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Do temperature and water depth influence microcrustacean hatching responses from floodplain wetland sediments?

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Abstract. Microcrustacea in ephemeral wetlands produce dormant eggs to escape prolonged dry conditions. These eggs can hatch on inundation, although in most cases not all eggs hatch during a single wetting event. Incomplete hatching can reflect bet-hedging strategies, but also the presence or absence of environmental cues that stimulate hatching. This study examines the effects of environmental cues likely to change for wetlands in the future, namely, temperature and water depth. Surface sediments collected from dry anabranches of the Macintyre River floodplain (eastern Australia) were inundated under two temperature regimes (warm and cool) in microcosms of two depths (shallow and deep). Hatched microcrustacea were sampled for 6 weeks. The abundance and assemblage composition of microcrustacea varied by temperature but not by depth. Although the total abundance was greater under warm conditions, the effect of temperature diminished over time. Temperature also had a greater effect on non-ostracods, with 144% more non-ostracods being hatched under warm than under cool conditions. Thus, changes to temperature during inundation periods arising from global climate change or river regulation are likely to influence the abundance and composition of microcrustacean assemblages, especially among non-ostracods, which will influence food availability for larval and juvenile native fish and, hence, recruitment.

Keywords: climate change, dryland river, egg bank, environmental cues.

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Introduction

Microcrustacea produce dormant eggs to survive prolonged dry periods in temporary water bodies (Cáceres 1997; Brendonck and De Meester 2003; Brendonck *et al.* 2017). The subsequent rewetting of the waterbody stimulates diapausing eggs to break dormancy, to take advantage of the short wet periods available to complete their life cycle, recruit new generations and add more eggs to the egg bank.

However, simply hatching in response to wetting can have negative consequences. If all eggs hatch following a wetting event that does not result in successful completion of life cycles, the egg bank will be depleted without replenishment. This can happen because the wetting event may be too brief, or the habitat quality conditions created by the event unsuitable (e.g. low food resources or poor water quality), to allow successful completion of life cycles and production of diapausing eggs.

To prevent the catastrophic depletion of the microcrustacea egg bank and increase the chances of successful completion of lifecycles, microcrustacea can follow two strategies. First, they can utilise a bet-hedging strategy, whereby not all eggs hatch in response to the same wetting event. This means that if an event does not result in the production of more diapausing eggs, for whatever reason, at least some eggs will remain to hatch in subsequent events. Second, eggs can respond to more complex suite of environmental cues than simply being wet. These cues can act to better predict the aquatic conditions created by the wetting event. Thus, the likelihood of the environmental conditions being suitable or not suitable, as indicated by environmental cues, stimulates or suppresses microcrustacea hatching (Nielsen *et al.* 2003; Richmond *et al.* 2006; Ekau *et al.* 2010).

Although the two strategies, namely, bet hedging and responding to environmental cues that predict conditions, differ in the sense that one works through protection and the other through prediction, both are likely to involve a response to environmental cues. In the case of predicting the environmental conditions, environmental cues are obviously fundamental. In the case of bet-hedging, the variation in hatching response to a wetting event is likely to be driven by within-population variation in hatching response to environmental conditions.

There is substantial empirical evidence that the capacity to hatch in response to environmental cues exists among microcrustacea. Factors such as high salinity, low dissolved oxygen concentrations and pesticides have all been shown to reduce the abundance and richness of hatched microcrustacea (Nielsen *et al.* 2007; Ning *et al.* 2015; Goździejewska *et al.* 2016; Portinho *et al.* 2018).

Strategies such as bet-hedging and responding to environmental cues that may predict post-hatching conditions are

particularly important for microcrustacea in dryland river systems subject to variable and unpredictable wetting regimes. This is because if wetting is variable and unpredictable, there is a greater chance that any one event may not be suitable for successful recruitment. By contrast, in systems subject to more regular and predictable wetting, such as those experiencing a regular spring pulse, the need to 'hedge bets' or 'predict' environmental conditions is not so great because each event is likely to produce conditions suitable for recruitment.

Australian dryland rivers are particularly variable and unpredictable (Puckridge *et al.* 1998; Bunn *et al.* 2006) and thus microcrustacea in these systems are likely to rely heavily on strategies such as bet-hedging and using environmental cues to stimulate hatching responses. Importantly, these dryland river systems are also subject to anthropogenic alteration as a result of water resource development (WRD) and, like rivers worldwide, climate change (Kingsford 2000; Howden *et al.* 2003; CSIRO 2008; Kingsford *et al.* 2017). In combination, these anthropogenic changes have affected a range of variables that have the potential to both act as hatching cues and influence subsequent recruitment success within the microcrustacea population (van Vliet *et al.* 2013; James *et al.* 2016).

