Cladocera resting egg banks in temporary and permanent wetlands

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ABSTRACT

Cladocerans are important filter-feeders transferring energy up the food web to different invertebrate and vertebrate predators. Along the flood period, cladocerans are one of the primary food sources for juvenile fish in floodplain. Resting egg banks allow cladoceran populations to overcome the environmental stress, related to several limnological changes, including complete drying of temporary wetlands. After drought, resting egg banks influence cladoceran community attributes during the cyclic and successional processes driven by episodic flood events. In this study we compared the taxonomic richness of active (from the water column) and dormant (from the sediment) Cladocera assemblages and analyzed the structure of resting egg banks, comparing the diversity, abundance and apparent viability/unviability of the eggs, between six temporary and six permanent wetlands, located along the Ovens River Floodplain, Victoria, Australia. The qualitative analysis shows higher taxonomic richness in active assemblages from temporary (24 taxa) than permanent (13 taxa) wetlands compared to dormant assemblages present in resting egg banks (9 taxa) from temporary and permanent wetlands. However, richness was influenced by taxonomic level of identification, with the majority of resting eggs only being identified to the taxonomic level of family (i.e. Chydoridae). Total taxa richness within egg banks was similar between wetland types, however, on average higher Shannon’s diversity of resting eggs was found within permanent (1.53) than temporary (0.82) wetlands. This is likely to be due to more stable wetlands not providing appropriate cues to trigger dormancy induction or breakage for specific populations, leading to higher values of evenness in permanent than temporary wetlands. Comparing permanent and temporary wetlands, higher abundance of resting eggs (more than four times) consisting of higher abundance of unviable eggs and similar viable egg abundance to permanent wetlands, was found within temporary wetlands, suggesting that the increased resting egg abundance in temporary wetlands is balanced by the losses due to factors such as predation, parasitism or other physical damage, during the terrestrial phase. Despite resistant outer shell structure, this study highlights that the damage to egg integrity is intensified in wetlands that undergo dry phases. Cladoceran resting egg banks represent the potential assemblage to recover after disturbance events such as drying, and information about these is important to ensure appropriate management and conservation of floodplain biodiversity.

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INTRODUCTION

Floodplains and their associated wetlands are vital to the maintenance of biological diversity at the landscape scale, providing many ecosystem services and functions. However, due to a range of anthropogenic influences many floodplains and associated wetlands are now highly impacted (Petts and Amoros, 1996; Kingsford, 2000). Within a floodplain complex there is a mosaic of wetlands that vary in morphology, hydrology and water quality characteristics that create a heterogeneity of aquatic habitat in floodplains and consequently, high biological diversity (Ward, 1998; Nielsen and Brock, 2009).

In southeast Australia, as in several regions of the world, many lowland rivers have been regulated by damming, reducing the extent of flooding on downstream floodplains and wetlands (Kingsford, 1995). The Ovens River, located in the Murray River Watershed, is one of the few rivers in south eastern Australia that is largely unregulated within the Murray-Darling Basin and has recognized importance to native fish recruitment (MDBA, 2018). Nevertheless, research undertaken within the region of the Ovens River floodplain has indicated that since European settlement, sedimentation rates in wetlands have increased as a consequence landscape usage (Davies et al., 2018). Increased sedimentation rates has been linked to decreases in wetland and floodplain productivity, as indicted by declines in macrophyte abundance (Thoms et al., 1999; Gell, 2019). Within this and other floodplain systems, flooding drives pulses of primary and secondary production (Junk et al., 1989). During these flood events many fish move onto the
floodplain to feed on the abundant food resources, one of the primary food sources for juvenile fish are cladocerans (Humphries et al., 1999). Cladocerans play an essential role in the food web of these systems, consuming algae, detritus, bacteria and protozoa (Porter et al., 1979; Smirnov, 2013), before being consumed both by larger invertebrates, fish, and filter-feeding waterbirds (De Bernardi et al., 1987, Jenkins and Boulton, 2007).

The cladocerans are among the invertebrate groups that produce resting eggs to avoid adverse conditions, such as drying, poor water quality, predation or lack of resources (Radzikowski et al., 2018), and reportedly have the potential to remain viable for 100's of years although viability declines with age (Amsinck et al., 2007). Cladoceran resting egg banks are found in many different aquatic environments (Ning and Nielsen, 2011) and have a role in conferring resilience of communities and the recovery of aquatic communities after disturbance (Brock et al., 2003).

