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Environmental Flows Rapidly Increase Zooplankton Abundance in a Regulated Lowland River

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ABSTRACT

Zooplankton are important parts of the food web that support the survival of larval fish in floodplain rivers. Zooplankton abundance and community structure are sensitive to flow-driven changes in the environment, which have been heavily impacted by river regulation with dams. Environmental flows (e-flows) are managed dam releases designed to restore a degree of natural ecological functioning to regulated rivers. Native fish spawning can be triggered by e-flows, but it is not well understood whether these flows can stimulate instream zooplankton production in an appropriate timeframe to support feeding by fish larvae in their first weeks of life. This study aimed to investigate the immediate and longer-term impacts of a planned dam release during the drought of 2018 in the Macquarie–Wambuul River of New South Wales, Australia, on the abundance of zooplankton and associated environmental variables. Dissolved organic carbon, nitrogen oxides (NOx) and chlorophyll *a* increased significantly at the onset of the e-flow. The zooplankton community was dominated by Cladocera (also named Diplostraca). The significant drivers of zooplankton community structure were NOx, temperature and river level. The start of the e-flow coincided with a significant increase in cladoceran densities, which resulted in up to $36.2 \times 10^9 \pm 1.5 \times 10^9$ Cladocera d^{-1} being exported through the study sites. Increased zooplankton exports were maintained for at least 6 weeks after the onset of the e-flow. These findings demonstrate that e-flows during drought can stimulate increased zooplankton abundance within appropriate timeframes to support the survival of native fish larvae.

1 | Introduction

Zooplankton are integral components of riverine food webs. They allow energy to flow from heterotrophic microbes and phytoplankton to higher-order consumers, such as fish (Degerman et al. 2018; King 2005). Zooplankton abundance and community structure are sensitive to multiple environmental drivers, including dissolved organic carbon (DOC) (Hitchcock, Mitrovic, Hadwen, Roelke, et al. 2016; Mitrovic et al. 2014), temperature, dissolved oxygen and turbidity (Ning et al. 2013), many of which are governed by river flow regimes (Balzer, Hitchcock, Kobayashi, et al. 2023).

Flow magnitude, velocity, frequency and timing also have direct impacts on riverine zooplankton populations (Bunn et al. 2006; Hitchcock, Mitrovic, Hadwen, Growns, and Rohlfs 2016). Large inflows can increase water velocity and inundate disconnected in-channel or floodplain habitats, causing bulk transport of zooplankton from highly productive still waters and littoral zones to the main river channel (Dole-Olivier et al. 2000; Ning et al. 2010). When conditions are suitable for reproduction, eggs are deposited in river channel and floodplain sediments (Nielsen et al. 2000), forming egg banks that are resistant to long periods of drying and environmental stress (Dole-Olivier et al. 2000). When dried sediments are rewetted during times of high flow,

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large influxes of zooplankton are possible within days (Boulton and Lloyd 1992; Chaki et al. 2021a; Nielsen et al. 2000).

The natural flow regime of many major rivers worldwide has been heavily modified by river regulation (Nilsson et al. 2005). Regulating structures, particularly dams, change the magnitude, timing and frequency of river flows downstream of the dam (Maheshwari et al. 1995), intersect longitudinal connectivity with river headwaters and decrease lateral connectivity with the floodplain (Ward and Stanford 1995). The lentic environment in dams can also change the concentration and chemical composition of dissolved organic matter and inorganic nutrients (Baldwin et al. 2010), change river temperature (Michie et al. 2020) and alter biotic communities in waters released from the dam (Facey et al. 2022). These changes in flow can have large impacts on downstream zooplankton communities, including changes in community composition, diversity and abundance downstream of the dam (Czerniawski and Domagala 2014; Sługocki et al. 2021). Dams can also act as a source of zooplankton to the downstream river, though this will be minimal in large dams that release hypolimnion bottom waters (Lair 2006).

Zooplankton production supports the growth and recruitment of several threatened native fish species in the highly regulated rivers of Australia's Murray–Darling Basin (MDB) (King 2005; Tonkin et al. 2006). Nearly 70% of mean annual inflows to the MDB are captured by dams, and natural flow regimes have consequently been severely impacted (Maheshwari et al. 1995; MDBA (Murray-Darling Basin Authority) 2011). To mitigate the detrimental impacts of river regulation, river managers can use environmental flows (e-flows) to mimic components of the natural flow regime and restore a degree of natural ecological functioning to degraded river systems (Arthington 2012). E-flows are releases of water held within a dam, or restrictions on extracting river flows, intended to improve the health of the river system. River managers design e-flow plans to meet specific ecological objectives, often including support of threatened native fish populations. For example, Golden perch (*Macquaria ambigua*) spawning in the northern MDB can be triggered by planned e-flow peaks during winter–spring (Stuart and Sharpe 2022). Their eggs hatch within 1 week of flow onset and drifting larvae require relatively high densities of zooplankton prey for up to 20 days to survive (NSW DPI 2015; Tonkin et al. 2006). Although e-flows can be effective at triggering spawning events, they may not be able to provide adequate food for juvenile survival and recruitment within the required timeframe (Bunn et al. 2006; Ye et al. 2020). For example, e-flows on the lower Murray River from 2014 to 2019 were effective at stimulating golden perch spawning, but not at supporting juvenile recruitment (Ye et al. 2020). Validating the success of e-flows in stimulating zooplankton abundance is important to ensure the desired outcomes of e-flow events for riverine consumers are met.