Most obviously, climate change and, to a lesser extent, WRD through changes to seasonality of flooding, are likely to affect temperature. Temperature has the potential to affect microcrustacea through direct physiological effects on hatching and development and indirect effects on the suitability of the aquatic habitat created by inundation. For example, the mortality rate of hatched microcrustacea is increased both in high (>30°C) and low (<15°C) temperatures (Heinle 1969; Vandekerkhove *et al.* 2005). Temperature also helps increase primary production in the habitat, which leads to higher microcrustacea growth after hatching (Schalau *et al.* 2008). Conversely, higher temperature reduces dissolved oxygen concentrations, which, as noted above, can supress microcrustacea hatching (Ning *et al.* 2015).

Hydrological changes arising from WRD and climate change may also affect potential cues. For example, water depths are affected by climate change and WRD as a result of changing flood magnitudes and frequencies. In an adaptive sense, water depth could be an effective cue because it is a good predictor for duration of inundation and habitat heterogeneity (Hamilton and Lewis 1990). There is also an obvious mechanism in the form of water pressure that would enable eggs to respond to variations in depth.

Although there is a potential for temperature and water depth to act as cues for microcrustacea hatching, few studies have explored their effects (Nielsen *et al.* 2002; Vandekerkhove *et al.* 2005; van Vliet *et al.* 2013; Jones and Gilbert 2016).

In light of these knowledge gaps, this study tests whether temperature and water depth act as cues for the hatching of microcrustacea from eggs in the egg banks of temporary floodplain wetlands. On the basis of the potential adaptive advantages of hatching response to temperature and water depth, the following two hypotheses are proposed:

1. In relation to temperature, we hypothesise that hatching assemblages will vary with temperature and that higher temperature will result in greater numbers because of the adaptive advantages of higher primary productivity and metabolic rates facilitating higher growth rates and greater reproductive success. We further hypothesise that the temperature effect will be stronger early in the post-inundation phase because any temperature effect driving faster development and hatching of eggs will diminish with time as eggs developing more slowly under cool conditions reach hatching stage.
2. In relation to depth, we hypothesise that hatching communities will vary with depth (facilitated through a response to ambient water pressure), with greater numbers being likely to hatch from deeper microcosms on the basis of the adaptive advantages that deeper habitats are likely to provide more resources and a greater range of microhabitats than are shallow habitats and the longer inundation periods associated with higher depths.

Materials and methods

Study sites and sediment collection

Sediments were collected from 16 dry anabranches of the Macintyre River floodplain in February 2018. The Macintyre River drains the Border Rivers catchment in south-eastern Australia. The study area covered roughly 90 km of river floodplain downstream of Goondiwindi on the New South Wales–Queensland border (Fig. 1). All the anabranches are temporary and flood about four times a year to once in 2 years Chaki *et al.* (2021).

The anabranches were selected using a random stratified design to incorporate a range of flood frequencies. This approach was taken so that the study could test for patterns in relation to flood frequency in a separate study (Chaki *et al.* 2021). Soil samples were collected at each of two randomly selected locations in each of the 16 anabranches. These locations were selected to represent relatively deep relatively shallow points within each anabranch. At each of the two locations in each anabranch, we selected an area of 1 m^2 and collected five soil samples (S1–S5; 10 cm × 10 cm × 2 cm) by using a spade from within this area, with samples being positioned as four samples in each corner of 1-m^2 area (S1–S4) and in the centre of the area (S4). Soil samples were placed in zip-lock bags to transport back to the laboratory. The soil samples were then disaggregated and sieved to remove large pieces of organic matter. Although the anabranches had no surface water, the soils varied in moisture content. Thus, to achieve uniform starting conditions, all wetland sediment was dried at 35°C for 24–48 h before the inundation trial. The soil samples (S1–S5) collected from each location were pooled and subsampled, with each subsample being randomly assigned to treatment in a crossed design.

Laboratory trials

For each subsample, we placed ~210 g soil into a microcosm consisting of a 10-cm-diameter acrylic plastic tube, sealed at the base. This amount of soil sample resulted in the sample filling the tube to an approximate depth of 3 cm. The microcosms were then filled with water that was a mix of river water collected from the field site (40%) and rainwater (60%). This mix was used to ensure that any chemicals in the local river water that may have served as cues to hatching were included in the microcosms. A 100% river water fill was not used because of logistic issues associated with transporting the required volume

