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RESEARCH ARTICLE

Inundation of different river bank heights influences organic matter concentrations and zooplankton abundance

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Abstract

Regulation and water extraction change flow regimes in lowland rivers, affecting ecosystem functions and wetting patterns of riverbanks. River connectivity to lateral environments is crucial for organic matter cycling and the life cycles of diapausing microinvertebrates. While extreme hydraulic periods (floods and cease-flow) are well-studied, the impact of small to medium flows on riverine carbon flux is less understood. We conducted a mesocosm study to examine litter, nutrient, and zooplankton contributions from different bank heights in the Mehi River, Australia. Sediment from three bank heights (lower, lower + middle, and lower + middle + upper) was added to 1000 L mesocosms. Upper bank heights had more organic matter, leaf litter, and live plant coverage. Sediment from upper and middle banks increased organic carbon and phosphorus concentrations. Zooplankton abundance was higher in treatments with upper bank sediment compared to lower bank sediment. Zooplankton communities varied, with rotifer taxa including *Keratella valga* and *Filinia passa* in upper bank treatments. We estimated zooplankton biomass contributions under current regulated hydrology and compared them to a predevelopment scenario without water extraction. Regulation has reduced zooplankton input from banks by about 8.8%. Inundating higher banks increases carbon and microinvertebrate availability for food webs compared to only inundating lower sections. These findings inform effective flow management strategies and highlight how targeted environmental water use can enhance lowland river ecosystem productivity.

The interaction between the flow regime and biophysical environment is an important factor influencing the health and productivity of river ecosystems (Bunn and Arthington 2002). This is particularly true in lowland rivers (Thoms and Sheldon 2000). In lowland rivers, periods of flood and low flows play a controlling role for many biogeochemical and ecological processes (Biggs et al. 2005; Junk et al. 1989). Flooding is a natural disturbance that maintains diverse floodplain and riparian habitats and vegetation, deposits and transports organic matter and nutrients, and supports biota with life-history traits adapted for wetting and drying periods. Conversely, low and stable flows can concentrate dissolved organic matter and nutrients, increasing primary production and supporting the growth and development of larval and juvenile fish (Bernhardt

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et al. 2022; Hitchcock and Mitrovic 2015a; Rolls et al. 2012). Although significant progress has been made in understanding the ecological importance of connectivity during large floods and the disconnection during low-flow periods, the importance of small hydrological events that punctuate extremes is less well understood (Poff and Zimmerman 2010).

Freshes (sometimes referred to as in-channel flows or flow pulses) are distinct short-term increases in discharge above recent average conditions (Puckridge et al. 1998). During freshes, water levels increase and inundate benches and low-lying sections of riverbanks but are generally not of sufficient magnitude to break banks and inundate floodplains. Bank profiles of lowland rivers contain diverse mosaics of organic matter and geomorphic structures, such as benches (Sheldon and Thoms 2006; Southwell 2008). Assessments of litter and surface sediment organic matter have shown that concentrations are typically higher on upper sections of river banks compared to the lower bank due to proximity to riparian vegetation and reduced frequency of inundation (Sheldon and Thoms 2006). It is therefore likely that the magnitude of fresh flow may be important for mobilizing organic matter and nutrients into the water column. The input of allochthonous materials into the river channel is an important process in supporting microbial and microinvertebrate production in many lowland systems (Balzer et al. 2024; Reid et al. 2008).

Lowland river organisms possess life history adaptations that enable them to exist under highly variable climate and flow conditions (Thoms and Sheldon 2000). Zooplankton species in lowland river ecosystems produce dormant eggs that can persist for multiple years in dry sediment (De Stasio 1990; Hairston 1996). The emergence of zooplankton from egg banks following inundation of floodplain environments leads to increases in biomass and biodiversity of zooplankton in the adjoining main stems of rivers (Ning and Nielsen 2011; Panarelli et al. 2021). The spatial distribution of zooplankton eggs across bank heights in rivers is sparsely studied. Researchers investigating the spatial variability of zooplankton egg banks have shown taxonomically distinct communities between rivers and floodplain egg banks (Ning and Nielsen 2011); more frequently inundated floodplains have a higher abundance and diversity of hatched zooplankton (Havel et al. 2000), and longer inundation may lead to increased egg abundance (Chaki et al. 2021). Riverine food webs are governed not only by the quantity of hatching zooplankton, but also by the interaction between bottom-up forces such as food availability (Hitchcock et al. 2016a; Zeug and Winemiller 2008) and top-down pressure from predation (Persson et al. 1988), as well as a broad suite of abiotic factors that include habitat, temperature, and flow characteristics (e.g., velocity, duration, frequency, magnitude) (Hitchcock et al. 2024; McInerney et al. 2023; O'Brien et al. 2025; Roach 2013).

River regulation and extraction have significantly impacted the natural flow-regimes of rivers globally (Grill et al. 2019). In particular, the frequency of freshes can be dramatically impacted by river regulation. For example, in the Murray-Darling Basin, Australia, freshes and bankfull flows have been reduced by 70–73% (Sheldon et al. 2024). This may have wide-reaching impacts on food web productivity and organic matter dynamics in rivers (Baldwin et al. 2016). In spite of a broad recognition of the utility of environmental flows as the primary management lever for the mitigation of river regulation impacts on ecosystems (Arthington 2012; Poff and Matthews 2013), fine-scale flow-ecology relationships remain poorly understood.

Here, we explore how inundating different heights of riverbanks can influence the availability of basal food resources for river food webs, including organic matter concentrations and zooplankton communities. We undertook a month-long mesocosm experiment using sediment sourced from different bank heights of the Mehi River, Australia. Following the wetting of sediment in mesocosm enclosures, organic carbon, nutrients, zooplankton, and chlorophyll *a* (Chl *a*) were monitored weekly for 4 weeks, and the results were used to estimate the contribution of zooplankton to the river from bank inundation under different flow scenarios. We expect that zooplankton biomass from sediments collected at lower bank heights will be higher than those collected from higher up the bank during the initial stage of the experiment due to more frequent inundation and potential for increased diapause eggs being deposited. However, we hypothesize this relationship will be less clear toward the end of the experiment if food resources are greatest in treatments with sediment from higher on the bank.

Materials and methods

Field site location

The Mehi River is a lowland river in northern NSW, Australia, located between the towns of Moree and Collarenebri (Fig. 1). The Mehi River is part of the broader Gwydir River catchment (26,500 km^2) within the Murry-Darling Basin, Australia. The landscape and flow regime of the catchment has been highly modified to support irrigated agriculture. Copeton Dam regulates discharge in the river upstream of Moree, while at Moree the system becomes more braided with multiple anabranches. A weir controls discharge between the mainstem of the Gwydir River and the Mehi River, and a series of smaller weirs and diversions regulate downstream hydrology. The Gwydir and Mehi River flow from east to west and join the larger Barwon River (flowing north to south). Rainfall (Average annual ~ 585 mm), and subsequent river discharge volume is interannually highly variable. The Mehi River's surrounding catchment has been extensively cleared for both irrigated and dryland cropping as well as grazing, with fringing riparian vegetation (predominantly River redgum, *Eucalyptus camaldulensis*) remaining along most of the river length. Soils on the banks of Mehi River and the surrounding