For floodplain rivers, variability in riverine flows dictate the periods of connectivity between the river and associated floodplain wetlands and, in general, those wetlands lower on the floodplain will have more extended periods of connectivity and often retain permanent water compared to those wetlands further from the river that have shorter periods of connectivity and are often more temporary. The frequency of connection is dictated by the size of the river flow and extent of floodplain inundation (Nielsen et al., 2020). Connectivity between the river channel and wetlands promote dispersal of biota between wetlands. During periods of disconnection wetlands become harsh environments for many aquatic organisms. To avoid these harsh conditions the production of resting eggs by cladoceran becomes important and provides a means of dispersal in time (De Stasio, 1989). This temporal dispersion is essential during the terrestrial phase in temporary wetlands, increasing the dependency on resting egg production and hatching from dormant eggs.

As a consequence of the mosaic of wetland types on the floodplain, individual wetlands have differing successional trajectories that drive the observed high biodiversity within these systems (Ward, 1989). Flooding causes less disturbance to the biota within permanent wetlands compared to temporary wetlands. In permanent wetlands flood pulses are less intense, causing shifts in water quality and have the potential to introduce new species during the connection period. In temporary wetlands the disturbances are harsher. These wetlands dry and re-fill irregularly and biota have adaptations to persist during these adverse conditions. As the duration of the dry period increases the ability of a dormant egg to persist decreases (Nielsen et al., 2013; Eskinazi-Sant’Anna and Pace, 2018). In tropical systems, hatching of some cladoceran species or genotypes is benefited from short desiccation events, of at least 8 months (Vargas et al., 2019). However, Jenkins and Boulton (2007) suggests drying longer than a few decades may adversely impact recovery of microinvertebrate populations in Australian arid zone floodplain rivers.

The aim of this study was to compare the structure of cladoceran resting egg banks between temporary and permanent wetlands. In addition, we also compared the taxonomic richness between resting egg banks and communities present within the water column. We test the hypothesis that temporary wetlands will contain a higher diversity, abundance (total eggs) and losses (unviable eggs) of resting eggs in comparison to permanent wetlands and (ii) that the community in the water column will be a sub-set of the community contained in the dormant egg bank.

METHODS

Dormant and active cladoceran assemblages were sampled from the sediment and water column of six temporary and six permanent wetlands, along a 5-kilometer length of the Ovens River Floodplain, Australia (Fig. 1). The distance between two temporary wetlands did not exceed 5.3 x 10^2 meters, while the distance between two permanent wetlands reaches until 3.8 x 10^3 meters, and two permanent wetlands are much closer to temporary than other permanent. When flooding occurs, all wetlands are connected. Once floodwaters recede many of these wetlands can be classified as either permanent or temporary (Quinn et al., 2000).

Wetlands were sampled on the 17th October 2017, when the wetlands were isolated and the volume of water was decreasing. Water depths in the temporary wetlands varied between being dry (one wetland) to depths of less than 20 cm. At the time of sampling the permanent wetlands were turbid with fringing patches of emergent vegetation and no observable submerged vegetation. In contrast the temporary wetlands had a diversity of submerged vegetation.

Complementary information about Ovens River floodplain hydrologic dynamic can be seen in Quinn et al. (2000), King et al. (2003) and Marren and Woods (2011).

Egg assemblage

Within each wetland, sediment was sampled from six randomly selected locations, including littoral and limnetic zones with inundated sediment (except in one dried temporary wetland), and combined into a single integrated sample for each wetland. Samples were collected to a depth of 10cm using a 4cm diameter corer. Coring is an effective method of dormant egg collection and is an aggregation of eggs across multiple years and takes into account the vertical mixing of sediments and
eggs within a wetland (De Stasio, 1989; Bachmann et al., 2018). In these wetlands, 10 cm represents an aggregation of a relatively short time period of 5 years given estimated sedimentation rates of 2 cm per year within the region (Thoms, 1995). Within each wetland the six cores gave a combined sampled surface area of 302 cm² and a sample volume of 3,016 cm³. As cladoceran eggs are typically greater than 200 µm in size, the sediment was sieved through a 200 µm sieve and the retained material was examined for resting eggs.