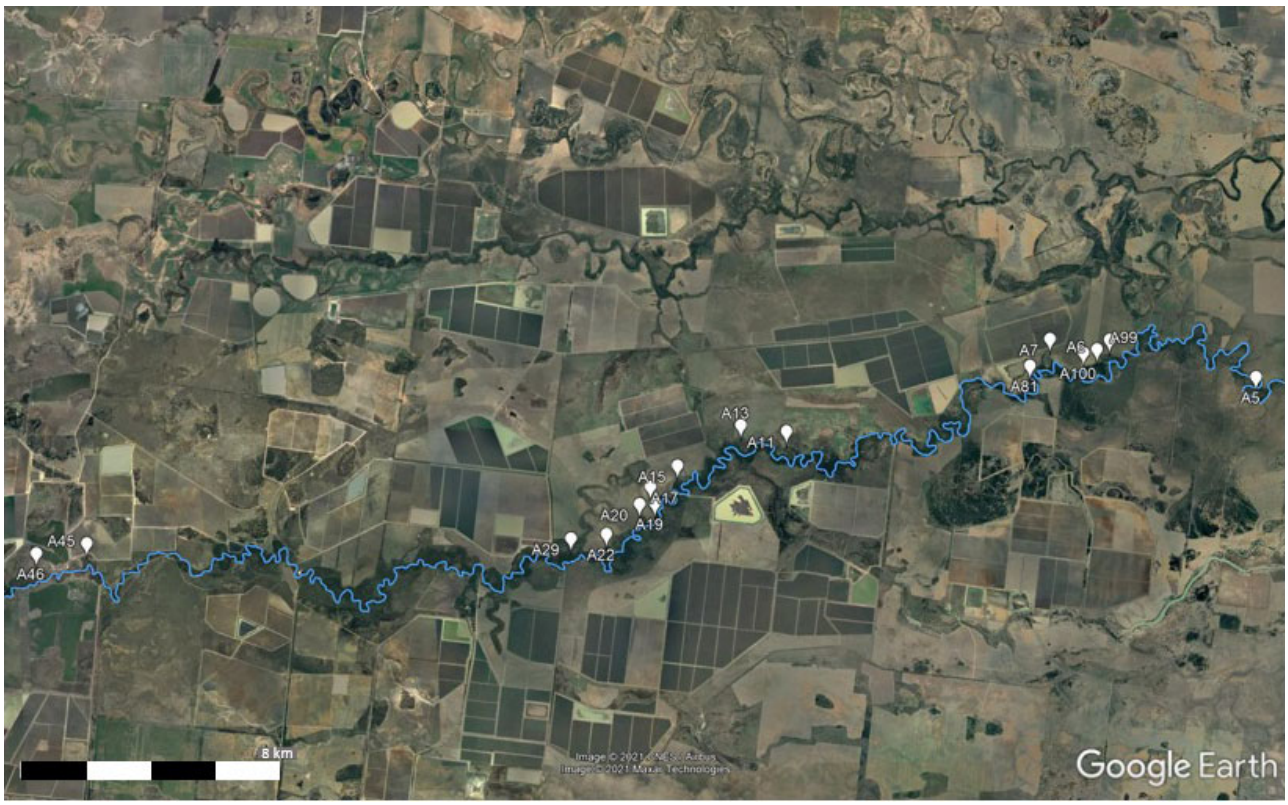

Fig. 1. The locations of the selected sites on the Macintyre River floodplain.

of water back to the laboratory. Before use, all water was filtered through 50-µm mesh sieve to avoid introducing any microcrustacea that may have been present in the river water.

To test for an effect of depth on hatching, the microcosms consisted of tubes of two different depths. Practical and logistical factors limited the depth contrast to 40 cm for the deep treatment against 15 cm for the shallow treatment. Although relatively small, this depth difference was deemed sufficient on the basis of the likely contrast in habitat quality and heterogeneity in wetlands of 40-cm and 15-cm depths. It is noteworthy too that, on the basis of a regional potential evaporation rate of ~5 mm day^{-1}, this contrast is likely to correspond to a difference in persistence of ~50 days (Reid *et al.* 2017). Two of the subsamples from each anabranch sediment sample were placed in the deep tubes and the remaining two were placed in the shallow tubes.

To test the influence of temperature on microcrustacea hatching, these tubes were then placed into one of two temperature controlled rooms in a glasshouse. One room was subject to a cool-temperature regime centred on ~20°C and the other was subject to a warm-temperature regime averaging ~4°C higher. The 4°C difference was based on the estimated warming in Australia since 1910 of 1.44 ± 0.24 (CSIRO 2020), projected ongoing warming, combined with shifts in the seasonality of inundation, resulting in more flooding occurring during warmer months (CSIRO 2020). Temperatures in each room were varied to mimic diurnal fluctuations of ~8–10°C. These regimes resulted in the cool treatment experiencing median and mean temperatures of 19.5°C and 21°C respectively, and a range from 17.5°C (10th percentile) to 24.5°C (90th percentile) for most of the trial period. The warm treatment experienced median and mean temperatures of 24.1°C and 24.3°C respectively, and a range from 19.5°C (10th percentile) to 29.5°C (90th percentile) for most of the trial period. Temperatures were recorded every hour over the duration of the trial. Thus, each subsample from each sediment sample was subject to a different treatment combination of deep versus shallow and warm versus cool. All treatments experienced the same light–dark regime based on local ambient light (day–night).

Microcosms were sampled on eight occasions over 6 weeks from 22 May to 4 July 2019. Sampling was conducted twice weekly to avoid reproduction by emerged individuals (Nielsen *et al.* 2007; Ning and Nielsen 2011). After 2 weeks, biweekly samples were combined for analysis. Samples from the first 2 weeks were kept separate to assess temporal variation in hatching that has been shown to be more pronounced during the days immediately after inundation (Eskinazi-Sant'Anna and Pace 2018). Sampling was conducted by siphoning the water into a measuring cylinder, with care not to agitate the soil, and filtering the decanted water through a 50-µm-mesh sieve. The retent of sieved water was preserved in 75% ethanol for later analysis.