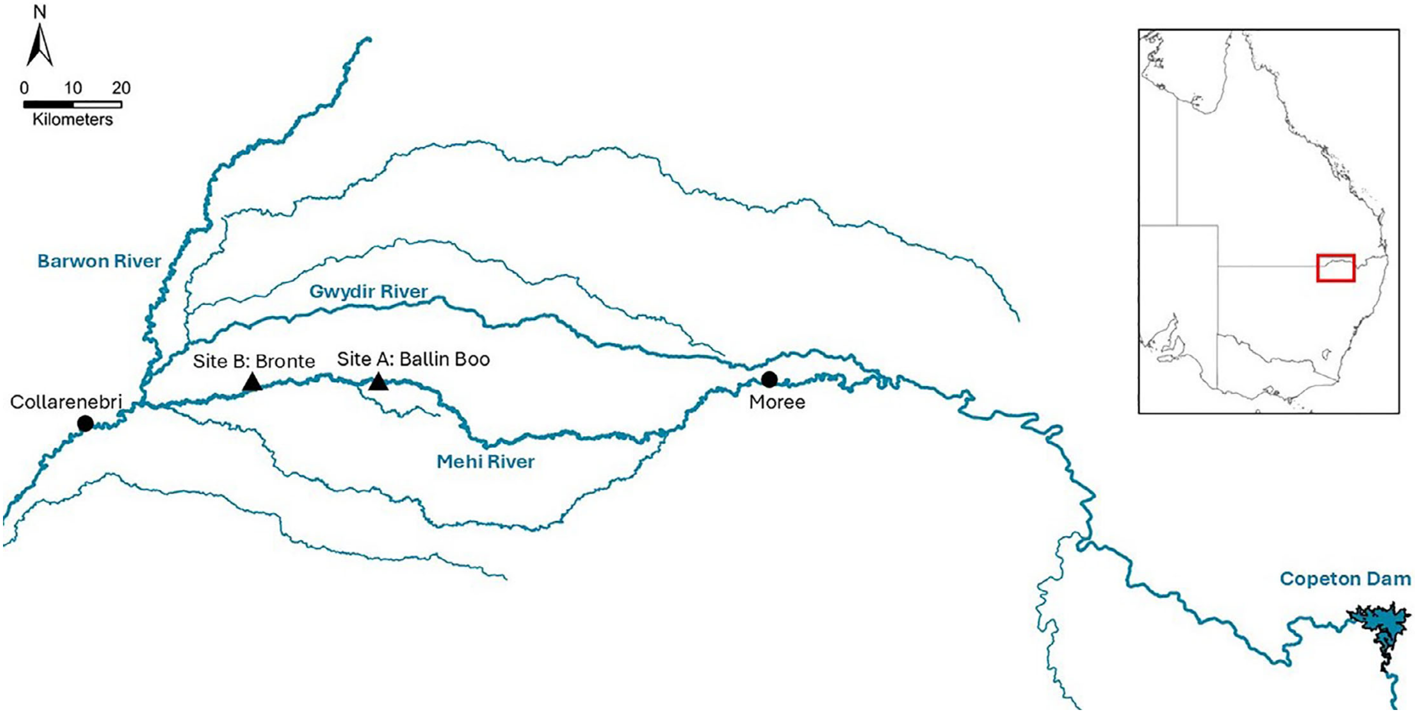


Fig. 1. Sampling locations on the Mehi River, Australia. Site A, Ballin Boo, and Site B, Bronte, are located in the lowland section of the catchment.

lowland areas are dominated by fine clay, with proportions in the upper 5 cm of the soil horizon > 60% (NSW-DPIE 2020). This results in naturally occurring high suspended sediment and turbidity within the water column. Water is managed via the Gwydir River Water Sharing Plan and the system receives environmental flows via several mechanisms including held water released from dams, restrictions on pumping during certain flow events, and a maximum annual extraction limits. Two locations were chosen as sites for this study: Site A, the Mehi River at Ballin Boo and Site B, the Mehi River at Bronte (Fig. 1). Sites were primarily selected as they were immediately downstream of gauging stations, which river height and flow recorded daily, as well as their accessibility and ease of collection and transport of large amounts of sediments.

Experimental design and field sampling

Sampling of sediment occurred on the 25th and 26th of January 2022 (at sites B and A, respectively). Sediment was collected from three bank heights at each site. Bank heights selected were low (sediment directly next to water level [~ 10 cm range]), middle (1 m above water level), and upper (2 m above water level). These heights were chosen following inspection of both sites in order to create a practical working distance between treatments to avoid disturbance and contamination and to represent the main range of bank inundation during fresh flows and are equal to approximately the 45th, 90th, and 97th percentiles of flows (calculated over the years 2012–2021). This is equivalent to discharge rates of 13.8, 360, and 1080 ML d^{-1}, respectively (Supporting Information Fig. S1). Both sites had similar inundation histories, and flow at each site remained at or below the height during sampling for the previous 4 weeks.

At each site, 50 m transects were established at low, middle, and upper bank heights. A hypsometer (Haglof Vertex Laser VL400) was used to determine the heights of transects relative to existing river gauging station height demarcations and current river height. Sediment was collected from 1 m × 0.59 m randomly selected quadrats along each transect by scraping and removing with hand trowels all leaf litter, live plants, and the first 3 cm of sediment within each quadrat. From the low section of the bank, 15 full quadrats and 3 half quadrats (0.5 m × 0.6 m) were collected; for the middle bank, 6 full quadrats and 3 half quadrats were collected; and for the upper bank, 3 full quadrats of sediment were collected. Sediment was placed in bags, and the weight of each bag was measured prior to transporting back to the mesocosm facility at the University of Canberra. It was not possible to maintain the vertical structure of the sediment during collection and transport. A photograph of every transect was taken prior to sediment collection to determine the percent cover of leaves, twigs, bark, live plants, and bare soil. Sediment was collected from five additional randomly selected intervals at each bank height and stored in bags for the determination of sediment organic matter content.

The mesocosm experiment took place from the 31st January to 1th March 2022 at the University of Canberra's mesocosm

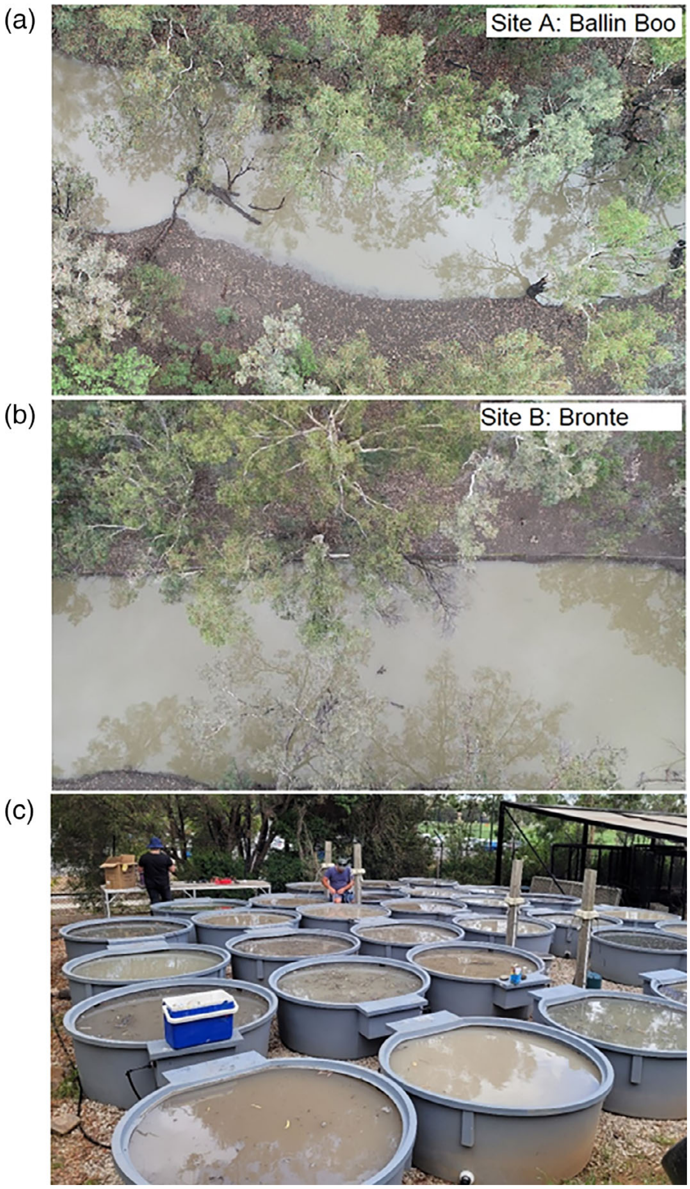


Fig. 2. Photographs of sampling locations and experimental facility. (**a**) Site A—Mehi River at Ballin Boo, showing a section of the bank sampled in the bottom part of the photo. (**b**) Site B—Mehi River at Bronte showing a section of the bank sampled in the top half of the photo. (**c**) Mesocosm facility at the University of Canberra. 1000 L mesocosms are each fitted with a pump, providing constant flow and connected to dechlorinated water system to ensure water levels are maintained throughout the experiment. Photographs of the sites were taken on the day of sampling via drone.