Fig. 1. Sampling sites in permanent and temporary wetlands on the Ovens River floodplain, North-eastern Victoria.
Resting eggs were separated from the sediment under a stereomicroscope and identified to genus or family, using morphological egg characteristics outlined in Vandekerkhove et al. (2004) and Coronel et al. (2009). The eggs were quantified according to two categories: viable and unviable based on appearance (Fig. 2). Eggs deemed unviable showed signs of either predation, parasitism, or other signs of physical damage to the embryo. Additionally, representatives of each morphological group of eggs were incubated at 22°C under a 12/12-hour light dark cycles, which allowed the identification of some species when hatching was observed.

Active assemblage

Semi-quantitative samples of the active assemblages were sampled from the water column of each wetland using a plankton net (50 µm mesh; 30 cm diameter) by horizontal subsurface hauls of approximately 2 meters. The use of net hauls allows for an assessment of the taxonomic richness of the active community but not the abundance of individuals in the community. Five temporary wetlands were considered to water column assemblage, because one of them was dry. The samples were preserved in 90% ethanol and identified to species using darkfield microscopy and relevant taxonomic keys (Smirnov and Timms, 1993; Benzie, 1998; Smirnov, 1996; Orlova-Bienkowskaja, 2001; Van Damme and Dumont, 2008; Sinev, 2016).

Statistical analysis

The statistical stats package in the “R Development Core Team” (2015) was used to evaluate differences between cladoceran assemblage from temporary and permanent wetlands. Data was checked for normality (Shapiro-Wilk test) and homoscedasticity (Levene test), with data transformation (log10(x+1)) performed only on abundance data, One-way Analysis of Variance (ANOVA) was used to compare differences between wetland type on the following variables: total abundance of resting eggs, viable egg abundance, unviable egg abundance, taxonomic richness in water column (active organisms), taxonomic richness in sediment, egg evenness (Pielou’s evenness), egg diversity (Shannon H’) and abundance to each taxon. Non-metric Multidimensional Scaling (nMDS), based on a Bray-Curtis dissimilarity matrix, was used to display patterns of community composition, and Jaccard distance to presence and absence of taxa, between wetland types. Analysis of Similarities (ANOSIM) was

Fig. 2. Resting eggs appearance: A) viable with preserved embryo, Aloninae (above) and Ceriodaphnia (below); B) unviable with damaged embryo, Daphniidae (above) and Simocephalus (below).
used to test the significant difference of the taxonomic egg bank composition between wetland types.

RESULTS

Water column communities

Taxonomic richness in the water column was significant higher in temporary wetlands compared to the permanent wetlands (Tab. 1, Fig. 3A). In total, 27 species of cladocerans were recorded from the water column of the 11 wetlands sampled, with 23 species present in temporary wetlands and 13 in the permanent wetlands. Of these 14 were exclusive to the temporary wetlands and 4 to the permanent wetlands (Tab. 2).

Nonmetric multidimensional scaling of the water column community data (presence-absence data) indicates community composition differs between wetland types (Fig. 4). These differences were confirmed by ANOSIM (R=0.7067; p=0.002). The differences between communities were primarily driven by *Coronatella* spp. which was only found in the temporary wetlands and *Simocephalus* cf. *elizabethae* in permanent wetlands (Tab. 2). *Bosmina meridionalis* and *Simocephalus expinosus* group sp1 were found in both types of wetlands, but *B. meridionalis* was more common in temporary and the second more common in permanent wetlands (Tab. 2, Fig. 4).

Egg-bank communities

In contrast to what was observed in the water column community, overall taxonomic richness of resting egg banks was similar between wetland types, while average taxonomic richness was significantly higher in the egg bank of the permanent wetlands compared to the temporary wetlands (Tab. 1, Fig. 3B). In total only 9 taxa were recorded from the sediment of all wetlands and most taxa were common across both types of wetland with only *Moina tenuicornis* unique to temporary wetlands (Tab. 2).

