

# Multiple hatching events in clam shrimp: Implications for mate guarding behaviour and community ecology

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**Large branchiopods rely on dormant eggs to subsist in an ephemeral environment. Only a portion of the accumulated egg bank breaks dormancy when pools are filled, which is a bet-hedging strategy. Hatchings have been assumed to be discrete; however, multiple emergences have been reported for tadpole shrimp and fairy shrimp. We monitored the hatching frequency of the clam shrimp *Limnadia badia* in 35 pools on four granite outcrops in Western Australia. Here we report the occurrence of multiple hatching events, discuss their role as a secondary form of bet-hedging, and speculate on the implications for mating behaviour and community dynamics.**

**Keywords:** Bet-hedging strategy, Branchiopoda, *Limnadia badia*, Spinicaudata, temporary pool ecology.

## Introduction

THE Branchiopoda are crustaceans with a cosmopolitan distribution in inland freshwater and saline ponds and lakes on every continent, excluding Antarctica. The clam shrimp, fairy shrimp and tadpole shrimp are known collectively as the 'large' branchiopods. The majority of these organisms are found in temporary habitats and all share similar life-history adaptations to life in ephemeral pools. To survive in these unpredictable environments they produce eggs that undergo dormancy during the dry season as encysted gastrula<sup>1,2</sup>. When pools are inundated following rainfall events, the cysts can hatch and rapidly develop through several naupliar stages, mature and then reproduce while the pools remain filled<sup>3</sup>. However, not all cysts hatch during any given hydration period and this leads to the development of an egg bank in the pool sediment<sup>4</sup>. Cysts have been reported<sup>5</sup> to accumulate to densities of  $10^3$ – $10^5$ /m<sup>2</sup>, and yet percentages of the egg bank that hatch during one hydration have been reported to be as low as 2.8% in species of fairy shrimp<sup>6</sup>. This variable hatching is recognized as a bet-hedging strategy in which the reproductive output of individuals is spread

across several different hydration events<sup>4,7</sup>. This helps alleviate risks to survival of the population when a pond dries out before the hatched offspring reach reproductive maturity.

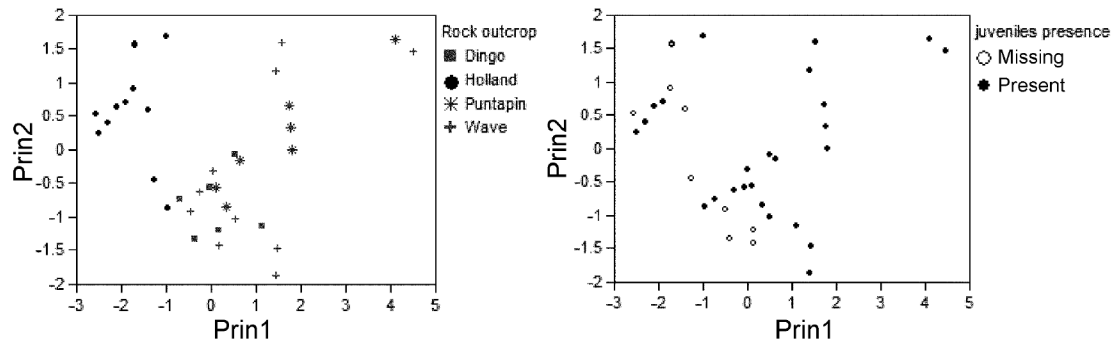
The mechanism by which hatching is induced is not well understood. Temperature and oxygen concentration are known to play a role<sup>8,9</sup>, but it is unclear how some cysts are stimulated to hatch while others maintain dormancy through a hydration event. Further, much effort has been focused on bet-hedging in an environment that could dry quickly after the initial hydration and hatching event, such as temporary pools in the desert<sup>1–3</sup>. Alternatively, particularly during wet seasons, ponds will fill and subsequent rains may keep them filled throughout the entire season, extending beyond the life cycle of the shrimp. In this situation, multiple hatching events throughout the life of the pool have been described in species of both fairy shrimp<sup>10</sup> and tadpole shrimp<sup>11</sup>. Here we discuss multiple hatching in a clam shrimp, *Limnadia badia* (Wolf, 1911).

We measured physio-chemical parameters of temporary pools on granite rock outcrops in Western Australia in relation to immediate vs delayed hatching of *L. badia*. We speculate as to whether delayed hatching is a secondary bet-hedging strategy or strictly a response to new exposure to hatching cues. Finally, we discuss how multiple hatching events result in the overlap of cohorts and the mixing of juvenile and adult life stages in these pools. We propose that the overlap of cohorts will have consequences in mating behaviour and temporary pool ecology.