facility. The experiment was performed using 1000 L round plastic enclosures (1.5 m diameter, 0.57 m deep), each filled with dechlorinated water (Fig. 2). Each mesocosm was fitted with a ballcock to automatically add additional dechlorinated water to ensure volumes remained consistent at all times between mesocosms. Mesocosms contained an aerator pump to provide a circular flow within enclosures of approximately 0.1 m s^{-1} which was chosen as it is similar to water velocities during low flows in similar lowland rivers (Mallen-Cooper and Zampatti 2020) and would minimize ongoing disturbance of sediment. Each pump was fitted with a small aeration tube to ensure enclosures did not become hypoxic. Three experimental treatments were used for the experiment which consisted of added sediment from different bank heights: Low (L), Low + Middle (LM), and Low + Middle + Upper (LMU). Each treatment had three replicates. These treatments were selected to determine the potential differences between bank heights, as well as to account for any potential interactions from mixing sediment across different bank heights as may happen during flow events. The L treatment received three bags of sediment from the low bank, the LM treatment 1.5 bags from the low bank and 1.5 bags from the middle bank, and the LMU treatment one bag from the low bank, 1 bag from the middle bank and 1 bag from the upper bank. Sediment was added to mesocosms on Day 0 of the experiment (48–72 h after collection) and mixed and spread by hand evenly across the base of each enclosure prior to filling with water. Sediment volume added to mesocosms was determined to create coverage across the entire base of the mesocosm equivalent to 3 cm in depth, with the total weight of sediment added to each being 20–24 kg.

Sampling, laboratory procedures, and statistical analysis

Sampling occurred at Days 4, 8, 16, 23, and 29 of the experiment. Turbidity, temperature, conductivity, dissolved oxygen, and pH were measured with a Horiba U54 multiparameter meter. All carbon and nutrient samples were filtered using 0.45 μm polycarbonate filters and stored in pre-washed and sample-rinsed 50 mL polyethylene terephthalate (PET) bottles and frozen. Dissolved organic carbon (DOC) samples were analyzed in the laboratory by the High Temperature Combustion Method (APHA 2005). Dissolved total nitrogen (DTN) and dissolved total phosphorus (DTP) were analyzed using a segmented flow analyzer (FS3100, OI Analytical, TX, USA) according to standard methods (APHA 2005). Chlorophyll *a* samples were taken on Days 8, 16, 23, and 29 by filtering 500 mL of water onto GF/F filters. Filters were frozen until subsequent determination by Standard Methods (APHA 2005) using the grinding technique and acetone as a solute with correction for phaeophytin.

Zooplankton samples were collected on Days 8, 16, 23, and 29 of the experiment using a 5 L depth integrated sampler (total 10 L collected) and passed through a 20 μm plankton net, stored in 125 mL PET bottles, and preserved with a 70% v/v ethanol solution. In the laboratory, samples were concentrated to 10 mL. A 1 mL pipette and a Sedgewick-Rafter counting chamber were used for subsampling and counting of zooplankton. The tip of the pipette was cut to make a 4 mm diameter opening so larger zooplankton would not be undersampled. Zooplankton were counted until 100 individuals of each group were identified or at least 50% of the sample was counted. Zooplankton were identified to the highest taxonomic level feasible via keys of Shiel (1995) and Bayly (1992).

Statistical analysis and flow scenario modeling

Differences between riverbank heights of cover types and sediment organic matter content were tested via one-way ANOVA using SPSS (Ver. 28.0). Differences between treatments, time, and site for DOC, DTP, DTP, Chl *a*, turbidity, and total zooplankton were tested via a mixed model with repeated measures analysis using SPSS. Data were first $\ln(x + 1)$ transformed and tested to ensure homogeneity of variance. Estimated marginal means test was used to test for pairwise comparisons where the main test was significant. Differences in zooplankton community were tested using permutational multivariate ANOVA (PERMANOVA), with three fixed factors (site, time and treatment) with PRIMER + PERMANOVA software ver. 6 (Anderson 2001). We calculated Bray–Curtis similarities based on log transformed zooplankton abundances and tested homogeneity of variance with PERMDISP (Anderson et al. 2008). Pair-wise *t*-tests were employed with PERMANOVA to test which treatments and time periods were significantly different. Monte Carlo asymptotic *p*-values were generated to increase the number of permutations tested during *t*-tests. Rare taxa were excluded (species that were not recorded in each replicate of at least one treatment at a minimum of one time point). SIMPER analysis was used to determine which species contributed the most to differences between treatments. Principle coordinates analysis (PCO) was used to visualize changes in community structure.

To estimate the potential contribution from the inundation of different bank heights under different water management scenarios, we calculated the total average zooplankton abundance in each mesocosm treatment per m^2 for Mehi at Ballin Boo site (based on 1000 L mesocosm and 1.5 m^2 of sediment collected and added to each mesocosm). We converted zooplankton abundance to dry weight biomass using median estimates for copepods, cladocera, and rotifers from previous studies (Dumont et al. 1975). We then calculated the potential monthly zooplankton biomass input by multiplying the surface area of the bank inundated per linear river km for each month by the zooplankton dry weight per km^2 on Day 23. Two different hydrological scenarios were provided by the NSW Department of Primary Industries Water: a current scenario and a natural or predevelopment scenario (that is if no dams or water extraction existed) (for detailed information on model development and calibration, *see* NSW Department of Planning and Environment 2022). The relationship between river height within the channel and bank inundation was calculated using the linear model $\ln(m^2 \text{ inundation} = 1.2871 + (0.5217 \times [\text{river height} + 1]))$. The model was calculated using elevation data collected by photogrammetry using images captured with a DJI Phantom 4V2 drone and processed using the WebODM software. The value used each month varied depending on the maximum bank height inundated (that is if river inundation height only reached lower bank level the values from the lower bank treatment were used, if the maximum inundation height reached middle bank height, the values from the LM treatment were used, etc.). We note that these modeling calculations are used to explore how bank inundation under different water management scenarios may impact river zooplankton populations rather than provide discreet predictions.

Results

Ground cover varied significantly between riverbank heights and sites ($p < 0.01$; Fig. 3a,b). At Site A, ground cover at the low transect was significantly different ($p < 0.01$) from the middle and high transects, with an increased amount of bare sediment and lower levels of live plants, leaves, twigs, and bark. At Site B, ground cover was significantly different between all riverbank heights ($p < 0.05$) with decreasing bare soil coverage with height up the riverbank and increasing coverage of live plants, bark, twigs, and leaves. There was also a significantly higher ($p < 0.01$) coverage of leaves and bark for the low transect at Site A compared to Site B. Sediment organic matter content was significantly different between riverbank heights but not between sites ($p < 0.01$; Fig. 5c). At Site A, sediment from the upper transect level had significantly higher ($p < 0.05$) organic matter compared to the middle bank height, and in turn, the middle bank height had significantly higher organic matter than sediment from the low bank height. At Site B, the upper transect had significantly higher ($p < 0.01$) organic matter than the lower transect, and there were no significant differences between the upper and middle, or middle and low transects.

Organic carbon concentrations varied significantly between treatments, sampling day, and time (Fig. 4a,b; Table 1). At Site A, DOC was significantly higher ($p < 0.05$) on Day 4 in the LM and LMU treatments compared to the L treatment, and remained highest in the LMU treatments throughout the experiment. At Site B, DOC was significantly higher ($p < 0.05$) in the LMU treatment compared to the L treatments at Days 4, 8, 23, and 29, and higher than the LM treatment at Days 4 and 23. The LM treatment was significantly higher ($p < 0.05$) than the L treatment at Day 8 only.