The abundance of eggs in the sediment of the temporary wetlands was significantly higher than what was recorded from the permanent wetlands (Tab. 1, Fig. 3C). Although there were more eggs recorded from the sediment of the temporary wetlands these eggs were more likely to be unviable (Tab. 1, Fig. 3D) with only approximately 30% of eggs assessed as viable compared to 55% in the permanent wetlands (Tab. 1, Fig. 3E). Differences in the abundance of eggs and taxonomic richness was also reflected in the Shannon diversity index (H') and Pielou’s evenness index with both measures significantly higher in the permanent wetlands compared to the temporary wetlands (Tab. 1, Fig. 3F-G).

Differences in abundance of resting eggs of some taxa were shown between wetland types (Fig. 5). Aloninae, Chydoridae, *Daphnia* spp. and *Moina* spp. (Tab. 1, Fig. 5A, C, E and G) were more abundant in the permanent wetlands, and one species of Daphniidae and *Simocephalus* spp. were more abundant in the temporary wetlands (Tab. 1, Fig. 5D, I), although these differences were not significant. Significantly more eggs of *Ceriodaphnia* spp. and *M. tenuicornis* were found within the sediment of the temporary wetlands (Tab. 1, Fig. 5B,

| Variable dependent | MS     | F value | p       |
|--------------------|--------|---------|---------|
| Diversity index    | 1.178  | 23.58   | 0.001***|
| Evenness index     | 0.193  | 9.00    | 0.013*  |
| Taxonomic richness (sediment) | 16.333 | 11.14 | 0.007** |
| Taxonomic richness (water column) | 50.430 | 5.51 | 0.043*  |
| Total resting egg abundance | 1.075 | 7.06 | 0.024*  |
| Unviable resting egg abundance | 2.123 | 12.79 | 0.005** |
| Viable/Unviable proportion | 0.176 | 7.61 | 0.020*  |
| Aloninae           | 3.060  | 4.77    | 0.054   |
| Ceriodaphnia spp.  | 4.248  | 13.84   | 0.004** |
| Chydoridae         | 1.068  | 1.44    | 0.258   |
| Daphniidae (sp)    | 0.667  | 0.62    | 0.451   |
| Daphnia spp.       | 1.733  | 0.87    | 0.372   |
| D. lumholtzi       | 11.194 | 18.57 | 0.001** |
| Moina spp.         | 2.043  | 1.65    | 0.227   |
| M. tenuicornis     | 16.310 | 19.04 | 0.001** |
| Simocephalus spp.  | 0.806  | 3.10    | 0.109   |

*** 0.001; **0.01; *0.05.
H) and significantly more eggs of *D. lumholtzi* were present in the sediment of the permanent wetlands (Tab. 1, Fig. 5F).

Nonmetric multidimensional scaling of the egg bank community (abundance data) corroborated the differences in community composition between wetland types (Fig. 6). These differences were confirmed by ANOSIM (R=0.602; p=0.007).

Fig. 3. Assemblage attributes (mean ± standard deviation) of the resting egg banks in permanent (P) and temporary (T) wetlands in the Ovens River floodplain. ***0.001; **0.01; *0.05.
DISCUSSION

The temporary wetlands, in this study, have a variable disturbance, pattern with drying occurring during most summer periods and re-filling of wetlands from the river occurring when winter-spring rainfall occurs. In permanent wetlands the disturbance is less variable. In these wetlands, water is retained across all seasons, but changes in water quality occur slowly as these wetlands shrink in size during the summer months and increase once winter-spring rainfall occurs and the wetlands are reconnected to the river. In both wetland types, seasonal changes in water availability promote physical and chemical changes and introduce new species that are either competitors for resources or predators (Junk et al., 1989). In combination these factors promote seasonal succession of many zooplankton species including cladoceran in wetlands (Nielsen et al. 2002). These changes have the potential to promote large alterations in cladoceran assemblages. Even considering the important ecological connectivity between floodplain lakes distant up to $10^4$ meters (Jenkins and Boulton, 2003), in our results, despite of the proximity among wetlands, several parameters were significant different between temporary and permanent wetlands, reinforcing the evidence of specific characteristics to resting egg bank structure according to type of wetlands.

