et al., 2013).

Zooplankton community concentration and composition were significantly different between high and low flow periods (PERMANOVA, $p=0.001$ at both sites). Changes in the zooplankton community following flow events may reflect changes in available food resources such as trophic strategies more suited to utilising post-flow resources dominate. Similarity percentage analysis indicated large shifts in the rotifer community between high and low flow periods from *Keratella*, *Brachionus* and *Filinia* at high flow to *Synchaeta*, *Brachionus* and *Trichocerca* at low flow. Redundancy analysis found changes in zooplankton concentration and structure were strongly correlated to Chl-*a* concentrations at both sites. Booms in zooplankton often coincide with increases in phytoplankton concentration (Basu and Pick., 1997; Shiel et al., 2006); this was seen in this study during November and December 2016 at Site 1 and November 2016 and October 2017 at Site 2. These findings suggest phytoplankton growth and consumption may be the main

source of energy used by zooplankton within the Namoi River, particularly in its mid-lower reaches. This is consistent with the river productivity model (Thorp & Delong, 1994) and other studies in freshwater systems (Thorp & Delong, 2002; Oliver & Merrick, 2006), which have found autochthonous production to fuel the bulk of metazoan production in rivers. However, in the Namoi River, the river productivity model seems to apply only in warmer months of the year. We further hypothesize that there may be temporal seasonal switches between allochthonous (Junk et al., 1989) and autochthonous (Thorp & Delong, 1994) energy as the dominant driver of zooplankton abundance.

DOC was also significantly correlated to changes in some rotifers, cyclopoid copepods and cladocerans, albeit it less strongly than phytoplankton. We found during and after high flow events primarily bacterivorous rotifer genera (Arndt, 1993) in-particular *Brachionus*, *Keratella* and *Filinia* dominated the rotifer community. Further, *Brachionus* and *Keratella* have been found to significantly increase in concentration after DOC additions in a mesocosm study on the Namoi River, suggesting the ability to indirectly exploit DOC inputs via heterotrophic pathways (Mitrovic et al., 2014). In contrast, bacterivory in some of the rotifer genera that dominated during low flow periods such as *Synchaeta* and *Trichocera* has been found to be insignificant, possibly due to their feeding apparatus unsuitable for bacterivory (Boon & Shiel, 1990; Arndt, 1993). Cyclopoid copepods and the cladoceran *Chydorus* also increased markedly during flow events. Cyclopoids are raptorial feeders and known to prefer ciliates and soft-bodied rotifers as food sources (Jurgen & Jeppesen, 2000; Barnett et al., 2007), leading to a 'semi-dependence' on DOC for nutrition (Berggren et al., 2014). *Chydorus* spp. dominated the cladoceran community during flow events and have previously been correlated with both DOC concentration and bacterial biomass (Hitchcock et al., 2016a, b).

Several previous studies have found DOC to play an important though highly variable role in supporting secondary production in freshwater food webs (Carpenter et al., 2005; Berggren et al., 2018; Balzer et al., 2023). The findings of this study suggest the energy pathway supporting secondary growth in riverine food webs changes seasonally and is highly flow dependant. Changes in the zooplankton community

assemblage across flow categories suggested heterotrophic production (resulting from DOC inputs) was at least partially supporting zooplankton growth during and after flow events. However, this heterotrophic support appeared to be complimentary to phytoplankton production during all in-channel flows, with only the large September flood suppressing phytoplankton growth. Our results suggest riverine food webs are dynamic and use both autotrophic and heterotrophic production as energy sources with flow events playing a critical role in the influence of either energy source. As already stated, further seasonal studies are also warranted to characterise DOC to determine its origins and transformation pathways under different flow conditions.

Implications for understanding lowland river food webs

Booms in fish population density have been linked to flood events and the energy pulses related to floodplain inundation (Junk et al., 1989; Puckeridge et al. 1998; Jenkins & Boulton, 2007). These increases are likely the result of increased recruitment and survival of fish following the post-flow increases in diversity, density and biomass of lower trophic-level components such as phytoplankton, bacteria and zooplankton seen in this and other studies (Jenkins & Boulton, 2003; Costelloe et al., 2005; Mitrovic et al., 2014). Several native Australian fish [Silver Perch *Bidyanus bidyanus* (Mitchell, 1838), Golden Perch *Macquaria ambigua* (Richardson, 1845) and Murray Cod *Maccullochella peelii* (Mitchell, 1838)] are reliant on zooplankton as a key food source throughout their larval and juvenile growth stages (Humphries, 1999; King, 2005). Thus, booms in zooplankton after flow events have been linked to increases in native fish density (Balcombe et al., 2005). From our results and those of Shiel et al., (2006), flow events may affect zooplankton populations from weeks to several months post-flow, depending on the size and timing of the flow event. The nutrients and organic matter mobilised by flow events and their influence on in-stream primary and secondary production may therefore play an important role in the broader survival and post-flow recruitment of native fish species.