Nitrogen concentrations were significantly different between day, site, and treatment. Concentrations were significantly higher for treatments LM compared to L at Day 4 for both sites and Day 8 for Site B, and significantly higher for the LMU treatment compared to the L treatment at Day 4 for Site B and Day 8 for Site A (Fig. 4c,d; Table 1). Phosphorus concentrations varied significantly ($p < 0.05$) between day, site, and treatment and were significantly higher ($p < 0.05$) in the LM

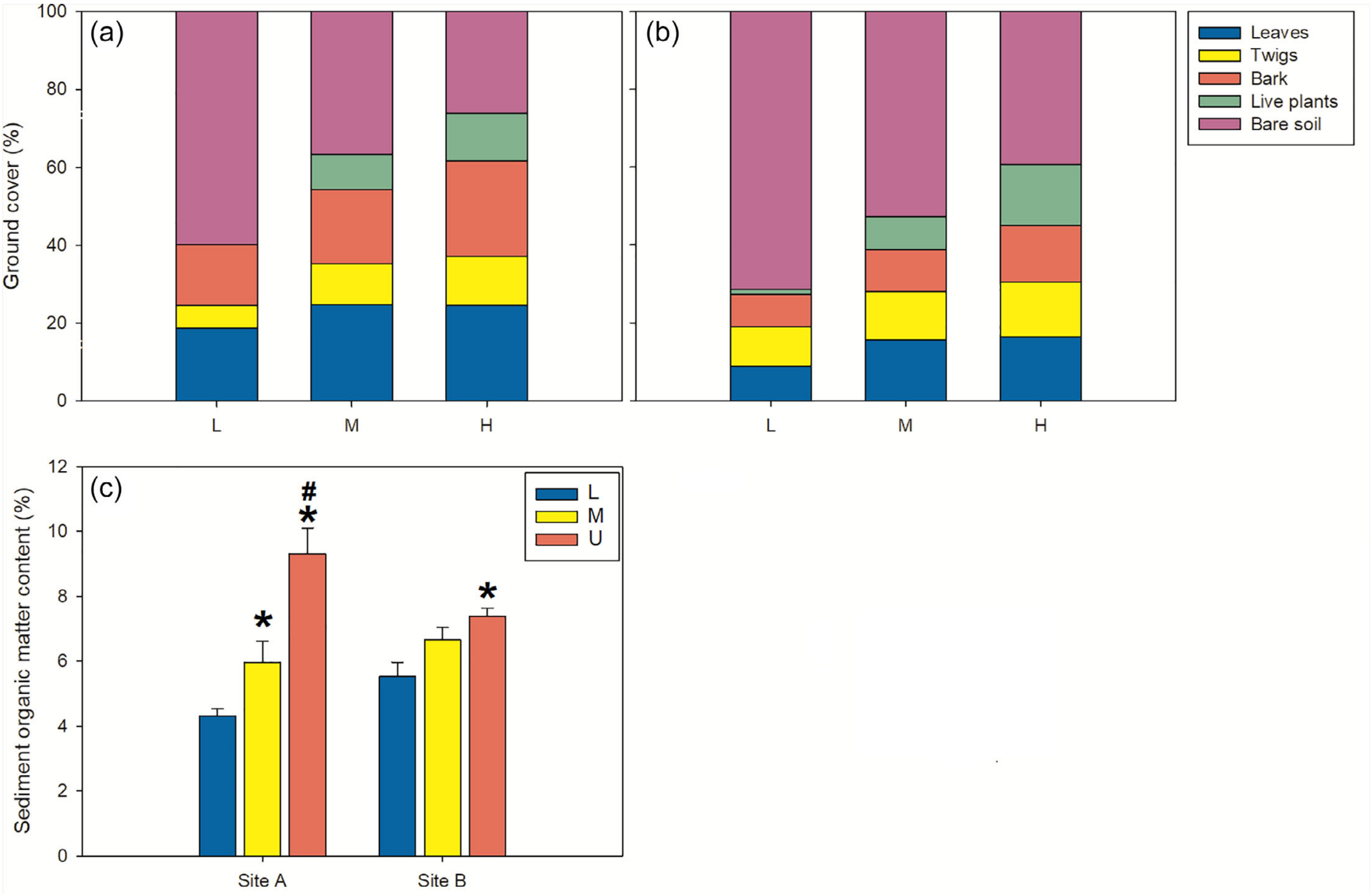


Fig. 3. Initial bank and sediment conditions for sites on the Mehi River. (**a**) The percentage of leaf litter and bare ground cover for transects at Site A, Mehi at Ballin Boo, and (**b**) Site B Mehi at Bronte. (**c**) Mean (± SE, $n = 5$) Percentage organic matter content in the sediment for the transects on the Mehi River. * denotes treatment significantly different to the L treatment, and # denotes treatment significantly different to LM treatment.

and LMU treatments compared to the L treatment (Fig. 4e,f) and higher in the second half of the experiment compared to the first half.

Chlorophyll *a* concentrations remained low at all times during the experiment. Concentrations varied significantly between treatments, day, and site (Fig. 5a,b; Table 1). At Site A concentrations were significantly higher in the L treatment compared to LM treatment at all times, and the LMU treatment at Day 8. At Site B Chl *a* concentrations were overall higher compared to the Site A. The only significant difference between treatments for Site B occurred at the start of the experiment at Day 8 when Chl *a* was significantly lower the LMU treatment compared to the other treatments. Turbidity varied significantly ($p < 0.05$) between treatments, day, and site (Fig. 5c,d; Table 1). Turbidity was typically significantly higher in the L treatment compared to LM and LMU, and was higher in mesocosms with sediment from Site A compared to B. Overall turbidity in the water column reduced with time over the experiment. Other measures taken did not vary clearly between including water temperatures (ranged 14.7–22.5°C), conductivity (0.119–0.173 ms cm^{-1}), pH (7.20–7.96) and dissolved oxygen (59–112%).

Zooplankton abundance showed significant differences ($p < 0.01$) between treatments, day, and site (Fig. 6a,b; Table 1). At the start of the experiment, zooplankton abundance did not vary between treatments. From Day 16 onward, zooplankton abundance was significantly higher ($p < 0.05$) in the LMU treatment compared to the L and LM treatments at Site A but not Site B. In the last week of the experiment, zooplankton abundance was significantly higher ($p < 0.05$) for LMU compared to L at Days 23 and 29 for both Site A and B mesocosms, and the LM treatment was higher than the L treatment at Day 23 for Site A.

Zooplankton community was significantly different between days, treatment, and height (Supporting Information Tables S1, S2; Fig. 6c,d). Rotifers dominated the zooplankton community at Days 8 and 16, with the highest abundances being *Keratella valga*, *Filinia passa*, *Brachionus urceolans*, and *Polyarthra* sp. as well as high numbers of copepod nauplii (Fig. 7). The same rotifer species remained the most dominant