The sieved water was returned to its original tube, and each tube was topped up to its original depth using the same mix of river and rainwater to maintain the same water level through the trial.

Microcrustacean identification and enumeration

Preserved samples from each microcosm and sampling occasion were enumerated in a Sedgewick–Rafter counting chamber and identified under a Zeiss Stemi 2000-C (Carl Zeiss International, Jena, Germany) dissecting microscope at between ×10 and ×100 magnification. Microcrustacea were assigned to morphotypes and given provisional taxonomic identifications by using a range of taxonomic guides (Smirnov and Timms 1983; Shiel 1995). Identified morphotypes were photographed, and provisional identifications were confirmed by experienced microcrustacean taxonomists (Koen Martens, Stuart Halse and Rochelle Petrie, pers comm.). Cladocera and copepods were identified to family level, and ostracods were identified to genus level where possible.

Statistical analysis

For statistical analysis, all counts were converted to the abundance of individuals emerged per square metre of sediment. From these count data, several response variables were considered to test the effects of depth, temperature and time on hatching. These included taxon richness of hatched microcrustacea, total abundance of hatched microcrustacea, and total abundance of hatched ostracods, total abundance of hatched non-ostracods, as well as the assemblages of all microcrustacea (ostracods and non-ostracods).

The effects of temperature, water depth and sampling time on the hatched microcrustacean assemblages were explored using permutational multivariate ANOVA (PERMANOVA) with temperature (2 levels), water depth (2 levels) and week (8 levels: 0.5, 1, 1.5, 2, 3, 4, 5, 6 weeks) as fixed factors by using the software program PRIMER-E (v.7) with the PERMANOVA + add-on (Anderson *et al.* 2008).

The PERMANOVA of abundances (total, ostracod and non-ostracod) analysis was performed using resemblance matrices calculated from Euclidean distance similarity measures of square-root-transformed count data to reduce the influences of abundant taxa (Clarke and Gorley 2015). Comparisons of taxon richness were also performed on resemblance matrices calculated from Euclidean distance measures of non-transformed count data (Clarke *et al.* 2014). The PERMANOVAs of assemblages were performed using resemblance matrices calculated from Bray–Curtis similarity measures of taxon count data square-root transformed to down-weight the influence of very abundant taxa (Anderson *et al.* 2008). The model used for abundance, richness and assemblage data is as follows:

$$\begin{aligned}&\text{Abundance/Richness/Assemblage} = \text{Te(Temperature)}\\&+ \text{Tu(Tube size; small and large)} + \text{We(Duration of inundation)}\\&+ \text{Te} \times \text{Tu} + \text{Te} \times \text{We} + \text{Tu} \times \text{We} + \text{Te} \times \text{Tu} \times \text{We}\end{aligned}$$

Results

The effects of temperature and depth on microcrustacean abundance and richness

The total number of microcrustacea hatched from the sediment varied by temperature (Fig. 2*a*, Table 1). Total abundance was 20.73% higher in warm conditions than in cool-temperature conditions (Fig. 2*a*). Total abundance also varied by sampling time (Fig. 2*b*, Table 1), without there being any interaction among

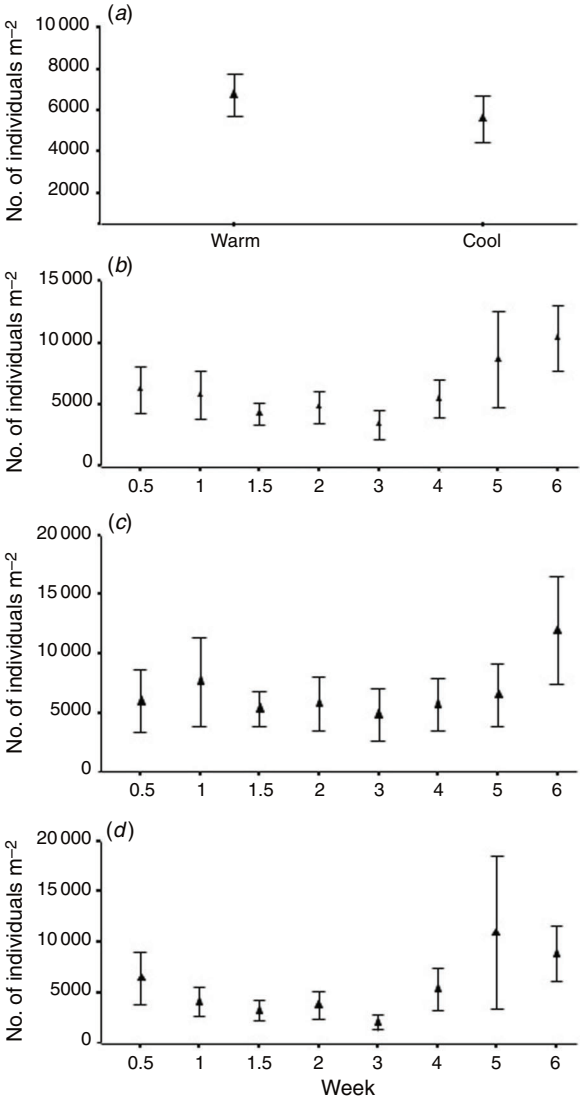

Fig. 2. Contrasts in the number of microcrustacean individuals hatching from warm and cool treatments (*a*) in different sites and (*b*) over the weeks of inundation period, and (*c*, *d*) contrasts in the number of microcrustacean individuals hatched over the weeks of inundation period from warm and cool treatments. Error bars are standard errors.