The aim of this study was to investigate the immediate and longer-term impacts of a planned dam release e-flow on riverine zooplankton abundance in a major regulated river in the MDB and attempt to understand the underlying mechanisms of any change. To achieve this, zooplankton, DOC, inorganic nutrients and water quality were sampled at two sites on the Macquarie-Wambuul River before, during, and after a spring e-flow designed to support flow-dependent fauna during the 2017–2019 drought. It was hypothesised that the e-flow would import DOC and nutrients from dry river benches, resulting in increased zooplankton abundance in the following weeks.

2 | Methods

2.1 | Study Sites

The Macquarie–Wambuul River is located in central New South Wales, Australia, and is regulated by Burrendong Dam, one of the largest inland dams in New South Wales (capacity 1680 GL, catchment size 13,900 km^2). Land use in the river catchment is over 90% agricultural, dominated by grazing and dryland cropping (Green et al. 2011). The flows of the Macquarie-Wambuul River support multiple threatened fish species and sustain the Macquarie Marches, a Ramsar-listed wetland (Commonwealth of Australia 2023). E-flows are utilised in the Macquarie-Wambuul catchment to maintain or improve the health of river-dependent ecosystems, with specific objectives of increasing instream productivity and supporting the growth and recruitment of native fish populations (NSW DPIE 2020).

Sampling was conducted in the mid-reaches of the Macquarie–Wambuul River at Rawsonville, 150 km downstream of Burrendong Dam, and again at Narromine, ~50 km further downstream, to ensure results were not site-specific (Figure 1).

2.2 | Study Design and Sampling

The sampled e-flow spanned July–December 2018 and was comprised entirely of water released from Burrendong Dam (CEWO 2018). The planned hydrograph consisted of two distinct components relevant to this study, each with specific ecological objectives (Table 1). The spring flow component of the e-flow included a steep increase in discharge from 6.4 to 29 m/^{3} s^{-1} designed to imitate a natural rainfall-driven flow pulse.

To capture the short- and longer-term impacts of the e-flow, sampling was conducted regularly from May 2018 to January 2019, with sampling effort intensified to weekly at Rawsonville during the rising limb and peak of the spring flow component of the e-flow hydrograph. Mean daily river discharge and river level data was obtained from Water NSW (2023) gauging sites located as close to the sample sites as possible: gauge 421001 was used for Rawsonville and gauge 421127 for Narromine. The 50-year flow percentiles for the Rawsonville gauge were 5th: 1.7, 50th: 14.5 and 95th: 100 m^3 s^{-1}.

To determine concentrations of DOC, nitrogen oxides (NOx) and reactive phosphorus (RP) duplicate 200 mL samples of river water were filtered through 0.45 μm PES syringe filters and immediately frozen until analysis (APHA 2024b, 2024c, 2024a). DOC concentrations were then quantified using a Shimadzu TOC-L total organic carbon analyser, and nutrient concentrations were determined by a Lachat QuickChem 8500 series 2 flow injection analyser. Standard curves, analytical blanks, spiked matrices and certified reference materials were used for quality control. Chlorophyll *a* (chl-a) was collected by filtering

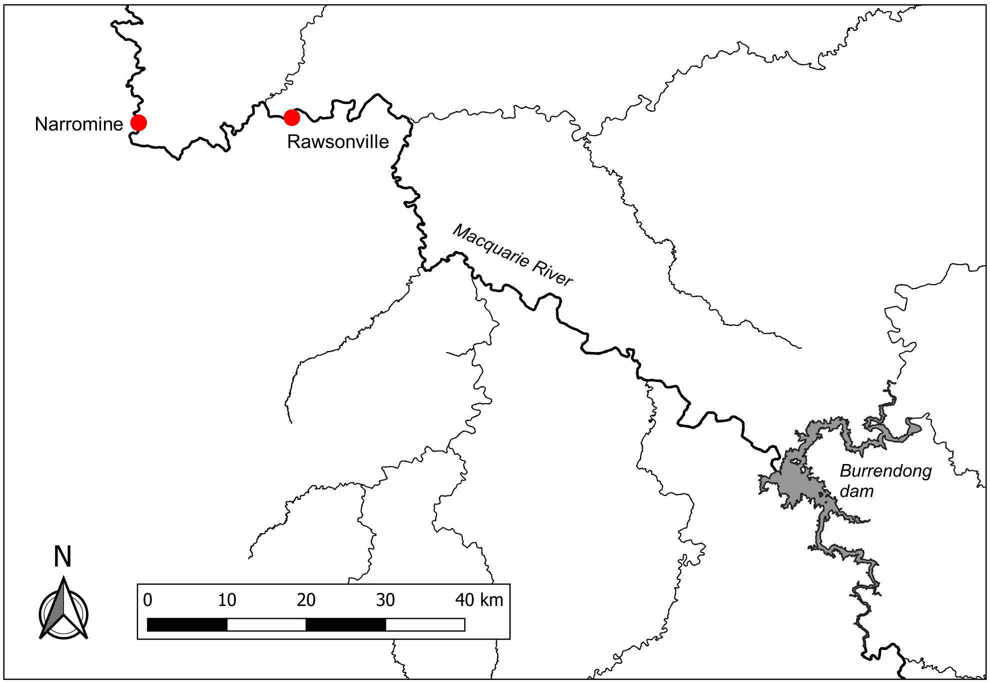

FIGURE 1 | Map showing two study sites on the Macquarie–Wambuul River, New South Wales, Australia. [Color figure can be viewed at wileyonlinelibrary.com]

TABLE 1 | Table showing planned hydrograph components of the 2018 winter–spring e-flow on the Macquarie –Wambuul River and their major ecological aims (CEWO 2018).