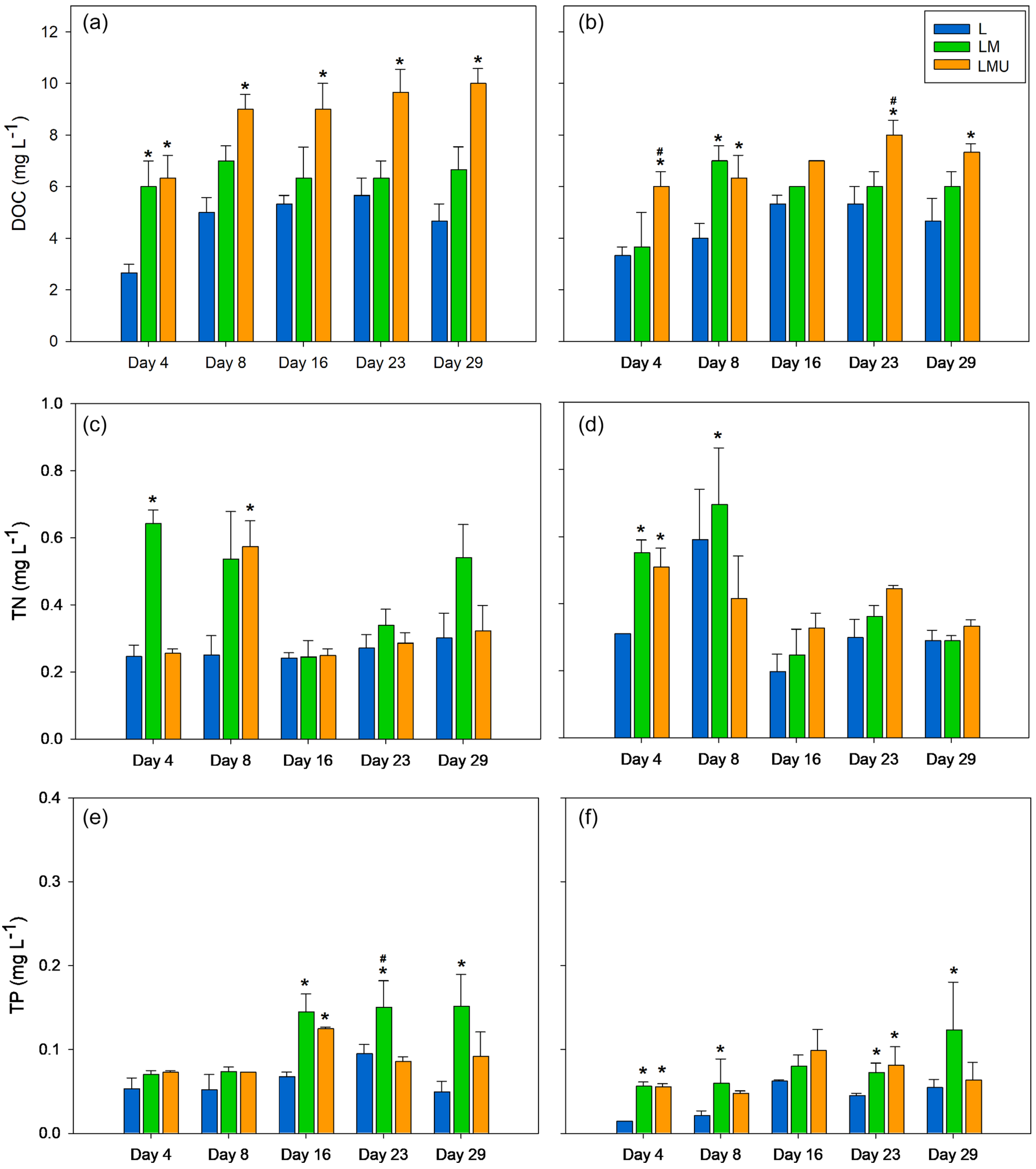


Fig. 4. Nutrient results for Mehi River mesocosm experiment between Days 4 and 29. (**a**) Dissolved organic carbon concentrations for Site A, and (**b**) Site B. (**c**) Dissolved total nitrogen concentrations for Site A, and (**d**) Site B. Dissolved total phosphorus concentrations for Site A (**e**), and (**f**) Site B. Error bars are standard error, $n = 3$. * denotes treatment significantly different to the L treatment, and # denotes treatment significantly different to LM treatment.

Table 1. Results of mixed model ANOVA (with repeated measures) for DOC, DIN, SRP, NTU (turbidity), ChlA (chlorophyll *a*), and Zoop (total zooplankton abundance). Values are *F*-values. ns = not significant, $^*p < 0.05$, $^{**}p < 0.01$, $^{***}p < 0.001$. $n = 3$.

	DOC	DTN	DTP	NTU	ChlA	Zoop
Day	7.33***	19.70***	3.26*	8.99***	3.411*	158.21***
Site	5.99*	17.90***	13.22**	81.38***	36.11***	4.99 ns
Treatment	32.11***	13.33***	17.86***	30.33***	10.39***	43.43***
Day × Site	0.51 ns	14.34***	14.15***	3.12***	11.27***	6.91***
Day × Treatment	2.32*	6.37***	2.82*	0.89 ns	2.95*	7.95***
Site × Treatment	1.30 ns	2.71 ns	1.5 ns	2.25 ns	3.56*	3.88*
Day × Site × Treatment	1.56 ns	4.67***	2.04 ns	1.38 ns	1.437 ns	1.98 ns

throughout, though by Day 29, rotifers declined in numbers, with only *K. valga* and *F. passa* remaining in higher abundance. Large zooplankton were present from Day 16, with the cladocera *Moina tenuicornis* and calanoid copepod *Boeckella triarticulata* as the dominant species. Egg-bearing adult females of *B. triarticulata* were visible in samples from Day 16. Egg-bearing individuals of the rotifers *K. valga* and *B. urceolans* were visible from Day 8. Zooplankton community structure

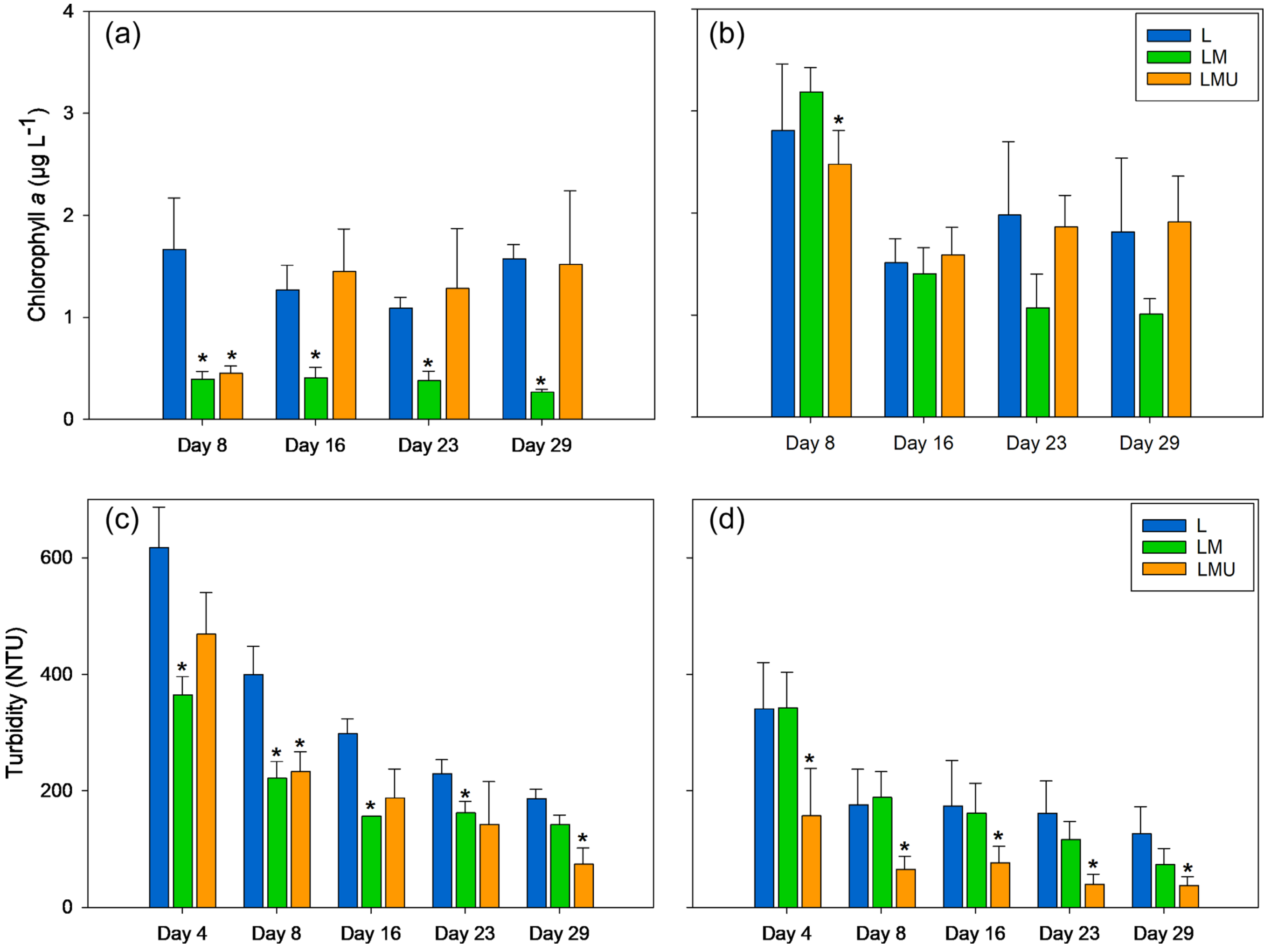


Fig. 5. Chlorophyll *a* (Chl *a*) and turbidity results for Mehi River mesocosm experiment. (**a**) Planktonic Chl *a* concentrations for Site A and, (**b**) Site B. (**c**) Turbidity measurements for Site A, and (**d**) Site B. Error bars are standard error, $n = 3$. * denotes treatment significantly different to the L treatment, and # denotes treatment significantly different to LM treatment.