The aquatic biodiversity in floodplain-wetland complexes dominated by ephemeral wetlands is supported by the resilience of the dormant communities to drying and, allow the communities to recover when the wetland re-floods (Brock et al., 2003). Hydrological disturbance in temporary pools, defined as “frequency of successful inundations and average duration that pools remain dry”, can be a determinant of richness, composition, and structure of the associated aquatic communities (Brendonck et al., 2017). This study has shown that the composition of cladoceran communities differs between temporary and permanent wetlands. In the water column, these differences were driven by more species occurring

| Unique - Temporary wetlands | Unique - Permanent wetlands | Common - Both wetland types |
|-----------------------------|-----------------------------|----------------------------|
| Water column                |                             |                            |
| Aloninae (1 species)        | Graptoleberis testudinaria (Fisher, 1851) | Aíona cf. gutta Sars, 1862 |
| Alona intermedia Sars, 1862 | Ovalona pulchella (King, 1853) | Bosmina meridionalis Sars, 1904 |
| Alona quadrangulares (O.F. Müller, 1776) – group sp.1 | Simocephalus cf. elizabethae (King, 1853) | Ceriodaphnia cf. quadangular (O.F. Müller, 1785) |
| Archepleuroxus baylyi Smirnov & Timms, 1983 | Simocephalus (Echinocudus) sp. | Flavalona cf. costata (Sars, 1962) |
| Ceriodaphnia cf. laticaudata P. E. Muller, 1867 | | Picripleuroxus cf. quasidenticulatus (Smirnov 1996) |
| Chydorus cf. clelandi Henry, 1919 | Pleuroxus cf. inermis Sars, 1896 | |
| Chydorus cf. eurinotus Sars, 1901 | Scapholeberis kingi Sars, 1903 | |
| Chydorus cf. sphaericus (O. F. Müller, 1776) | Simocephalus exspinosus (De Geer, 1778) – group sp.1 | |
| Coronatella cf. poppei (Richard, 1897) | Simocephalus exspinosus (De Geer, 1778) – group sp.2 | |
| Coronatella cf. rectangular (Sars, 1861) | | |
| Coronatella sp.1 | | |
| Daphnia sp.1 | | |
| Diaphanosoma cf. unguiculatum Gurney, 1927 | | |
| Picripleuroxus sp.1 | | |
| Pseudomoina lemnae (King, 1853) | | |
| Egg bank | | |
| Moina tenacicornis Sars, 1896 | Aloninae | Ceriodaphnia spp. |
| | | Chydorinae |
| | | Daphnia spp. |
| | | Daphnia cf. lumholtzi Sars, (1885) |
| | | Daphniidae |
| | | Moina spp. |
| | | Simocephalus spp. |
in temporary wetlands, with more than 50% of the active species occurring only within these systems. This highlights the importance of temporary wetlands as biodiversity hotspots within floodplains. In contrast, to the findings in the water column the taxonomic richness of the resting egg bank was lower in the temporary wetlands compared to the permanent wetlands, even as the equitability, resulting also in lower taxonomic diversity. The differences between the two wetland types is likely to be as a consequence of reduced variability in the hydrology of the permanent wetlands. This reduced variability leads to an accumulation of dormant eggs in the sediment of the permanent due to the loss of cues that trigger dormancy breakage (Nielsen et al., 2000).

Dormant eggs of most cladoceran species are known to accumulate in sediment over long time periods (Brendonck and De Meester, 2003; Alekseev, 2007; Radzikowski, 2013), and have been suggested to potentially provide a useful estimate of the diversity of zooplankton communities (May 1986, Vandekerkhove et al., 2004; Coronel et al., 2009). However, in this study, the community of cladocerans in the water column at the time of sampling differed from what was present in the egg bank, with more species occurring in the water column. This difference between communities present in the water column and what is found in sediment has also been previously recorded in other studies (Pallazo et al., 2008; Santangelo et al., 2015; Gehard et al., 2017). The differences are likely to reflect issues with identifying ephippia to lower taxonomic groups leading to an underestimation of the resting egg bank community. Resting egg identification is a difficult task, because important taxonomic characteristics (head pores, postabdomen, antennae, antennula and trunk limbs) are not present in resting eggs. Even valve characteristics as marginal setae and denticles can be lost during the permanence in the sediment (Panarelli et al., 2019).