Hydrograph component	Dates	Approx. discharge at Rawsonville ($m^3 s^{-1}$)	Major ecological aims
Winter pre-wet	15 July–17 August	6	Prime system to increase efficiency of spring flow
Spring flow	18 August–early December	17–29	Support inundation dependent fauna and flow generalist/specialist fish instream (Murray cod, spangled perch, eel-tailed catfish), and inundate wetlands

duplicate 500 mL samples of river water through a 0.7 μm glass fibre filter (Whatman GF/F) and immediately frozen until analysis. Chl-a was then extracted using the standard boiling ethanol method (APHA 2024d) and concentration was quantified with a Cary 60 UV–vis spectrophotometer. Water quality parameters included electrical conductivity, pH, temperature and dissolved oxygen concentration and were measured in triplicate using a Hydrolab Surveyor with MS5 Minisonde.

For zooplankton abundance, triplicate samples were collected from free-flowing areas of the river channel > 1 m in depth, located > 3 m apart from each other. A 10 L container was repeatedly filled with water from approximately 20 cm below the surface to a total volume of 70 L, which was passed through a 35 μm plankton net and concentrated to 100 mL (Suthers et al. 2019). Concentrated samples were then preserved in > 70% ethanol until counting. Zooplankton were then identified to order level with a dissecting microscope and S-tray using the taxonomic guide of Shiel (1986). To estimate how increases in zooplankton density could translate to prey availability for fish, the daily zooplankton export through each site was calculated as the number of individuals per litre multiplied by the daily discharge through each site on the day the sample was collected.

2.3 | Statistical Analysis

All statistical analysis was carried out using R Statistics version 4.4.0 (R Core Team 2024). Plots were generated with *ggplot2* and maps created using QGIS (QGIS.org 2024; Wickham 2016). Differences in environmental variables and zooplankton abundance between e-flow components were tested using ANOVA and Tukey's post hoc comparisons with the *car* package (Fox and Weisberg 2019). Assumptions of normality and homogeneity were validated using Shapiro–Wilk and Levene's tests and log or square-root transformations used to meet assumptions where necessary. To investigate relationships between zooplankton abundance and environmental variables, Pearsons correlations tests were performed with a natural log transformation to reduce the effect of outliers. To understand the impact of environmental variables on zooplankton taxa, redundancy analysis was conducted with the *vegan* package (Oksanen et al. 2022). Environmental variables were standardised and zooplankton data was natural log transformed with *vegan*'s decostand function to reduce the impact of outliers. Variables were selected based on the literature, preliminary plots and stepwise selection. Best model fit was assessed using adjusted-R^2 and ANOVA-like permutation tests (Legendre et al. 2011). For ordination plots, data were grouped by flow component using the date ranges outlined in Table 1, with additional groups created to describe samples taken outside of the planned e-flow period ("Before e-flow" and "After e-flow, irrigation"). The "Winter pre-wet" flow component was unable to be included in the redundancy analysis due to missing chl-a data.

3 | Results

3.1 | Hydrology

Sampling occurred between May 2018 and February 2019, which was during an intense drought period, characterised by below-average rainfall and inflows in the MDB (BOM 2024). Maximum discharge during the initial peak of the spring flow component was $39.4\,\mathrm{m^3\,s^{-1}}$ at Rawsonville and $37\,\mathrm{m^3\,s^{-1}}$ at Narromine (Figure 2). Flows had not exceeded this magnitude at the sample sites for nearly 7 months (Water NSW 2023). During the sampling period, tributary inflows below the dam were entirely from the Bell River ($<0.9\,\mathrm{m^3\,s^{-1}}$) and comprised <9% of total discharge at Rawsonville during low flow and <5% during the spring flow component of the e-flow (Water NSW 2023). Burrendong Dam was at ~35% of effective full storage at the time of the e-flow and water temperatures were approximately 3°C–4°C lower downstream of the dam compared to upstream, indicating water was released from the hypolimnion (Water NSW 2023).

3.2 | Physical and Chemical Changes

The spring flow component of the e-flow changed water chemistry at both sites. During the ascending limb and initial peak of the spring flow at Rawsonville, concentrations of DOC, NOx and chl-a spiked significantly for at least eight days (DOC $F_{3,11}=4.3$, $p=0.01$, *log*NOx $F_{2,12}=0.03$, $p<0.001$, chl-a $F_{3,14}=5.8$, $p=0.009$, Tukey's p all <0.04, Figure 3). DOC concentrations returned to pre-flow (the period before the onset of the e-flow) levels quickly after the initial flow peak, and chl-a and NOx returned to pre-flow conditions by late October (Figure 3). Substantial loads of detritus were observed in high-flow samples. Air temperature varied from 13°C ± 0.6°C to 30°C ± 1.3°C at both sites over the course of the study, and water temperature gradually increased from 9 ± 0.1°C to 31 ± 0.3°C between July 2018 and January 2019 (Figure 3).