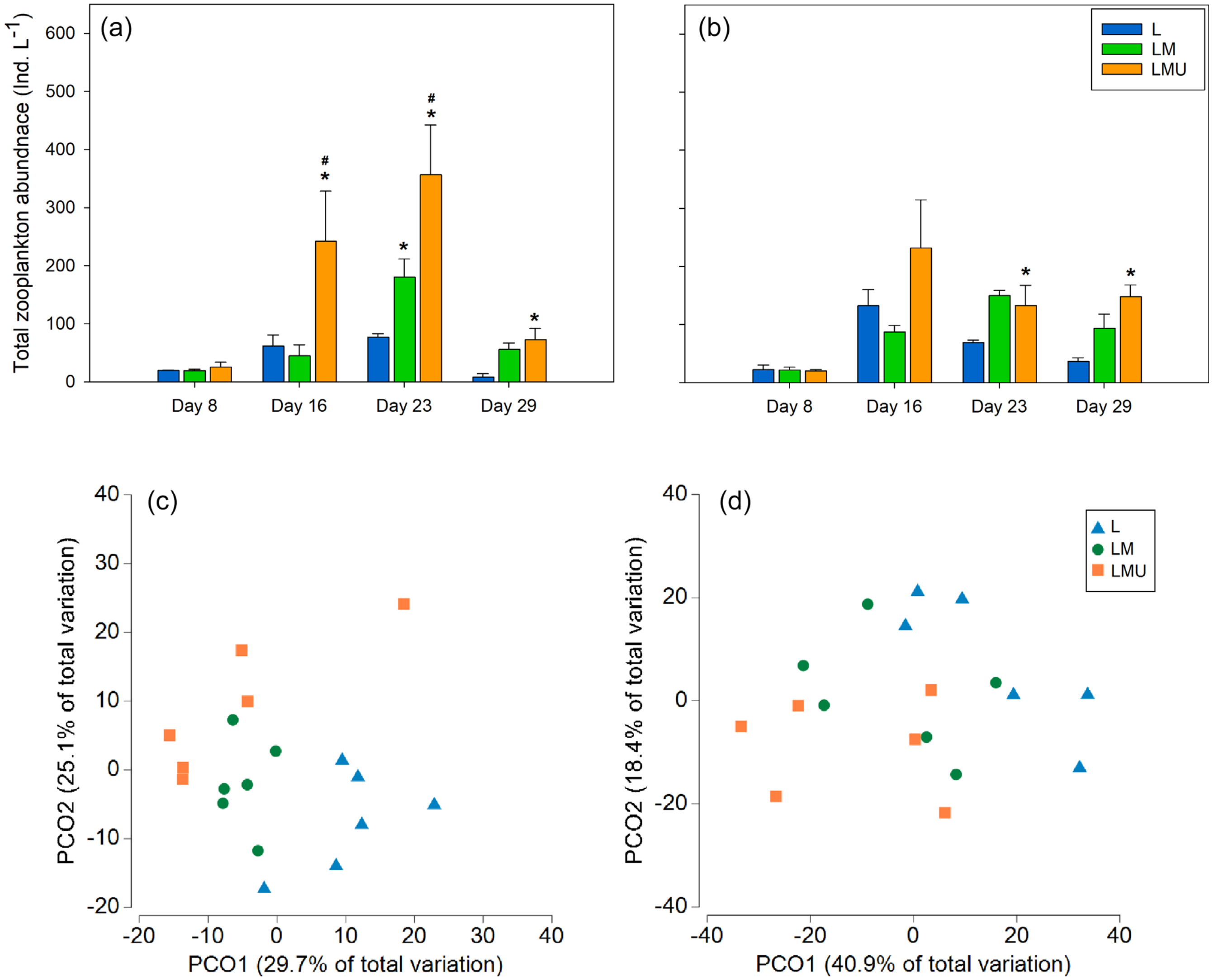


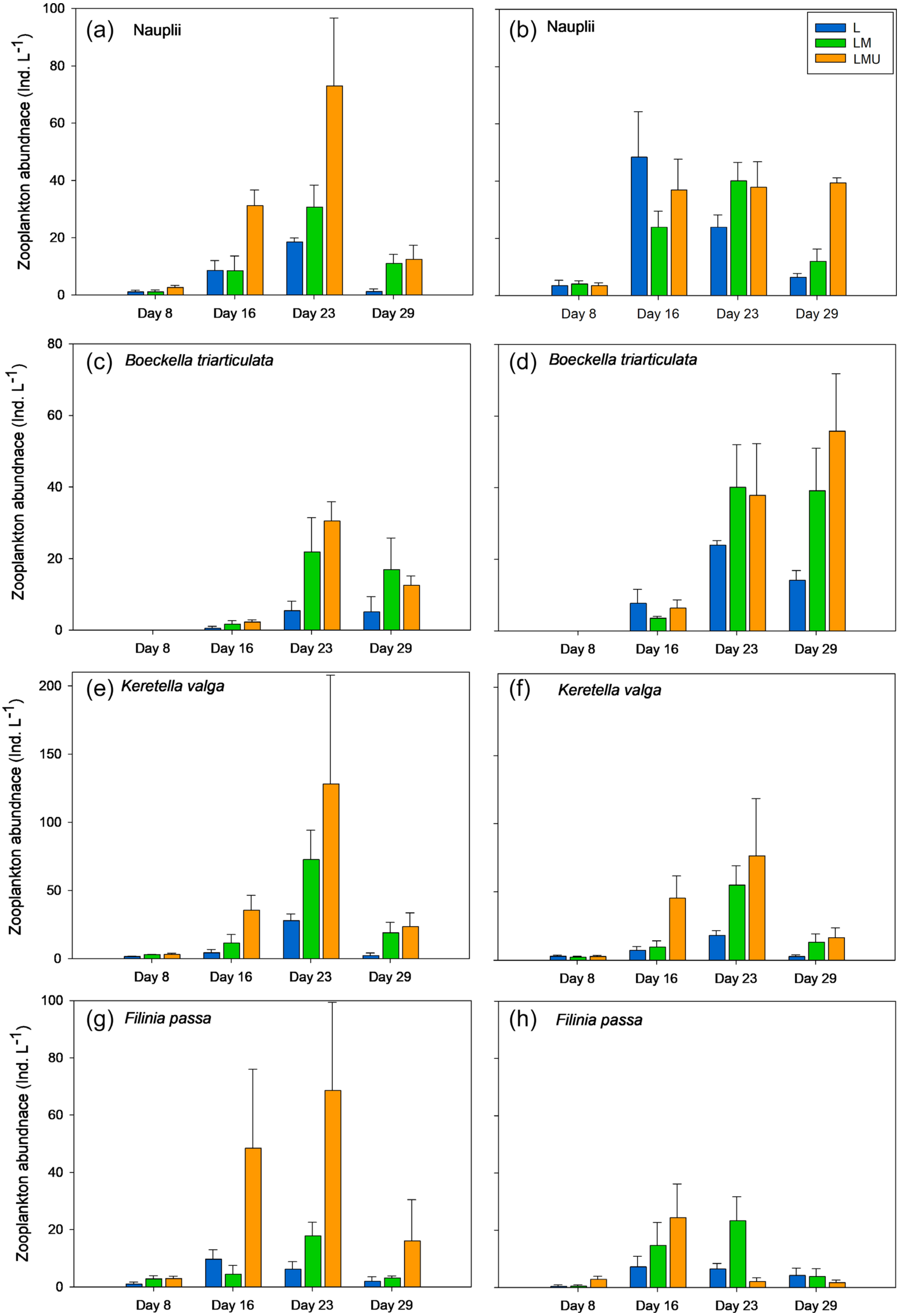
Fig. 6. Mean total zooplankton and difference in assemblage structure between treatments (**a**) Total zooplankton abundance at Site A. (**b**) Total zooplankton abundance at Site B. (**c**) PCO analysis of zooplankton community at Day 23, and (**d**) Zooplankton community at Day 29. Error bars for (a) and (b) are standard error, $n = 3$. * denotes treatment significantly different to the L treatment, and # denotes treatment significantly different to LM treatment.

was similar at both sites; the major differences were the presence of *Daphnia lumholtzi* and *Daphnia carinata* at Site B, while only *D. carinata* was present at Site A, and the presence of rotifer *Lepadella* sp. at Site B, which was largely absent at Site A. SIMPER analysis showed that for treatments that were significantly different, *B. triarticulata*, *M. tenuicornis*, *F. passa*, *K. valga*, *nauplii*, *and Polyarthra* sp. contributed the most to dissimilarity (Supporting Information Table S4).