Conclusion

Flow events were important for mobilising nutrients and organic carbon for the Namoi River, supporting our first hypothesis that nutrients and DOC would be related to discharge. Resources mobilised by flows appeared to support production via both autotrophic and heterotrophic pathways leading to large increases in zooplankton and phytoplankton concentration and changes in zooplankton community assemblage. However, phytoplankton and zooplankton booms during and after flows were not always related to the size of the flow event, with the timing and antecedent conditions of flows also playing an important role in defining the food web response to the flow event. These factors should be considered for the effective management of flow events in lowland rivers. Further, our data suggests the protection of small and medium flow events may be important for maintaining ecosystem health and processes. Future research targeting long-term data sets encompassing a much wider range of flows (particularly in-channel flows) would greatly increase our ability to model lower food web responses to flow events.

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Data availability The data sets generated and analysed during the current study are available from the corresponding author upon reasonable request.

Declarations

Conflict of interest The authors declare there was no conflict of interest during this work.

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References

- Anderson, M. J., R. N. Gorley & K. R. Clarke, 2008. *Permanova+ for Primer: Guide to Software and Statistical Methods*, PRIMER-E, Plymouth:
- APHA, 2005. *Standard Methods for the Examination of Water and Wastewater*, 21st ed. American Public Health Association, Washington:
- Arndt, H., 1993. Rotifers as predators on components of the microbial web (bacteria, heterotrophic flagellates, ciliates)—a review. *Hydrobiologia* 255–256(1): 231–246. <https://doi.org/10.1007/BF00025844>.
- Arthington, A. H., 2015. Environmental flows: A scientific resource and policy framework for river conservation and restoration. *Aquatic Conservation: Marine and Freshwater Ecosystems* 25(2): 155–161. <https://doi.org/10.1002/aqc.2560>.
- Arthington, A. H. & S. R. Balcombe, 2011. Extreme flow variability and the “boom and bust” ecology of fish in arid-zone floodplain rivers: a case history with implications for environmental flows, conservation and management. *Ecology*. <https://doi.org/10.1002/eco.221>.
- Balcombe, S. R., S. E. Bunn, F. J. McKenzie-Smith & P. M. Davies, 2005. Variability of fish diets between dry and flood periods in an arid zone floodplain river. *Journal of Fish Biology*. <https://doi.org/10.1111/j.1095-8649.2005.00858.x>.
- Baldwin, D. S., M. J. Colloff, S. M. Mitrovic, N. R. Bond & B. Wolfenden, 2016. Restoring dissolved organic carbon subsidies from floodplains to lowland river food webs: a role for environmental flows? *Marine and Freshwater Research* 67(9): 1387–1399.
- Balzer, M. J., J. N. Hitchcock, W. L. Hadwen, T. Kobayashi, D. P. Westhorpe, C. Boys & S. M. Mitrovic, 2023. Experimental additions of allochthonous dissolved organic matter reveal multiple trophic pathways to stimulate planktonic food webs. *Freshwater Biology* 68(5): 821–836.
- Barnett, A. J., K. Finlay & B. E. Beisner, 2007. Functional diversity of crustacean zooplankton communities: towards a trait-based classification. *Freshwater Biology*. <https://doi.org/10.1111/j.1365-2427.2007.01733.x>.
- Basu, B. K. & F. R. Pick, 1997. Phytoplankton and zooplankton development in a lowland, temperate river. *Journal of Plankton Research*. <https://doi.org/10.1093/plankt/19.2.237>.
- Berggren, M., S. E. Ziegler, N. F. St-Gelais, B. E. Beisner & P. A. Del Giorgio, 2014. Erratum: contrasting patterns of allochthony among three major groups of crustacean zooplankton in boreal and temperate lakes (ecology (2014) 95 (1947–1959)). *Ecology* 95(11): 3230.