factors. Pairwise tests of weeks showed that the total number of hatched individuals was significantly different in 50% of the week-to-week comparisons (Table 2). Whereas in the warm treatment, the hatching number of microcrustacea increased gradually, except in Week 3 (Fig. 2*c*), in the cool treatment, there was a sudden increase in hatching in Week 4 or 5 and a decrease in Week 6 (Fig. 2*d*). The difference in abundance for each treatment in each sampling period resulted in the cumulative number of microcrustacea hatching in warm conditions for each microcosm being substantially greater over the inundation period (Fig. 3*a*).

The total number of non-ostracods hatched from sediment varied by temperature and week (Fig. 4*a*, *b*, Table 1). Two significant interactions were also found among factors whereby

Table 1. Permutational multivariate ANOVA (PERMANOVA) results for the analysis of hatched micrustacean taxon abundance, richness and assemblage composition with temperature (two levels), tube depth (two levels) and the weeks of sampling (8 levels) as factors

Factor	Degree of freedom	Sum of squares	Mean squares	*F*	*P*
Abundance					
Total abundance					
Temperature	1	9570	9570	3.65	**0.049**
Week	7	83 646	11 949	4.55	**0.001**
Ostracod abundance					
Week	7	42 713	6101.9	3.39	**0.002**
Temperature × Week	7	27 648	3949.6	2.19	**0.001**
Non-ostracod abundance					
Temperature	1	65 122	65 122	35.43	**0.001**
Week	7	2.45	35 056	19.07	**0.001**
Temperature × Week	7	81 031	11 576	6.29	**0.001**
Temperature × Tube depth × Week	7	30 224	4317	2.35	**0.034**
Full assemblage					
Temperature	1	9949.2	9949.2	3.42	**0.004**
Week	7	3.93	56 141	19.34	**0.001**
Non-ostracod assemblages					
Temperature	1	12 180	12 180	4.09	**0.004**
Tube depth	1	5586	5586	1.87	0.092
Tube depth × Week	7	28 114	4016	1.35	0.078
Ostracod assemblages					
Temperature	1	7447	7447	2.88	**0.017**
Week	7	4.09	58 483	22.6	**0.001**
Temperature × Week	7	27 381	3911	1.51	**0.028**

the effect of temperature varied by weeks, and the effect of temperature varied by tube depth, and weeks (Table 2). The temperature–week interaction reflects a pattern whereby hatching numbers increased gradually in the warm treatments from the beginning to the end of the inundation period (Fig. 4*c*), whereas in cool treatments, the hatching number was mostly low, with a peak in Week 5 (Fig. 4*d*). The cumulative effect of temperature over the inundation period resulted in almost 144% more non-ostracods hatching in the warm treatments than in the cool treatments (Fig. 3*b*).

The total abundance of hatched ostracods also varied by week (Fig. 5*a*), with a strong interaction between temperature and week (Table 1). This interaction reflects a pattern whereby the hatching pattern in the warm treatments fluctuated little from week to week (Fig. 5*b*), whereas the pattern in the cool treatments was for large fluctuations from week to week, with a gradual decrease in numbers after the first week to the third week and then a gradual increase from inundation from Week 4 to Week 6 (Fig. 5*c*). In contrast to non-ostracods, the cumulative number of ostracods hatched over the inundation period was actually higher in the cool treatments by 11%, although this did not translate to a significant temperature effect on abundance (Fig. 3*c*).

In total, 16 taxa (Table1S) were identified in this experiment, but species richness did not vary by temperature or depth and there were no significant interactions among factors.