Linear modeling of zooplankton emergence in mesocosm experiments revealed that for the period 1993–2022, there was an estimated average additional 6.3 kg per year (dry weight) of zooplankton per linear kilometer attributable to changes in river height wetting bank sediments (Fig. 8). In contrast, the estimation of additional biomass of zooplankton from changing river heights under a predicted natural hydrology was 0.6 kg per linear km higher (8.8%). Zooplankton biomass contributions varied between years (Fig. 8), with wetter years (1995, 1996, 2001, 2010, 2012, 2016, 2022) contributing more biomass to the river under the natural hydrology scenario. Under the current regulated river scenario, drier years (1998, 2006, 2014, 2017) had higher zooplankton biomass contributions.

Discussion

As hypothesized, our mesocosm experiments revealed that sediment collected from upper bank heights contained significantly more organic matter, leaf litter, and live plant coverage



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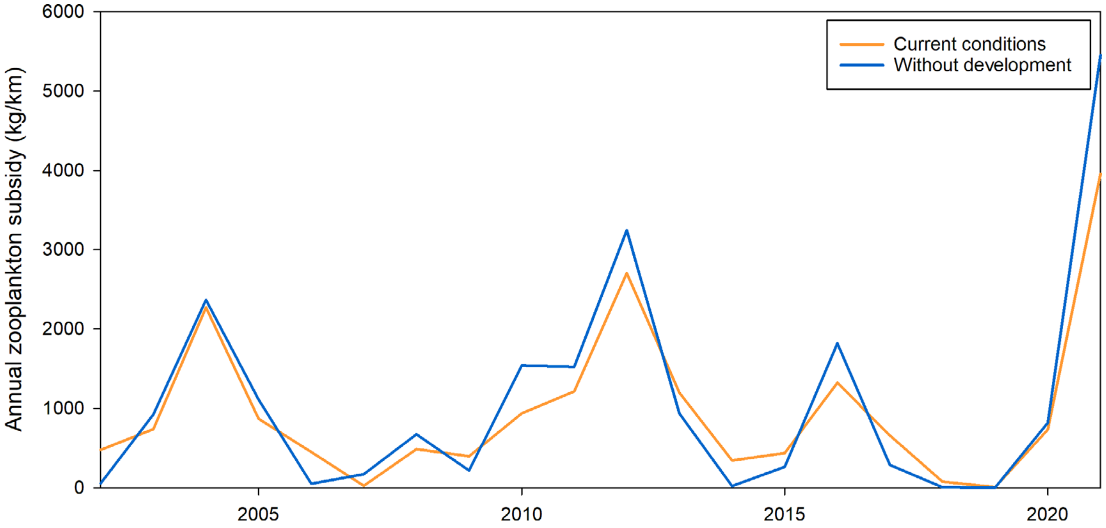

Fig. 8. Estimates of annual dry weight zooplankton input to the river from the banks per linear river km for the years 1993–2022. The two hydrological scenarios tested were current conditions and without development (which models hydrology without regulation or extraction). The shaded areas represent 95% confidence intervals.

than sediment collected from lower heights. This resulted in higher concentrations of organic carbon and phosphorus in mesocosms that received sediment from upper banks compared to just the low bank. We also hypothesized that zooplankton density would initially be higher in the treatment that received sediment from only the lower bank, as they are more frequently inundated, and that densities would become higher in treatments with sediment from the upper bank at the end of the experiment, as there would be additional food resources if organic matter concentrations were higher. Our results did not support the first part of this hypothesis, as zooplankton densities were not different between treatments at the start of the experiment and were, in fact, higher in the LMU treatment for one site at Day 16. The results did support the second part of the hypothesis, with zooplankton densities significantly higher in mesocosms that contained sediment collected from upper banks. Our results also showed that zooplankton communities were significantly different between treatments, with much higher numbers of the taxa *B. triarticulata, M. tenuicornis*, *F. passa*, *K. valga*, and *F. passa* emerging from the LMU treatment containing sediment collected from higher up the bank profile compared to the treatments that received only lower bank sediment.

Organic matter and nutrient dynamics

Concentrations of organic carbon were higher in the mesocosms with sediment from the upper and the middle bank compared to the lower bank. Similarly, sediment organic matter and percent litter cover vs bare soil showed the same pattern in relation to bank height. Other studies have found higher litter and organic matter loads closer to the riparian zone and suggest the proximity to terrestrial vegetation is an important factor (Sheldon and Thoms 2006). Vegetation cover and morphology of our study sites is similar to that of many lowland rivers globally (Carling and Petts 1992), though the variability of flow and inundation is typically much higher in Australian rivers compared to those of the northern hemisphere (Finlayson and McMahon 1988). Inundation frequency is another important factor that influences allochthonous inputs to river ecosystems (Xie et al. 2019). del Campo et al. (2021) recently showed leaf litter not only accumulates but undergoes chemical transformation leading to increased decomposition rates after wetting in dryland rivers. In this study, both sites and bank heights had been last inundated approximately 6 weeks prior to our sediment collection, and thus, litter accumulation was largely similar. Differences between treatments reflect spatial variations in bank height more so than recent inundation history. We expected that DOC inputs from the upper banks would be higher with greater litter accumulation time (Sutfin et al. 2016) and more duration between inundation events.

Bank sediments in lowland riverbanks undergo highly variable patterns of wetting and drying, resulting in complex nitrogen and phosphorus cycling patterns (Baldwin and

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Fig. 7. Mean zooplankton abundance for most common zooplankton taxa in the Mehi River mesocosm experiments. (**a**) mean nauplii abundance for Site A, and (**b**) Site B. (**c**) Mean abundance of *Boeckella triarticulata* for Site A, and (**d**) Site B. (**e**) Mean abundance of *Keratella valga* for Site A, and (**f**) Site B. (**g**) Mean abundance of *Filinia passa* for Site A, and (**h**) Site B. Error bars are standard error, $n = 3$.

Mitchell 2000; Schönbrunner et al. 2012). In our experiment, nitrogen concentrations were generally higher in mesocosms that received sediment from the middle and upper banks, highest in the first week of the experiment, and decreased in concentration thereafter. These results indicate the release of nitrogen and subsequent assimilation by microbes in banks was more rapid than can occur following the wetting of floodplain sediment (Kobayashi et al. 2009; Ostojić et al. 2013). Both nitrogen and phosphorus were higher in mesocosms with sediment from higher banks, indicating that similar to organic carbon, proximity to riparian vegetation is an important driver of nutrient concentrations derived from riverbanks. Phosphorus concentrations were slightly higher in the latter half of the experiment, which was unexpected. Potential reasons for this may be the gradual release of P from the hydrolysis of organic phosphorus facilitated by microbial production of exo-enzymes during the process of degrading complex organic materials (Richardson and Simpson 2011). In addition, heterotrophic bacteria that have a high affinity for P may have been nutrient limited, either by available carbon or nitrogen, thus allowing P accumulation later in the experiment (Hitchcock and Mitrovic 2013; Hitchcock et al. 2010). In rivers, anoxic conditions may be more common following larger freshes, and reduction processes may have an important role in nutrient release (Baldwin and Williams 2007). In our mesocosms, these processes were likely less important as they were kept aerated and dissolved oxygen never fell below 50%.

The nutrient and other key parameters observed in this study are within the same ranges as observed in the Mehi River. Recent water quality reporting at the same location as Site B found median scores for turbidity and nutrients of 165 NTU, 1.25 mg L^{-1} TN, and 1.8 mg L^{-1}TP (DECCEEW 2024). A previous study some of these authors have contributed to in the adjacent Namoi and Macquarie River catchment found DOC, Chl *a*, and zooplankton abundance all within similar ranges to this study (Balzer et al. 2024; O'Brien et al. 2025). This suggests the results observed in this experiment appear to represent conditions similar to those that occur in situ.

Microinvertebrate dynamics

Flow regimes play an important role in the life histories of many zooplankton species in lowland rivers. The variability of flow and flooding of wetlands and floodplains can lead to diverse assemblages of microinvertebrates emerging from sediment (Boulton and Lloyd 1992). Our results demonstrated that both zooplankton abundance and community structure significantly differed between bank height inundation. We hypothesize these results are likely due to a combination of differences in egg bank densities between bank heights and differences in basal resources (organic matter and nutrients) that may support ongoing production of emergent zooplankton populations.