3.3 | Zooplankton Response

Zooplankton responded strongly to the spring flow component of the e-flow. Mean abundance of the superorder Cladocera (also termed Diplostraca) significantly increased by a factor of >4 at the onset of the spring flow at Rawsonville, with a similar increase of >5 times seen at Narromine before and after the initial flow peak ($F_{3,31}=32.5$, $p<0.001$, Tukey's $p<0.001$, Figure 4). This resulted in maximum exports of $36.2\times10^9 \pm 1.5\times10^9$ Cladocera $\mathrm{d^{-1}}$ through Rawsonville and $15.1\times10^9 \pm 1.4\times10^9$ Cladocera $\mathrm{d^{-1}}$ through Narromine during the spring flow, 16 and 25 times higher than during the pre-wet component, respectively (Figure 5). Although not analysed, we noted that the family Chydoridae composed the majority of Cladocera in most samples. Cladoceran abundance did not change significantly during the pre-wet component of the e-flow compared with pre-flow (Tukey's $p=0.75$, Figure 4). Densities of taxa in class Copepoda

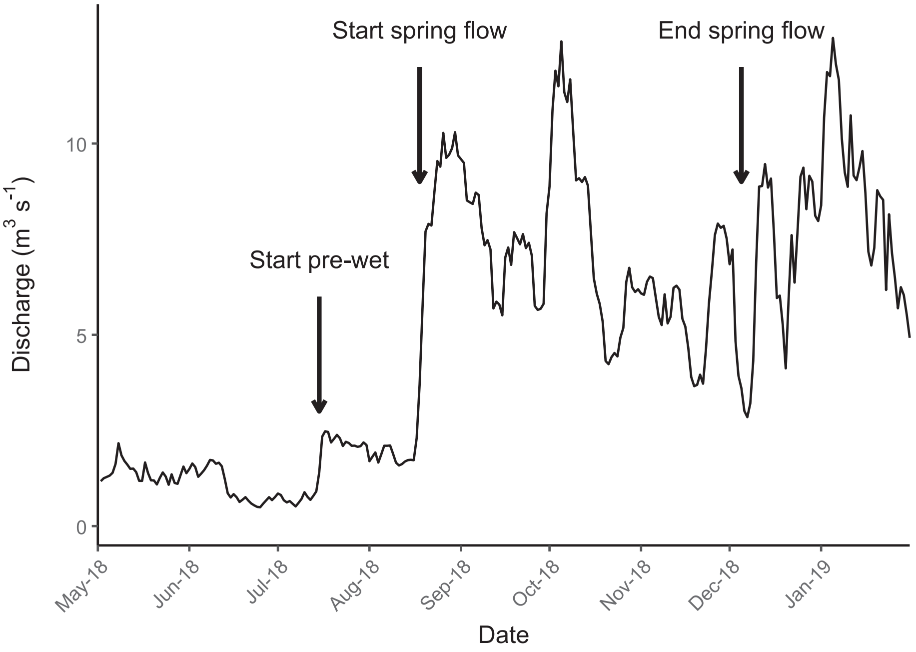

FIGURE 2 | Hydrograph of river discharge ($\mathrm{m^3\,s^{-1}}$) during an environmental flow event on the Macquarie–Wambuul River showing the flow components of a planned environmental flow event (CEWO 2018), as detailed in Table 1.