- Berggren, M., P. Bengtson, A. R. A. Soares & J. Karlsson, 2018. Terrestrial support of zooplankton biomass in northern rivers. *Limnology and Oceanography* 63(6): 2479–2492. <https://doi.org/10.1002/lno.10954>.
- Boon, P. I. & R. J. Shiel, 1990. Grazing on bacteria by zooplankton in Australian billabongs. *Marine and Freshwater Research*. <https://doi.org/10.1071/MF9900247>.
- Brett M. T., M. J. Kainz, S. J. Taipale & H. Seshan, 2009. Phytoplankton, not allochthonous carbon, sustains herbivorous zooplankton production. *Proceedings of the National Academy of Sciences of the United States of America*.
- Bunn, S. E. & A. H. Arthington, 2002. Basic principles and ecological consequences of altered flow regimes for aquatic biodiversity. *Environmental Management* 30(4): 492–507. <https://doi.org/10.1007/s00267-002-2737-0>.
- Bunn, S. E., P. M. Davies & M. Winning, 2003. Sources of organic carbon supporting the food web of an arid zone floodplain river. *Freshwater Biology* 48(4): 619–635. <https://doi.org/10.1046/j.1365-2427.2003.01031.x>.
- Carney, R. L., J. R. Seymour, D. Westhorpe & S. M. Mitrovic, 2016. Lotic bacterioplankton and phytoplankton community changes under dissolved organic-carbon amendment: Evidence for competition for nutrients. *Marine and Freshwater Research* 67(9): 1362–1373. <https://doi.org/10.1071/MF15372>.
- Carpenter, S. R., J. J. Cole, M. L. Pace, M. Van De Bogert, D. L. Bade, D. Bastviken, C. M. Gille, J. R. Hodgson, J. F. Kitchell & E. S. Kritzberg, 2005. Ecosystem subsidies: terrestrial support of aquatic food webs from ¹³C addition to contrasting lakes. *Ecology* 86(10): 2737–2750. <https://doi.org/10.1890/04-1282>.
- Clarke, K. R. & R. M. Warwick, 2001. Change in marine communities: an approach to statistical analysis and interpretation, 2nd ed. PRIMER-E, Plymouth:
- Cook, R. A., B. Gawne, R. Petrie, D. S. Baldwin, G. N. Rees, D. L. Nielsen & N. S. P. Ning, 2015. River metabolism and carbon dynamics in response to flooding in a lowland river. *Marine and Freshwater Research* 66(10): 919–927. <https://doi.org/10.1071/MF14199>.
- Costelloe, J. F., J. Powling, J. R. W. Reid, R. J. Shiel & P. Hudson, 2005. Algal diversity and assemblages in arid zone rivers of the Lake Eyre Basin, Australia. *River Research and Applications*. <https://doi.org/10.1002/rra.851>.
- Dalzell, B. J., T. R. Filley & J. M. Harbor, 2005. Flood pulse influences on terrestrial organic matter export from an agricultural watershed. *Journal of Geophysical Research: Biogeosciences*. <https://doi.org/10.1029/2005jg000043>.
- Dalzell, B. J., T. R. Filley & J. M. Harbor, 2007. The role of hydrology in annual organic carbon loads and terrestrial organic matter export from a midwestern agricultural watershed. *Geochimica Et Cosmochimica Acta*. <https://doi.org/10.1016/j.gca.2006.12.009>.
- den Meersche, K. V., P. V. Rijswijk, K. Soetaert & J. J. Middeburg, 2009. Autochthonous and allochthonous contributions to mesozooplankton diet in a tidal river and estuary: Integrating carbon isotope and fatty acid constraints. *Limnology and Oceanography* 54(1): 62–74.