Table 2. Pairwise test results of micrustacean species abundance and community composition over time in Macintyre River anabranches

All data were analysed by permutational multivariate ANOVA (PERMANOVA)

Week	0.5	1	1.5	2	3	4	5	6
Total abundance								
0.5		0.782	0.337	0.556	**0.017**	0.76	0.179	**0.032**
1			0.171	0.354	**0.002**	0.52	0.257	**0.05**
1.5				0.734	**0.05**	0.553	**0.016**	**0.001**
2					**0.033**	0.775	**0.053**	**0.01**
3						**0.025**	**0.001**	**0.002**
4							0.098	**0.016**
5								0.353
6								
Full assemblages								
0.5		**0.001**	**0.001**	**0.001**	**0.001**	**0.001**	**0.001**	**0.001**
1			**0.001**	**0.001**	**0.001**	**0.001**	**0.001**	**0.001**
1.5				**0.001**	**0.001**	**0.001**	**0.001**	**0.001**
2					**0.001**	**0.001**	**0.001**	**0.001**
3						**0.018**	**0.003**	**0.001**
4							0.724	**0.001**
5								**0.002**
6								
Non-ostracod assemblages								
0.5		**0.001**	**0.001**	**0.001**	**0.001**	**0.001**	**0.001**	**0.001**
1			**0.003**	**0.001**	**0.026**	**0.003**	**0.001**	**0.001**
1.5				0.136	0.068	**0.002**	**0.001**	**0.001**
2					**0.005**	**0.001**	**0.001**	**0.001**
3						0.307	**0.04**	**0.001**
4							0.504	0.184
5								0.349
6								
Ostracod assemblages								
0.5		**0.001**	**0.001**	**0.001**	**0.001**	**0.001**	**0.001**	**0.001**
1			**0.002**	**0.001**	**0.001**	**0.001**	**0.001**	**0.001**
1.5				**0.001**	**0.001**	**0.001**	**0.001**	**0.001**
2					**0.001**	**0.001**	**0.001**	**0.001**
3						**0.007**	**0.003**	**0.001**
4							0.465	**0.001**
5								**0.003**
6								

The effects of temperature and depth on microcrustacean assemblage composition

The PERMANOVA results showed significant differences in assemblage composition in relation to temperature and week but not in relation to depth treatment. Among major taxa, *Ilyocypris*, juvenile ostracod, *Cypretta* and *Ilyodromus* hatched in greater numbers and earlier in cool treatments than in warm treatments. In contrast, Chydoridae, Moinidae, Daphnidae, *Heterocypris* and Macrotrichidae hatched in greater numbers and earlier in warm treatments than in cool treatments. There were no interactions among factors for microcrustacea assemblages. Pairwise tests showed differences in hatched assemblage for all week-to-week comparisons except for the Week 4 to Week 5 comparison (Table 2).

The influence of the tested factors on the hatching appears to vary among taxonomic groups. The non-ostracod assemblages

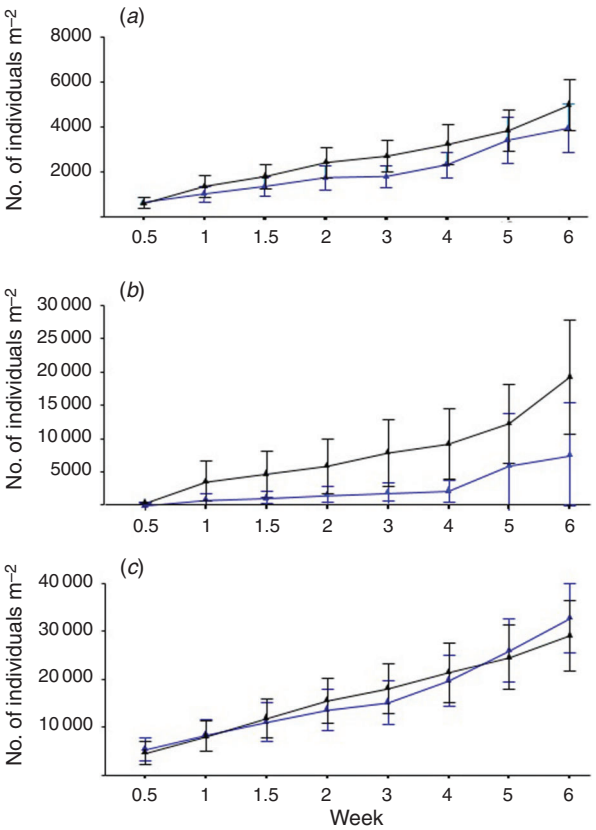

Fig. 3. (*a*) Contrasts in the cumulative number of hatched microcrustaceans, (*b*) non-ostracods and (*c*) ostracods per square metre from different temperatures for each week over the inundation period. The black and blue lines represent microcrustaceans hatched from warm and cool temperatures accordingly and the error bars are standard errors.