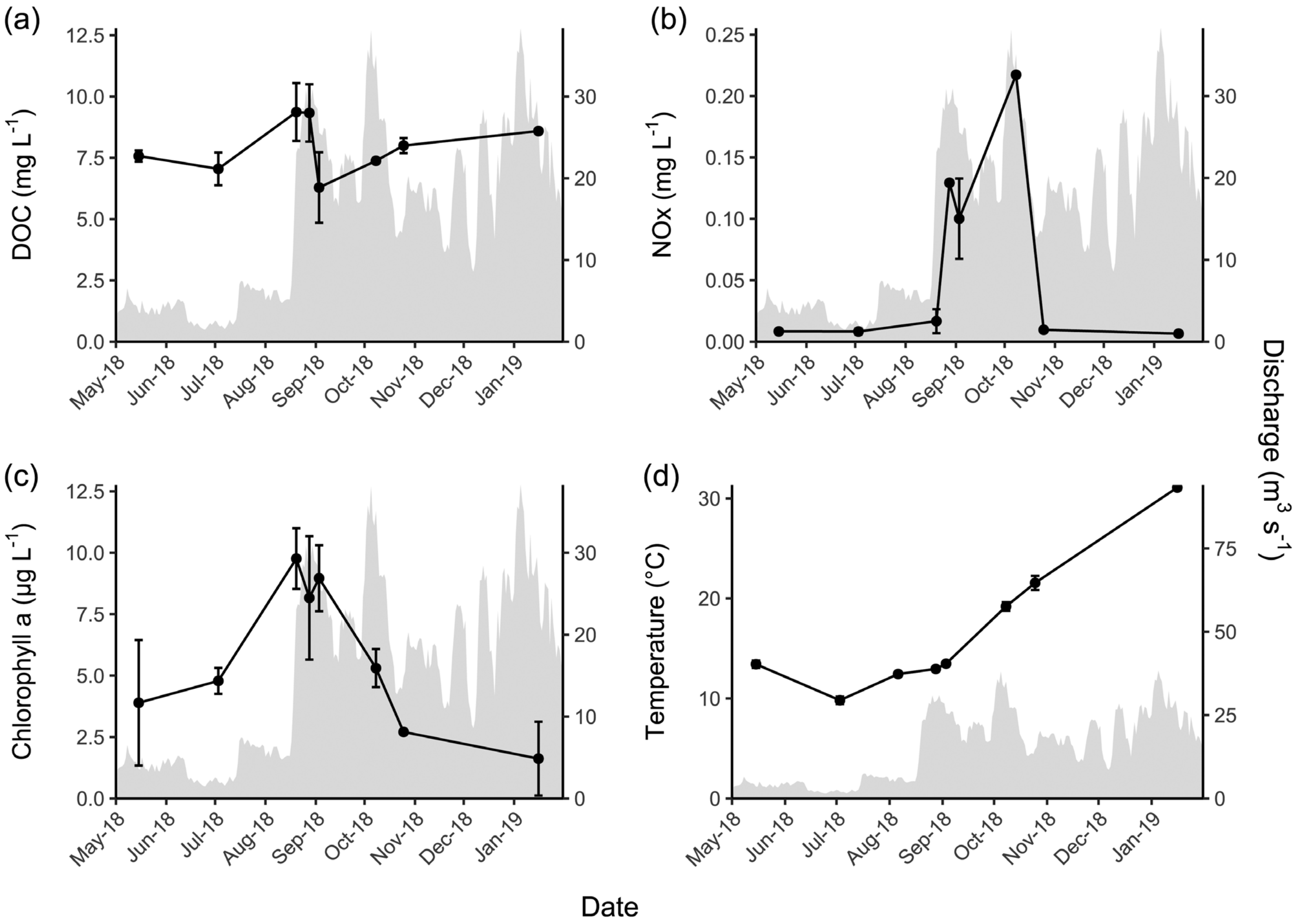

FIGURE 3 | Hydrographs of river discharge (m^3 s^{-1}) showing the corresponding concentrations of (a) dissolved organic carbon (DOC mg L^{-1}), (b) nitrogen oxides (NOx µg L^{-1}), (c) chlorophyll a (µg L^{-1}) and (d) water temperature (°C) during an environmental flow event at Rawsonville on the Macquarie–Wambuul River.

did not change significantly over the course of the study (all $p > 0.24$, Figure 4). All zooplankton densities returned to pre-flow levels by October.

Cladoceran abundance was significantly positively correlated with NOx ($R^2 = 0.30$, $p < 0.05$) and chl-a ($R^2 = 0.66$, $p < 0.001$). Both Cyclopoida and Cladocera were positively correlated with dissolved oxygen concentration ($R^2 > 0.31$, $p < 0.05$). Redundancy analysis found the significant drivers of zooplankton community composition to be NOx, temperature and river level (constrained inertia = 0.72, adjusted-$R^2 = 0.62$, $F_{3,9} = 7.5$, $p = 0.002$, Figure 6). Cladoceran abundance was in a similar multivariate space to samples taken during the spring flow component and was positively linked with NOx concentrations and river level (Figure 6). Copepods were clustered together in multivariate space and appeared inversely related to river level and temperature. Samples taken after the e-flow appeared most closely related to increased temperature (Figure 6).

4 | Discussion

It is important to understand how effective planned e-flows are at stimulating instream zooplankton production within an appropriate timeframe to support the recruitment of threatened native fish. This study demonstrates that zooplankton abundance can increase almost immediately in response to e-flows, with greater abundance lasting up to 60 days after the initial flow peak. These increases in food availability may be able to support higher trophic level taxa, including native fish larvae, during the first few weeks of life.

4.1 | Impacts on Water Chemistry and Chlorophyll a

The initial peak of the spring flow component of the e-flow corresponded with concentration peaks of DOC, NOx and chl-a. The short-lived pulse of DOC was likely mobilised from terrestrial organic material accumulated on dry river benches since the previous flow peak of greater magnitude nearly 7 months earlier. Similar DOC import was seen during an e-flow on the Snowy River and attributed to localised and riparian vegetation wetting (Rohlfs et al. 2016). The large pulse of NOx may have been released by the rewetting of sediments in the river channel, where nitrogen mineralisation can occur due to extended drying (Baldwin and Mitchell 2000). DOC and nitrogen pulses are often linked in river systems as they are both liberated by the microbial and photochemical processing of terrestrial organic matter (Aitkenhead-Peterson et al. 2003; Hitchcock and Mitrovic 2015;