There were distinct differences in egg bank communities between bank heights; there were rotifer taxa present at Day 8 and 16 in the LM and LMU mesocosms that were absent in the L mesocosms. These included *Euchlanis* sp., *Keratella australis*, *Platyias quadricornis*, and *Trichotria pocillum*. Limited information exists on how egg bank communities may vary between bank heights. Ning and Nielsen (2011) compared egg bank communities between wetlands and slackwater sections of rivers, finding 31 taxa present in total, with only 12 common to both environments. They suggest the differences in taxa may be due to respective abiotic and biotic forces for the two environments that may include direct influences (such as dispersal, sediment movement and mixing, patterns of hatching and emergence and degradation) and indirect influences (active population presence and dormancy induction patterns/cues of individual taxa). The presence of taxa in mesocosms receiving sediment from upper and middle sections of the bank that were absent in mesocosms that received sediment from the lower bank may be due to factors such as the proximity to the floodplain that may have distinct community and different microhabitats on the upper bank, including the presence of live plants that may provide habitat or refuge for some taxa (Choi et al. 2013).

Zooplankton abundance was significantly higher in the last 2 weeks of the experiment in the mesocosm receiving sediment from the upper bank, followed by middle sections of the bank. These results indicate that increased secondary production rather than purely increased emergence rate may be important since these differences were not visible at Day 8, and exploratory analysis of the relationship between zooplankton abundance and environmental variables found DOC to have a positive relationship with zooplankton abundance (Supporting Information Fig. S3). Further, the visible presence of reproductive individuals of the rotifers *Keratella* and *Brachionus* post-Day 8, and egg-bearing copepods visible from Day 16 provide additional support for elevated production. This also indicates how quickly populations can boom in situ following inundation. It is likely that the higher loads of organic matter supported microphagous rotifers that consume fine particulate organic matter and small protists directly, such as *F. passa* and *Brachionus* spp. Additionally, the higher organic matter loads likely supported increased biomass of bacteria, ciliates, and other protists, which can act as an important additional food subsidy to zooplankton. Other mesocosm studies have shown the addition of DOC can support increased zooplankton abundance mediated through intermediary protists (Balzer et al. 2023; Hitchcock et al. 2016b; Mitrovic et al. 2014; Tang et al. 2023). Further evidence that processes related to higher flows and bank inundation are important in understanding zooplankton dynamics in lowland rivers, a recent study on the Namoi River, Australia (the next major river south of the Mehi River) found zooplankton abundance during low flow periods ranged from 0.5 to 13 individuals L^{-1}, however, following high flows increased to between 231 and 1072 individuals L^{-1} (Balzer et al. 2024).

The unexpected lower zooplankton concentration in the low bank treatment, despite higher Chl *a* relative to the low-mid bank, challenges the assumption of direct bottom-up control in our experiments. Phytoplankton, particularly if dominated by diatoms as is often the case in lowland Australian rivers (Croome et al. 2011), can represent a high-quality food source rich in essential long-chain omega-3 polyunsaturated fatty acids (e.g., eicosapentaenoic acid) that enhance somatic growth and reproduction in animals (Brett et al. 2009). However, the observed discrepancy suggests other factors may have driven patterns. It is possible that abundant, high-quality resources in the low bank treatment promoted increased individual growth (McInerney et al. 2022), rather than numerical abundance in the zooplankton population. Alternatively, phytoplankton may have been dominated by poor food quality or unpalatable autotrophs, such as cyanobacteria. Future studies should consider determination of phytoplankton components and quantification of changes to consumer biomass when assessing the role of bottom-up controls of zooplankton communities.

Implications for restoring flows and managing lowland rivers

Central theories of river function in lowland rivers have conceptualized overbank flooding as the primary source of material that provides energy and drives river food webs (Junk et al. 1989; Junk and Wantzen 2004; Tockner et al. 2000). While over longer temporal scales it is true these large events transport massive amounts of organic matter and lead to huge booms in production (Cook et al. 2015), most of the time rivers are restricted to their channels and sources of energy driving them fluctuate. Thorp and Delong (1994) emphasized the importance of local production, highlighting local primary production in constricted lowland systems, but also the importance of inputs from the edge of the rivers, including the banks. Those ideas are similar to the out-welling hypothesis in estuarine systems (Odum 2000) that describes the importance of inputs from the banks and riparian zone during regular inundation as important productivity drivers. In lowland rivers, freshes have typically received less attention as an important hydrologic function driving river productivity and food webs (Hitchcock and Mitrovic 2015b). The results of this study demonstrate that fresh flows are likely vital processes promoting the productivity of lowland river ecosystems both in terms of microinvertebrate dynamics and biogeochemical cycling of organic matter through enhanced connectivity to riverbanks.

We estimated the contribution of bank inundation to zooplankton input to the river under two different flow scenarios, current conditions, and without development, to explore the implications of the results and provide an estimation of how river regulation has disrupted this ecological process. While the results showed an overall reduction under current conditions, zooplankton contribution from the bank inundation varied from year to year under the scenarios. During wetter years with higher flows, for example, 2016 and 2021, zooplankton inputs were much higher in the without development scenario. This is expected as the dam and water extraction reduce flows downstream, and in turn, the extent of bank inundation. However, during the onset of a dry period (for example 2014, 2017), when flow is typically low, the contribution of zooplankton input is higher under the current conditions scenario due to releases of water from the upstream Copeton Dam. The lowest contributions across the time period modeled occurred during the drought of 2018–2019, which was characterized by a period of cease-to-flow under both scenarios. Further research monitoring of in-situ zooplankton dynamics is needed to confirm this pattern.

In interpreting the implications of these results, there is uncertainty in assigning the relative importance of zooplankton contributions from bank sediment to river populations compared to longitudinal drift and in-water production. There are a few studies that report estimates of zooplankton production rates due to the time-consuming nature or reliability of methods (Kobari et al. 2022; Yebra et al. 2017), making comparisons to biomass inputs from bank sediments difficult. Riverine zooplankton may be considered to be ephemeral, have rapid generation times, and respond to external conditions rapidly (Hairston 1996 and references therein). For example, rotifer taxa can reproduce rapidly via parthenogenesis, resulting in a theoretical population doubling time of less than a week (Nandini et al. 2007). Zooplankton employ different physiological and reproductive strategies in response to environmental conditions such as drought and floods. Almost all zooplankton taxa of inland rivers have life-history traits related to dormancy (Hairston and Cáceres 1996). As the occurrence of dormancy is generally related to adverse environmental conditions, and lowland rivers regularly experience hydrologic and climatic extremes, it is likely these processes are relatively more important here compared to temperate systems with more consistent hydrology (Hairston 1996). Further research is needed to understand the relative importance of these processes to in-situ zooplankton production.

Here, we demonstrate the influence of variable in-channel hydrology on riverine organic matter flux. We provide clear evidence of the differences that occur when inundating riverbanks at different channel heights in relation to basal resource availability and zooplankton emergence. Management of individual flow components for ecological outcomes has become the mainstay of modern river and catchment management activities. Despite aspirations, river regulation for consumptive use limits the ability to deliver the minimum hydrological requirements to sustain ecosystem health (Sheldon et al. 2024). Acknowledging the limitations of our mesocosm study from one river, we provide useful information to assist managers responsible for environmental water delivery. Our work shows that the damming, regulation, and extraction of water from the Mehi Rivers has reduced zooplankton biomass additions caused by hydrological variation by as much as 8.8%. We provide information for how restoration of higher volume freshes can benefit lowland river ecosystems. We recommend further research is needed to understand the broader importance of zooplankton inputs from banks to broader riverine zooplankton dynamics.

Author Contributions

James N. Hitchcock: conceptualization, formal analysis, investigation, methodology, visualization, writing – original draft preparation, writing – review and editing. **Andrew J. Brooks:** conceptualization, formal analysis, investigation, methodology, writing – original draft preparation, writing – review and editing. **Tim Haeusler:** formal analysis, investigation. **Paul J. McInerney:** writing – review and editing. **Dane F. Parsons:** investigation. **Ross M. Thompson:** writing – review and editing.

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Conflicts of Interest

None declared.

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

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