- Drakare, S., P. Blomqvist, A. K. Bergström & M. Jansson, 2002. Primary production and phytoplankton composition in relation to DOC input and bacterioplankton production in humic Lake Öträsket. *Freshwater Biology* 47(1): 41–52. <https://doi.org/10.1046/j.1365-2427.2002.00779.x>.
- Fischer, H., F. Kloep, S. Wilzcek & M. T. Pusch, 2005. A river's liver—microbial processes within the hyporheic zone of a large lowland river. *Biogeochemistry* 76: 349–371.
- Furst, D. J., K. T. Aldridge, R. J. Shiel, G. G. Ganf, S. Mills & J. D. Brookes, 2014. Floodplain connectivity facilitates significant export of zooplankton to the main River Murray channel during a flood event. *Inland Waters* 4(4): 413–424. <https://doi.org/10.5268/IW-4.4.696>.
- Gawne, B., C. Merrick, D. G. Williams, G. Rees, R. Oliver, P. M. Bowen, S. Treadwell, G. Beattie, I. Ellis, J. Frankenberg & Z. Lorenz, 2007. Patterns of primary and heterotrophic productivity in an arid lowland river. *River Research and Applications*. <https://doi.org/10.1002/rra.1033>.
- Hecky, R. E. & P. Kilham, 1988. Nutrient limitation of phytoplankton in freshwater and marine environments: a review of recent evidence on the effects of enrichment. *Limnology and Oceanography*. https://doi.org/10.4319/lo.1988.33.4_part_2.0796.
- Hein, T., C. Baranyi, G. J. Herndl, W. Wanek & F. Schiemer, 2003. Allochthonous and autochthonous particulate organic matter in floodplains of the River Danube: the importance of hydrological connectivity. *Freshwater Biology* 48(2): 220–232. <https://doi.org/10.1046/j.1365-2427.2003.00981.x>.
- Hitchcock, J. N. & S. M. Mitrovic, 2015a. Highs and lows: the effect of differently sized freshwater inflows on estuarine carbon, nitrogen, phosphorus, bacteria and chlorophyll a dynamics. *Estuarine, Coastal and Shelf Science* 156: 71–82.
- Hitchcock, J. N. & S. M. Mitrovic, 2015b. After the flood: changing dissolved organic carbon bioavailability and bacterial growth following inflows to estuaries. *Biogeochemistry* 124: 219–233.
- Hitchcock, J. N., S. M. Mitrovic, W. L. Hadwen, D. L. Roelke, I. O. Gowns & A. M. Rohlfs, 2016a. Terrestrial dissolved organic carbon subsidizes estuarine zooplankton: An in situ mesocosm study. *Limnology and Oceanography* 61(1): 254–267. <https://doi.org/10.1002/lno.10207>.
- Hitchcock, J. N., S. M. Mitrovic, W. L. Hadwen, I. O. Gowns & A. M. Rohlfs, 2016b. Zooplankton responses to freshwater inflows and organic-matter pulses in a wave-dominated estuary. *Marine and Freshwater Research* 67(9): 1374–1386.
- Humphries, P., A. J. King & J. D. Koehn, 1999. Fish, flows and flood plains: links between freshwater fishes and their environment in the Murray-Darling River system, Australia. *Environmental Biology of Fishes* 56(1–2): 129–151. <https://doi.org/10.1023/a:1007536009916>.
- Humphries, P., H. Keckeis & B. Finlayson, 2014. The river wave concept: integrating river ecosystem models. *BioScience* 64: 870–882.
- Hunter, M. D. & P. W. Price, 1992. Playing chutes and ladders: heterogeneity and the relative roles of bottom-up and top-down forces in natural communities. *Ecology*. <https://doi.org/10.2307/1940152>.
- Irigoien, X. & J. Castel, 1997. Light limitation and distribution of chlorophyll pigments in a highly turbid estuary:

- the Gironde (SW France). *Estuarine, Coastal and Shelf Science*. <https://doi.org/10.1006/ecss.1996.0132>.
- James, C. S., M. C. Thoms & G. P. Quinn, 2008. Zooplankton dynamics from inundation to drying in a complex ephemeral floodplain-wetland. *Aquatic Sciences* 70(3): 259–271. <https://doi.org/10.1007/s00027-008-8034-0>.
- Jenkins, K. M. & A. J. Boulton, 2003. Connectivity in a dryland river: short-term aquatic microinvertebrate recruitment following floodplain inundation. *Ecology* 84(10): 2708–2723. <https://doi.org/10.1890/02-0326>.
- Jenkins, K. M. & A. J. Boulton, 2007. Detecting impacts and setting restoration targets in arid-zone rivers: aquatic micro-invertebrate responses to reduced floodplain inundation. *Journal of Applied Ecology* 44(4): 823–832.
- Johnson, E. B., C. Boys, J. Hitchcock, W. Hadwen, S. Fielder, J. A. Facey & S. M. Mitrovic, 2023. Terrestrial carbon additions to zooplankton prey influence juvenile estuarine fish growth. *Environments* 10(3): 50.
- Junk, J. Wolfgang., Bayley, B, Peter & R. Sparks, 1989. Junk et al. 1989—the flood pulse concept in river-floodplain systems. pdf. In *Canadian Journal of Fisheries and Aquatic Science*.
- Jürgens, K. & E. Jeppesen, 2000. The impact of metazooplankton on the structure of the microbial food web in a shallow, hypertrophic lake. *Journal of Plankton Research*. <https://doi.org/10.1093/plankt/22.6.1047>.
- King, A. J., 2005. Ontogenetic dietary shifts of fishes in an Australian floodplain river. *Marine and Freshwater Research*. <https://doi.org/10.1071/MF04117>.
- King, A. J., Z. Tonkin & J. Mahoney, 2009. Environmental flow enhances native fish spawning and recruitment in the Murray River, Australia. *River Research and Applications*. <https://doi.org/10.1002/rra.1209>.
- Kingsford, R. T., 2000. Ecological impacts of dams, water diversions and river management on floodplain wetlands in Australia. In *Austral Ecology*. <https://doi.org/10.1046/j.1442-9993.2000.01036.x>.
- Kobayashi, T. & A. G. Church, 2003. Role of nutrients and zooplankton grazing on phytoplankton growth in a temperate reservoir in New South Wales, Australia. *Marine and Freshwater Research* 5: 35. <https://doi.org/10.1071/MF02025>.
- Kobayashi, T., P. Gibbs, P. I. Dixon & R. J. Shiel, 1996. Grazing by a river zooplankton community: importance of microzooplankton. *Marine and Freshwater Research*. <https://doi.org/10.1071/MF9961025>.
- Kobayashi, T., R. J. Shiel, P. Gibbs & P. I. Dixon, 1998. Freshwater zooplankton in the Hawkesbury-Nepean River: comparison of community structure with other rivers. In *Hydrobiologia*. <https://doi.org/10.1023/a:1003240511366>.
- MDBA (Murray Darling Basin Authority), 2018. *River Flows and Connectivity: 2017 Basin Plan Evaluation*, Murray Darling Basin Authority, Canberra.
- Mitrovic, S. M., D. P. Westhorpe, T. Kobayashi, D. S. Baldwin, D. Ryan & J. N. Hitchcock, 2014. Short-term changes in zooplankton density and community structure in response to different sources of dissolved organic carbon in an unconstrained lowland river: evidence for food web support. *Journal of Plankton Research* 36(6): 1488–1500. <https://doi.org/10.1093/plankt/fbu072>.
- Nielsen, D. L., R. A. Cook, N. Ning, B. Gawne & R. Petrie, 2016. Carbon and nutrient subsidies to a lowland river following floodplain inundation. *Marine and Freshwater Research* 67(9): 1302–1312. <https://doi.org/10.1071/MF14390>.
- Ning, N. S. P., D. L. Nielsen, T. J. Hillman & P. J. Suter, 2010. The influence of planktivorous fish on zooplankton communities in riverine slackwaters. *Freshwater Biology*. <https://doi.org/10.1111/j.1365-2427.2009.02283.x>.
- Ning, N. S. P., B. Gawne, R. A. Cook & D. L. Nielsen, 2013. Zooplankton dynamics in response to the transition from drought to flooding in four Murray-Darling Basin rivers affected by differing levels of flow regulation. *Hydrobiologia* 702(1): 45–62. <https://doi.org/10.1007/s10750-012-1306-7>.
- Oliver, R. L. & C. J. Merrick, 2006. Partitioning of river metabolism identifies phytoplankton as a major contributor in the regulated Murray River (Australia). *Freshwater Biology*. <https://doi.org/10.1111/j.1365-2427.2006.01562.x>.
- Poff, N. L. & J. K. H. Zimmerman, 2010. Ecological responses to altered flow regimes: a literature review to inform the science and management of environmental flows. *Freshwater Biology* 55(1): 194–205. <https://doi.org/10.1111/j.1365-2427.2009.02272.x>.
- Poff, N. L. R., J. D. Allan, M. B. Bain, J. R. Karr, K. L. Prestegard, B. D. Richter, R. E. Sparks & J. C. Stromberg, 1997. The natural flow regime: a paradigm for river conservation and restoration. *BioScience*. <https://doi.org/10.2307/1313099>.
- Puckridge, J. T., F. Sheldon, K. F. Walker & A. J. Boulton, 1998. Flow variability and the ecology of large rivers. *Marine and Freshwater Research*. <https://doi.org/10.1071/MF94161>.
- Rees, G. N., R. A. Cook, N. S. P. Ning, P. J. McInerney, R. T. Petrie & D. L. Nielsen, 2020. Managed floodplain inundation maintains ecological function in lowland rivers. *Science of the Total Environment* 727: 138469. <https://doi.org/10.1016/j.scitotenv.2020.138469>.
- Rolls, R. J., A. J. Boulton, I. O. Grouns, S. E. Maxwell, D. S. Ryder & D. P. Westhorpe, 2012. Effects of an experimental environmental flow release on the diet of fish in a regulated coastal Australian river. *Hydrobiologia* 686(1): 195–212. <https://doi.org/10.1007/s10750-012-1012-5>.
- Rowland, S. J., 1996. Development of techniques for the large-scale rearing of the larvae of the Australian freshwater fish golden perch, *Macquaria ambigua* (Richardson, 1845). *Marine and Freshwater Research* 47(2): 233–242. <https://doi.org/10.1071/MF9960233>.
- Shiel, R. J., 1995. *A Guide to the Identification of Rotifers, Cladocerans, and Copepods from Australian Inland Waters*, Cooperative Research Centre for Freshwater Ecology, Australia.
- Shiel, R. J., J. F. Costelloe, J. R. W. Reid, P. Hudson & J. Pawling, 2006. Zooplankton diversity and assemblages in arid zone rivers of the Lake Eyre Basin, Australia. *Marine and Freshwater Research* 57(1): 49–60. <https://doi.org/10.1071/MF05101>.
- Stahl, D. A., J. J. Flowers, M. Hullar & S. Davidson, 2013. Structure and function of microbial communities. *The*