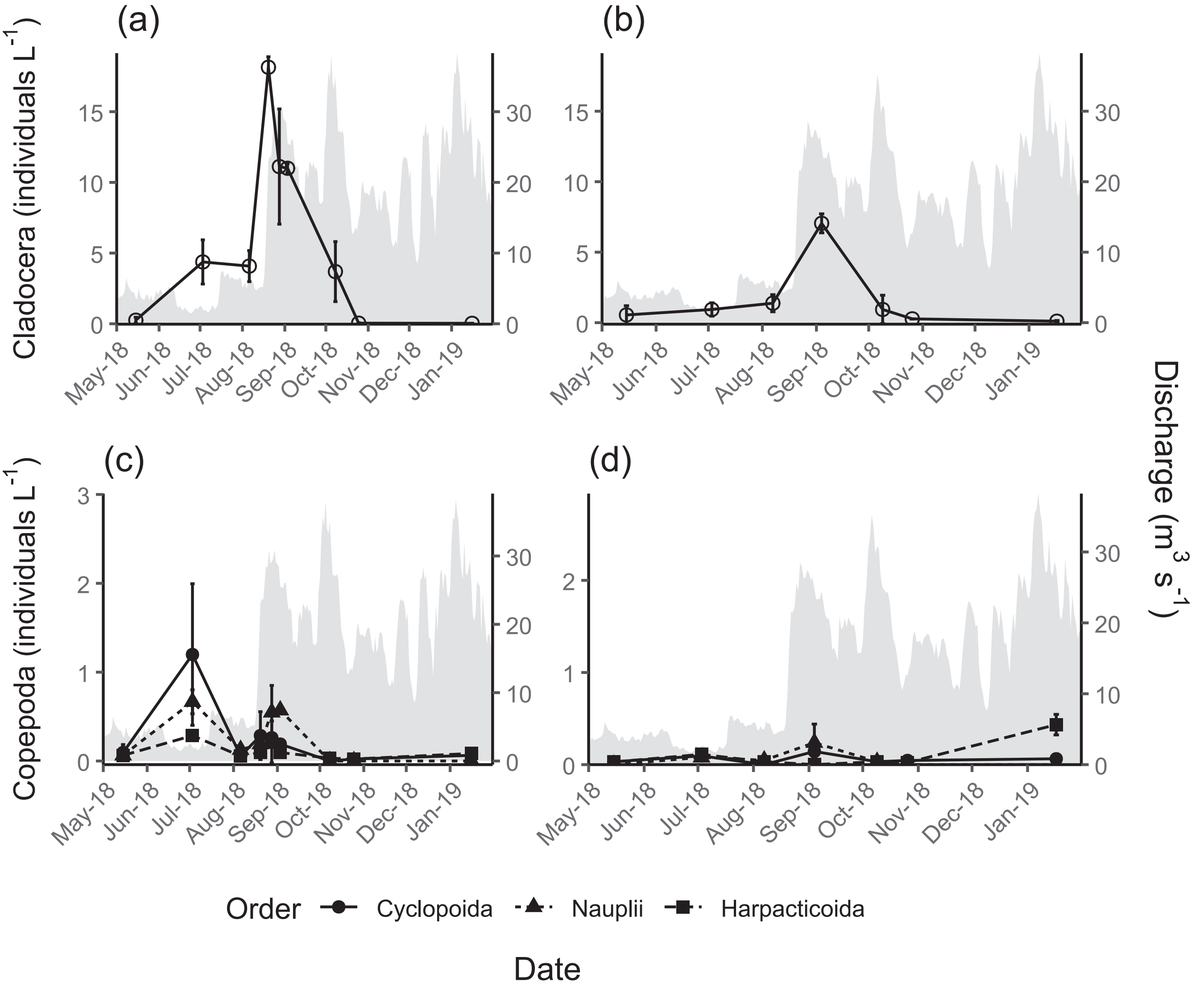

FIGURE 4 | Hydrographs of river discharge (m^3 s^{-1}) with corresponding zooplankton densities (individuals L^{-1}) during an environmental flow event on the Macquarie-Wambuul River for (a) Rawsonville order Cladocera, (b) Narromine order Cladocera, (c) Rawsonville class Copepoda and (d) Narromine class Copepoda.

Riggsbee et al. 2008). Increases in DOC and nutrients can support increased autotrophic and heterotrophic microbial production (Balzer, Hitchcock, Hadwen, et al. 2023), which was supported by the increase in chl-a observed during the spring flow peak in this study. Increases in flow velocity after extended periods of low flow can also cause benthic algal scouring, transporting scoured algae downstream and temporarily increasing instream chl-a concentrations (Davie and Mitrovic 2014). Substantial detritus observed in the e-flow samples suggests that some scouring may have occurred during the current study.

4.2 | Zooplankton Response to Spring Flow

Although the pre-wet component of the e-flow did not significantly impact riverine zooplankton abundance, there was a strong and immediate effect of the spring flow peak on cladoceran abundance. Increases in zooplankton abundance in response to flow have been observed to occur in the weeks following flow peaks (Balzer, Hitchcock, Kobayashi, et al. 2023; Shiel et al. 2006). In this study, the rapid increase in cladoceran densities occurred in tandem with the rising limb and initial peak of the spring flow hydrograph. The minimum time for chydorids (representing the majority of cladocerans in this study) to reach maturity and reproduce is approximately a week post-hatching (Dole-Olivier et al. 2000), so reproduction cannot account for this steep increase in abundance over such a short period of time. The positive association of cladoceran abundance with river level could indicate a link with the inundation of resting egg banks. Under favourable conditions, cladocerans can begin hatching from diapaused eggs within 1–2 days, with hatchings continuing to increase exponentially over the first week after which reproduction may begin (Boulton and Lloyd 1992; Nielsen et al. 2000). The high density of resting eggs required for such a sudden increase in abundance may have resulted from a diapause triggering event that coincided with a period during the previous year that had a similar extent of channel inundation to the e-flow (low food availability, for example, Alekseev and Lampert 2001). Alternatively, high resting egg densities could have been caused by an accumulation of diapaused eggs in the