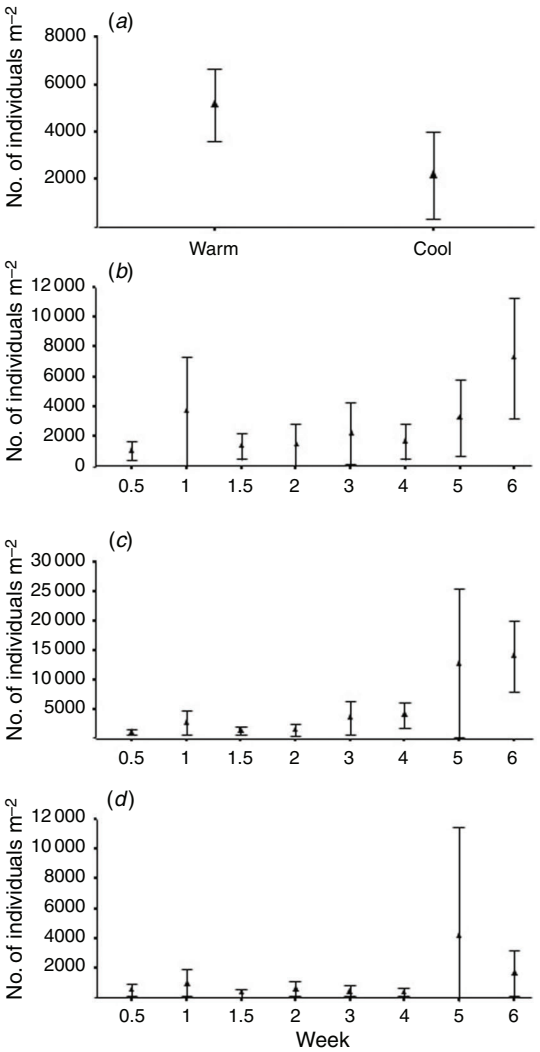

Fig. 4. (*a*) Contrasts in the number of non-ostracods hatched from warm and cool treatments in different sites, (*b*) contrasts in the number of hatched non-ostracods over the weeks of inundation period, and (*c*, *d*) contrasts in the number of hatched non-ostracods from warm and cool treatments over the inundation period. Error bars are standard errors.

varied by temperature and week, with there being no interactions among factors (Table 1). Pairwise tests of weeks showed that differences in non-ostracod assemblage compositions were observed for most combinations of weeks (Table 2).

The ostracod assemblages also varied by temperature and week (Table 1). Pairwise tests of weeks showed that hatched ostracod assemblages differed by all week combinations except Week 4 and Week 5 (Table 2). There was also a strong interaction between temperature and week for ostracod assemblages. In warm conditions, significant differences in assemblage composition were observed in pairwise tests of all combinations of weeks, with the exceptions of Week 1 and Week 1.5, Week 3 and Week 4, and Week 4 and Week 5. In contrast, in cool conditions, assemblage composition was significantly different for all week combinations except Week 4 and Week 5 (Table 2).

Discussion

Results of this study have demonstrated that environmental cues can influence what eggs hatch from the same egg bank. However, among the environmental cues tested, only temperature was found to have a detectable effect on the number and assemblage composition of microcrustacea hatching from the sediment. Water depth, despite its clear significance with respect to inundation duration (Hamilton and Lewis 1990) and habitat quality (Strachan *et al.* 2016), did not have a detectable effect on microcrustacea hatching, with the exception of an interaction among water depth, temperature and week affecting hatched non-ostracod assemblages.

With regard to the hypotheses, the findings support the first hypothesis that temperature influences microcrustacea hatching from the sediments, with ~20% more, on average, hatching from warm treatments. Temperature appears to increase hatching numbers of non-ostracods more than those of ostracods. The cumulative total of non-ostracods hatched over the full inundation period from warm-treatment microcosms was ~144% greater than that from the cool-treatment microcosms. In contrast, the cumulative total of ostracods hatched from the warm-treatment microcosms was actually 11% less than that of

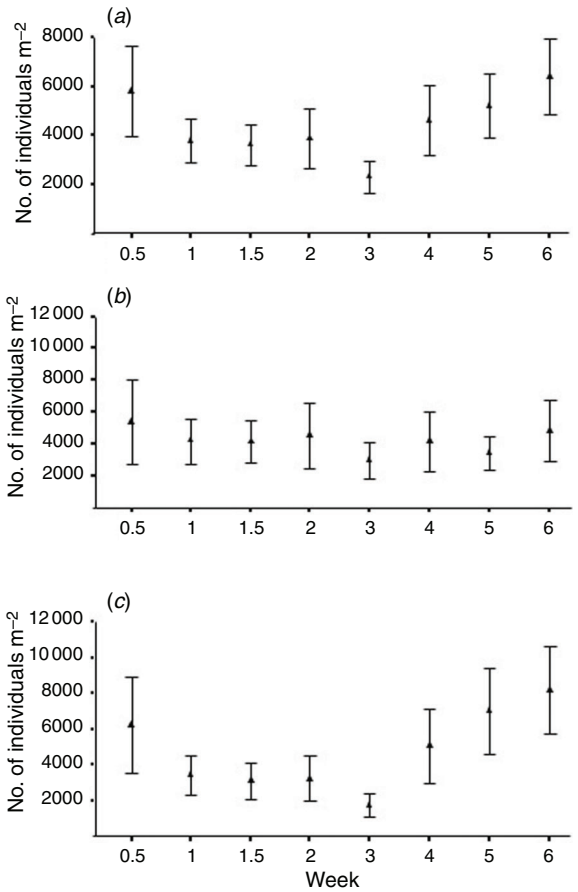

Fig. 5. (*a*) Contrasts in the number of hatched ostracods over the weeks of inundation period, and (*b*, *c*) contrasts in the number of hatched ostracods from warm and cool treatments over the inundation period. Error bars are standard errors.

ostracods hatched from the cool-treatment microcosms. Importantly, in warm and cool treatments, major changes happened in Weeks 5 and 6.