- Prokaryotes Prokaryotic Communities and Ecophysiology. https://doi.org/10.1007/978-3-642-30123-0_34.
- Sternberg, D., S. Balcombe, J. Marshall & J. Lobegeiger, 2008. Food resource variability in an Australian dryland river: evidence from the diet of two generalist native fish species. *Marine and Freshwater Research* 59(2): 137–144. <https://doi.org/10.1071/MF07125>.
- Thorp, J. H. & M. D. DeLong, 1994. The riverine productivity model: an heuristic view of carbon sources and organic processing in large river ecosystems. *Oikos*. <https://doi.org/10.2307/3545642>.
- Thorp, J. H. & M. D. DeLong, 2002. Dominance of autochthonous autotrophic carbon in food webs of heterotrophic rivers. *Oikos*. <https://doi.org/10.1034/j.1600-0706.2002.960315.x>.
- Townsend, S. A. & M. M. Douglas, 2017. Discharge-driven flood and seasonal patterns of phytoplankton biomass and composition of an Australian tropical savannah river. *Hydrobiologia* 794(1): 203–221. <https://doi.org/10.1007/s10750-017-3094-6>.
- Wallace, T. A. & D. Furst, 2016. Open water metabolism and dissolved organic carbon in response to environmental watering in a lowland river-floodplain complex. *Marine and Freshwater Research* 67(9): 1346–1361. <https://doi.org/10.1071/MF15318>.
- Westhorpe, D. P. & S. M. Mitrovic, 2012. Dissolved organic carbon mobilisation in relation to variable discharges and environmental flows in a highly regulated lowland river. *Marine and Freshwater Research* 63(12): 1218–1230. <https://doi.org/10.1071/MF12122>.
- Westhorpe, D.P., S.M. Mitrovic, & B.C., Chessman, 2008. Integrated Monitoring of Environmental Flows. Wetting terrestrial organic matter. IMEF Phase 1: 1998–2005.
- Westhorpe, D. P., S. M. Mitrovic, D. Ryan & T. Kobayashi, 2010. Limitation of lowland riverine bacterioplankton by dissolved organic carbon and inorganic nutrients. *Hydrobiologia* 652(1): 101–117. <https://doi.org/10.1007/s10750-010-0322-8>.
- Woodward, K. B., C. S. Fellows, S. M. Mitrovic & F. Sheldon, 2015. Patterns and bioavailability of soil nutrients and carbon across a gradient of inundation frequencies in a lowland river channel, Murray-Darling Basin, Australia. *Agriculture, Ecosystems and Environment* 205: 1–8. <https://doi.org/10.1016/j.agee.2015.02.019>.

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