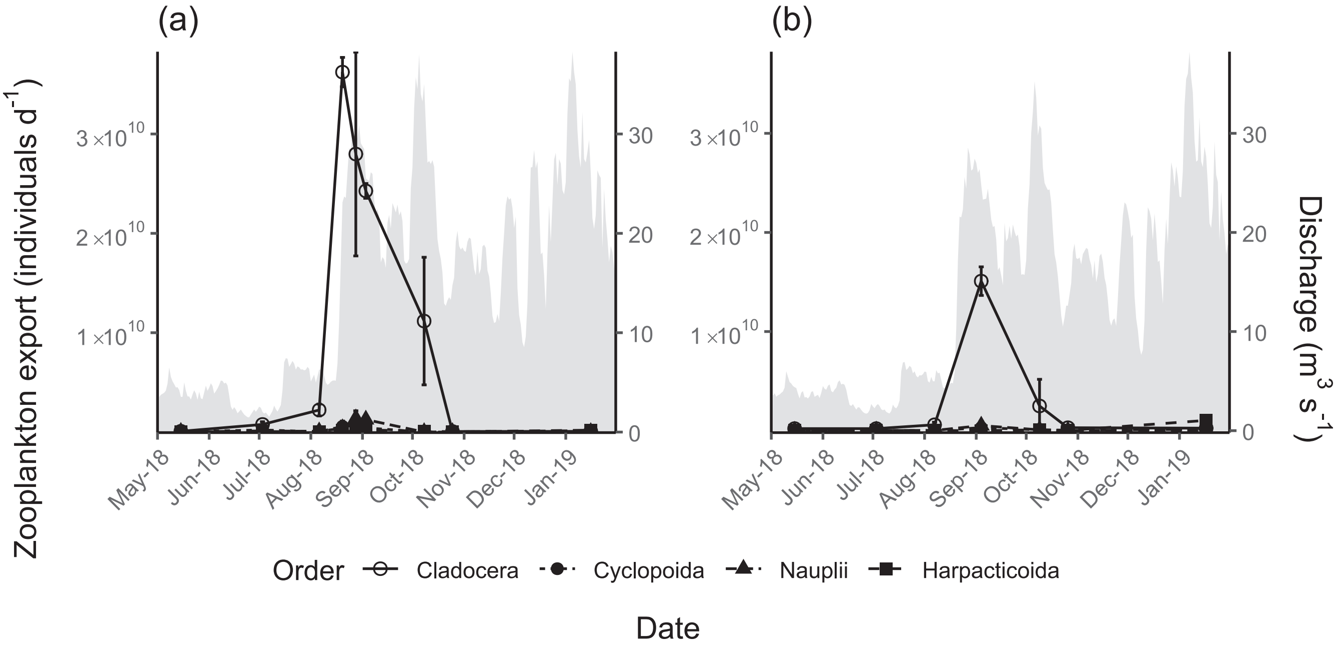

FIGURE 5 | Hydrographs of river discharge (m^{3}s^{-1}) with corresponding daily zooplankton export during an environmental flow event at (a) Rawsonville and (b) Narromine on the Macquarie–Wambuul River.

sediment over a prolonged period of inappropriate conditions for hatching (Nielsen et al. 2000). Epibenthic chydorids may also have been mobilised from benthic habitats or slackwaters by high water velocities during the initial stages of the e-flow, where they can accumulate in large numbers (Griggs et al. 1999; Nielsen et al. 2005).

Positive associations of cladoceran abundance with NOx and chl-a suggest populations were maintained through primarily autotrophic support, stimulated by increased nutrient availability (Ardón et al. 2021). Cladocerans can be bacterivores, detritivores or herbivores (Griggs et al. 1999), so it is probable that the terrestrial DOC pulse also contributed to increased zooplankton abundance through increased heterotrophic microbial production (Meunier et al. 2017). The impact of this terrestrial DOC influx may not have been captured in this study because changes in DOC chemical composition were not quantified. The humic- and fulvic-like components of terrestrial DOC can be more effective at supporting heterotrophic microbial production than the protein-like molecules dominant in slow-flowing or lentic waters (Guillemette et al. 2016).

The occurrence of the e-flow in this study during drought may have intensified the zooplankton response in comparison to a year of average rainfall. For example, the river had been nitrogen poor in the months preceding the e-flow, with NOx concentrations $<10\,\mu\mathrm{g\,L^{-1}}$, so the response to the e-flow may have been more pronounced than in a system where nutrients were more consistently available (Ardón et al. 2021). Additionally, scouring and transport of benthic algae accumulated during extended low flow may have provided an additional source of food for planktonic zooplankton (Davie and Mitrovic 2014), as well as liberating some zooplankton from epibenthic, littoral or slow-flowing refugia through advection (Dole-Olivier et al. 2000; Nielsen et al. 2005). Chydorids are often associated with both benthic and planktonic filamentous algal blooms (Griggs et al. 1999).

Seasonal changes were also important in driving community composition during this study, indicated by the strong inverse relationship of temperature and zooplankton abundance. Although bottom releases from thermally stratified dams can cause cold-water pollution downstream (Michie et al. 2020), thermal impacts on the Macquarie River appear to be limited to within 150 km of the dam wall (Burton 2001). This may explain why temperature changes at our sampling sites were gradual and did not appear linked to the change in flow magnitude, despite cooler temperatures below the dam wall compared to reaches upstream of the dam (Water NSW 2023). It is possible that the zooplankton response to e-flows may differ at sites closer to the dam outlet due to the influence of cold-water pollution; however, further research is needed to confirm this. Higher temperatures are usually linked to higher hatching abundances and reproductive rates in cladocerans (Dole-Olivier et al. 2000; Jones and Gilbert 2016), but the opposite effect was seen in this study. Chaki et al. (2021a) tested zooplankton hatching times in response to different temperature incubations, showing Cladocera taxa typically hatched faster at 20°C compared with warmer temperatures of 24°C. This inverse result is likely due to a combination of ecological factors, including specific taxon seasonality, flow-induced changes to populations and decreasing resource availability over the course of the study (Ardón et al. 2021; Shiel 1986).