A much higher abundance of cladoceran eggs was observed in the temporary wetlands (1.15 x 10^4 eggs.m^-2) compared to the more permanent wetlands (0.27 x 10^4 eggs.m^-2) during this study. These results are within the ranges (between 10^3 and 10^5 egg.m^-2) of egg abundance recorded from other cladoceran studies (Hairston et al., 1995; Iglesias et al., 2016). The key drivers of dormant egg production are changes in water quality, increased population density (crowding), predation and food quantity and quality (Brendonck et al. 2017). These changes in conditions result in substantial numbers of dormant eggs being produced. In wetlands with short hydroperiods with frequent occurrence of unfavourable conditions this may result in a continuous production of dormant eggs. In comparison, unfavourable events may occur more rarely in wetlands with a more stable hydrology, and dormant egg production may only occur sporadically (Gyllström and Hansson 2004; Brendonck et al. 2017).

Therefore, higher egg abundances within temporary wetlands may reflect the continuous production of resting eggs by cladoceran within these systems compared with the sporadic production in more permanent waterbodies. The highest number of unviable eggs was also reported for temporary wetlands. The higher damaged resting egg density, in part, may be due to the eggs of some species being more susceptible to factors that reduce viability such as age, predation, parasitism or physical damage (Redfield and Vincent, 1979; Gyllström and Hansson, 2004). Indeed, other studies have demonstrated that in temporary wetlands the numbers of eggs hatching decreases as the interval between flood events increases (Boulton and Lloyd, 1992; Jenkins and Boulton, 2007; Nielsen et al., 2013) and that survivorship may be species specific (Radzikowski, 2013).

The ability for a dormant egg to survive in temporary wetlands during the dry phase requires

**Fig. 4.** Nonmetric Multidimensional Scaling (nMDS of the taxonomic composition (presence/absence) of cladocera in the water column between the temporary (open circle) and permanent (closed circles) wetland (Stress = 0.12. Vectors abbreviations: Crec (Coronatella cf. rectangular), Coro (Coronatella spp.), Bmer (Bosmina meridionalis), Sexp1 (Simocephalus expinosus group sp1.), Seli (Simocephalus cf. elizabethae).**
specialised features such as thick envelopes and shells that help to protect them against the negative effects of adverse environmental factors, such as drying, freezing, mechanical damage, microbial invasion, predation, UV radiation or harmful chemicals (Alekseev, 2007; Amsinck et al., 2007). These features are likely to vary

Fig. 5. Taxonomic abundance (mean ± standard deviation) of the resting egg banks in temporary (T) and permanent (P) wetlands in the Ovens River floodplain. ***0.001; **0.01; *0.05.
among taxa (Gilchrist, 1978). It is known that cladoceran eggs can survive for decades but viability decreases over time (Piscia et al., 2012; Nielsen et al., 2013). Additionally, only a small proportion of viable dormant eggs will hatch in response to environmental cues (Cáceres and Tessier, 2003). This storage effect is an important mechanism for maintaining genetic diversity within populations (Hairston and Kearns, 2002). The egg viability had not confirmed by hatching in our study, being an inference related to appearance and age, but the unviable aspect had considered real damage in embryos. The significant difference in unviable eggs between temporary and permanent wetlands may indicate that higher resting egg production in temporary wetland can balance the losses during the dry phase. This represents a large energy investment to compensate losses under harsher conditions (biotic and abiotic) in these wetlands.

Understanding how wetting and drying regimes influence dormant eggs in permanent and temporary wetlands is important in developing management strategies to maximise the resilience of wetland ecosystems in the face of increasing aridity as a consequence of climate change to ensure a functioning and sustainable riverine-wetland landscape into the future.

CONCLUSIONS

In this paper we tested the hypothesis that the resting egg banks of cladocerans would be more diverse and abundant, including the higher density of inviable eggs, in temporary wetlands compared to more permanently inundated wetlands. Our results only partially support this hypothesis in that while there were significantly more eggs (mainly inviable eggs) in the sediment of temporary wetlands, there were on average lower taxonomic diversity within temporary wetlands.

The taxonomic richness was also much higher in water column than sediment, however this likely reflects limitations to resting egg identification and supports the need for advances in resting egg identification to improve the understanding of egg bank diversity. In temporary wetlands, the much higher resting egg density, suggest a possible adaptation to overcome loses due to drying of wetlands, however this needs further investigation.

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