Variations in hatching response in relation to temperature among taxonomic groups were further demonstrated by the significant differences in assemblage compositions between temperature treatments. This effect was particularly strong for concostracan branchiopods, which were absent in cool-treatment microcosms.

In addition, although there were no interactions among treatments for full assemblages, the effect of temperature on ostracod assemblage composition varied by week, with ostracod hatching numbers higher and more consistent through the trial period, whereas hatching numbers in the cool treatment were low, apart from Week 0.5 until Week 4. These hatching patterns partially support our hypotheses that any temperature effect would be stronger earlier in the post-inundation period.

These findings support several studies that have found that microcrustacea hatching increases in warm temperatures (Vandekerkhove *et al.* 2005; Dupuis and Hann 2009; Rajagopal *et al.* 2010; Jones and Gilbert 2016). Importantly, these previous studies compared hatching between seasons and thus left open the possibility that the observed patterns reflected responses to other seasonally aligned cues such as photoperiod. In the current study, temperature was isolated as a factor, so we can be confident that temperature is acting as a significant factor driving higher numbers of microcrustacea hatching as well as the compositional differences in the hatched assemblages.

Two mechanisms may be driving the higher hatching number under warm conditions. First, the response may be adaptive and reflect greater recruitment success under higher temperatures. This may arise because higher temperatures increase primary production and thus food availability. Therefore, the eggs that hatch in response to higher temperatures have a greater chance of survival and reproductive success, thus creating a selective advantage of higher hatching rates in response to higher temperatures (Vandekerkhove *et al.* 2005; Rajagopal *et al.* 2010). Second, the response may be physiological and reflect faster rates of egg development under warmer conditions (Hairston *et al.* 1995; Powlik *et al.* 1997; Yoshida *et al.* 2012; Chaves and Couto 2014).

In this study, the hatching pattern whereby the temperature effect was stronger for ostracods earlier during the period of inundation strongly suggests that the physiological mechanism is at least a factor. However, this does not rule out the possibility that the pattern also reflects an adaptive response.

In contrast to temperature, the study found little evidence that depth acted as a cue for microcrustacea hatching. Thus, we can reject the hypothesis that more eggs would hatch in the deeper microcosms.

There are three possible reasons for this result, namely

1. eggs are not able to detect water depth as a hatching cue;
2. eggs can detect depth, but there is no selective pressure to drive it to become a hatching cue; or
3. the amount of difference in depth we compared was not enough for eggs to detect and, hence, use as a cue.

In this study, some weak interactions were detected involving depth. The presence of these weak interactions, although difficult to interpret, provides some support for the hypothesis that the depth difference tested was not sufficient to produce a detectable response in the microcrustacea egg bank, despite the likely differences in habitat quality, heterogeneity and persistence between wetlands with depths of 0.45 m and 0.15 m. We suggest further testing using greater contrasts in depth to explore this possibility.

A previous study in the same floodplain by Chaki *et al.* (2021) showed that there were spatial differences in hatched microcrustacea linked to relative depth of inundation. Chaki *et al.* (2021) found that greater numbers of microcrustacea hatched from deeper regions of anabranches than from shallow regions. Chaki *et al.* (2021) interpreted those differences as a duration effect rather than the depth effect, arguing that duration of inundation differences drove differences in egg banks because of temporal patterns in hatching. The potential that depth may be a cue when larger contrasts are tested notwithstanding, the results of this study provide support for this interpretation.

Conclusions

This study has demonstrated that increased temperature will likely increase microcrustacea hatching. The results suggest that

temperature increases of about five degrees could increase the cumulative number of microcrustacea that hatch from the egg bank by 20% after 6 weeks of inundation. This effect is largely due to the response among non-ostracods, which showed an average increase of 144% in warmer conditions. The effect of temperature also varies over time, peaking, in relative terms, after 4 weeks of inundation when the cumulative abundance of hatched microcrustacea was 1.4 times higher in warm treatments for all microcrustacea and 1.08 times and 3.5 times higher for ostracod and non-ostracods respectively. Moreover, as non-ostracod microcrustacea are the preferred food for larval and juveniles fish, these results suggest that temperature increases may actually increase food availability for larval and juvenile native fish and contribute to their seasonal recruitment. However, we also assume that increasing temperature will be an advantage for microcrustacea hatching up to a certain temperature. At substantially higher temperatures, microcrustacea hatching may be suppressed as the thermal limits are reached and DO concentrations reduced. Therefore, the effects of larger increases in temperature need to be explored.

Although this study found no effects of depth on microcrustacea hatching, it is likely that any changes to flooding regime that influence depth will influence hatching in microcrustacea. This is because depth also affects the duration of inundation and inundation duration affects abundances and alters hatched assemblage compositions (Chaki *et al.* 2021).

Conflicts of interest

The authors declare that they have no conflicts of interest.

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