There was no significant effect of the e-flow on copepod populations in this study, though cyclopoid production has previously been shown to increase in response to flow-driven terrestrial resource pulses in regulated rivers (Balzer, Hitchcock, Kobayashi, et al. 2023; Ning et al. 2013). The inverse relationship between copepod taxa and river level suggests either a reduction in abundance through advection during the e-flow or high-flow evasive movement of taxa (Dole-Olivier et al. 2000; Viroux 2002). Copepods are generally strong swimmers and can cling to river substrates or move to low-flow refugia as water velocity increases

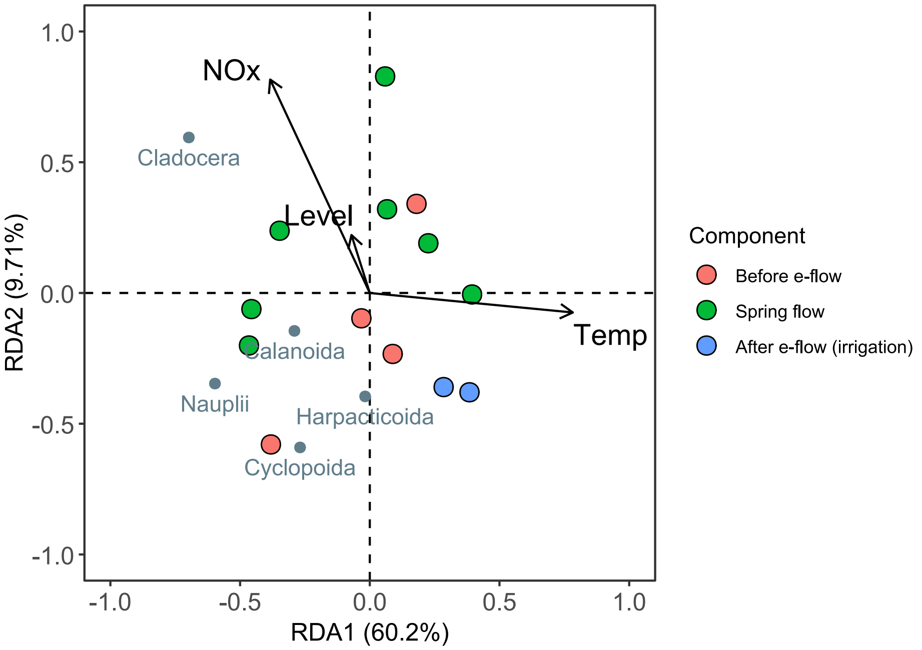

FIGURE 6 | Redundancy analysis showing the impact of environmental variables on zooplankton community composition before, during, and after an environmental flow (e-flow) event on the Macquarie–Wambuul River in winter–spring 2018. Dots represent the location of zooplankton taxa (grey) and sample means (coloured) in multivariate space. Note that no samples from the pre-wet component of the e-flow were included in this analysis due to insufficient data. [Color figure can be viewed at wileyonlinelibrary.com]

(Dole-Olivier et al. 2000), so it is possible population increases were not captured by the current sampling design. It is also possible that the temporal scope of the study did not align with the seasons when copepods were more abundant (Viroux 2002).

4.3 | Implications for Native Fish Recruitment

The increases in zooplankton abundance stimulated by the spring flow component of the e-flow could have substantial positive implications for native fish recruitment. During the initial spring flow peak, cladoceran export through the sites was over an order of magnitude greater than pre-flow conditions, with increased exports maintained for at least 6 weeks. The timing, location and prey size of this food pulse fit well with the larval food requirements of threatened flow-dependent and in-channel flow specialist fish species, including Murray cod, trout cod *Maccullochella macquariensis*) and spangled perch (*Leiopotherapon unicolor*) (NSW DPI 2015). For example, Murray cod larvae hatch and are adrift between 7 and 24 days after the initial flow peak triggers spawning (NSW DPI 2015). During this time, they require prey between 300 and 500 μm in width at a mean rate of ~7 individuals h^{-1} (Tonkin et al. 2006). In feeding trials, Murray cod larvae have shown a preference for cladoceran prey over similarly sized copepods (Tonkin et al. 2006) and gut contents analyses have found a significant contribution of chydorids to gut fullness when available as prey (Kaminskas and Humphries 2009; King 2005). Given the feeding rates of Murray cod larvae during their first weeks of life (~7 ind. h^{-1}; Tonkin et al. 2006), the volume of cladocerans flowing in the water column at the peak of the spring flow was enough to support the daily food requirements of ~220 million larvae, compared to ~13 million larvae pre-flow. It is worth noting that densities upwards of 250 individuals L^{-1} were required to support Murray cod larval survival in hatchery settings (Rowland 1992), where densities peaked at ~20 individuals L^{-1} in the current study. It is unclear how the reduced incidence of prey per litre would impact relative larval survival.

In contrast to the current findings, e-flows may not always be effective at providing appropriate food resources to support native fish recruitment. Some studies comparing low and high flow years have found higher levels of gut fullness and increased larval size during low flow years (Humphries et al. 1999; Kaminskas and Humphries 2009). It has also been argued that river productivity may be decreased by moderate flow pulses (i.e., flows that are neither low nor overbank) due to a disturbance of areas of high low-flow productivity alongside insufficient floodplain connectivity to create a resource pulse (Bunn et al. 2006). This study shows that e-flows can be very effective at providing a resource pulse and increasing instream zooplankton abundance when conducted after a prolonged period of low flow when instream nutrient availability is low. Such environmental watering events may be valuable in supporting native fish recruitment and maintaining the integrity of riverine food webs during droughts, which will become increasingly common as climate change progresses (Palmer et al. 2008; Stuart and Sharpe 2022).

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Data Availability Statement

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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