## Materials and methods

We undertook a field study in April–May 2007, of multiple pools on four granite outcrops in the wheatbelt area of southwestern Western Australia: Holland Rock (Shire of Kent, 33°21.259'S; 118°44.639'E; 12 pools), Dingo Rock (Shire of Lake Grace, 33°0.558'S; 118°36.321'E; 6 pools), Wave Rock (Shire of Kondinin, 32°26.712'S; 118°53.836'E; 10 pools), and Puntapin Rock (Shire of Wagin, 33°19.495'S; 117°23.941'E; 7 pools). Weathering

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**Figure 1.** (Left) Distribution of pools from different outcrops plotted against the first two principal component axes. (Right) Same plot for pools with and without juveniles. Positive values of the first principal axis correlate with low temperature, high DO, low pH, high salinity and high TDS ( $P < 0.0001$ ). Positive values of the second principal axis correlate with high temperature, low DO, high pH, high salinity and high TDS ( $P < 0.05$ ).

pools are abundant on these outcrops. Pools vary in size, depth, amount of substrate and vegetation, and they can be considered natural replicates, undergoing hydration during the same rain event. We studied these pools upon receiving confirmation from shire offices of significant filling after localized rains. The recent precipitation history of the outcrops (Figure 1) was reconstructed through the online database from the Australian Bureau of Meteorology ([www.bom.gov.au](http://www.bom.gov.au)). Each pool was sampled using two nets (one larger (2.0 mm) and one finer (0.5 mm) mesh) pulled sequentially through the pool for three minutes, covering the complete volume of the pond. Clam shrimp were identified as *L. badia* by the pyriform dorsal organ, lack of spine on the ventroposterior corner of the telson, and a sucker-like protrusion in the male movable finger characteristic of the genus, and further by the pronounced, elongated process of the apical club of the claspers and the lack of setae and spines in the caudal furca characteristic of the species<sup>12,13</sup>. Clam shrimp were collected in a sampling tray full of pool water, counted and sexed as males, females or juveniles (immatures). Males are easily recognizable by the first two pairs of thoracic appendages modified as ‘claspers’ to allow them to pair with females for mating. Females lack claspers and eggs are visible along the gonad or in the brood chamber. Juveniles are young, small, immature individuals, and their sex is typically not identifiable from morphological characteristics less than one week from hatching. Copresence of juveniles and adults in the same pool at the same time indicated multiple hatching. Size was recorded for a subset of specimens on Dingo Rock by measuring the longer axis of the carapace with a caliper. All specimens were returned to the pool after completing data collection.

The physio-chemical parameters, viz. temperature ( $^{\circ}\text{C}$ ), pH, salinity (ppt), total dissolved solids (ppt), and dissolved oxygen (mg/l), were recorded with a YSI 556 multi-probe system (YSI Incorporated). Mean depth of each pool was averaged from three measurements. Maximum

length, maximum width and mean depth were used to calculate the volume of pools, assuming the cross-sectional shape to be half of an ellipsoid. The pools present a great variation in morphology. We are aware that assuming a specific shape is an oversimplification and could underestimate the real volume of the pools in cases where the bottom is flat. Alternatively, the presence of loose rocks and boulders in the pools might result in an overestimate of the real pool volume. In the end, we find this measure is a good approximate for this type of study. Measurements were taken at 11:00 a.m. on the day population densities were assessed (Table 1).

Statistical analyses were performed in JMP 6.0 (SAS Institute Inc.).

## Results

In Table 1, we report the measurements of physio-chemical parameters for each of the 35 pools investigated. A principal component analysis was used to test the differences of water parameters between outcrops. The first principal component (PC1) accounted for 57.71% of the variation, PC2 accounted for an additional 22.01%, and both were significantly influenced by all parameters (Table 2). On plotting PC1 vs PC2, almost all the pools sampled on Holland Rock cluster independently from all the other pools (Figure 1). We performed a multivariate analysis of variance on PC1 and PC2, and found a significant difference among outcrops (Wilks’ Lambda  $P = 0.0058$ ). This implies that outcrops are not homogeneous with respect to physio-chemical characteristics (Table 3). To conform to the assumptions of normality, we log-transformed (PC1 + 10).

Regardless of the differences, multiple hatchings were found consistently across the four sampled outcrops (Figure 1; chi-square test on number of pools with and without juveniles across outcrop:  $P = 0.1152$ ); thus data were pooled for subsequent analysis. To investigate differential

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**Table 1.** Physio-chemical characteristics of the 35 granite outcrop pools, southwestern Western Australia, sampled during April–May 2007. Parameters were measured on different days at 11:00 a.m.

Rock outcrop	Pool	Sampling day	Temp. (°C)	DO (mg/l)	pH	Salinity (ppt)	TDS (ppt)	Mean depth (mm)	Volume (dm <sup>3</sup> )	Juvenile presence/absence
Holland	1	22 April 07	22.22	10.08	7.09	0.17	0.23	39.67	258.45	0
Holland	3	22 April 07	21.96	9.50	6.98	0.17	0.23	40.33	254.77	0
Holland	4	24 April 07	22.17	9.04	6.42	0.05	0.08	39.00	446.31	1
Holland	7	25 April 07	16.18	9.80	6.35	0.08	0.11	61.67	296.17	0
Holland	9	24 April 07	22.36	9.56	6.42	0.11	0.16	49.00	681.49	1
Holland	10	22 April 07	21.40	9.78	6.74	0.07	0.10	41.00	123.20	1
Holland	11	22 April 07	22.09	9.88	6.93	0.06	0.09	34.33	195.57	0
Holland	12	22 April 07	22.76	9.16	6.32	0.10	0.13	30.00	52.62	1
Holland	13	24 April 07	22.35	10.02	6.64	0.22	0.29	19.33	26.78	1
Holland	14	25 April 07	16.24	5.29	6.32	0.14	0.19	92.00	4037.58	0
Holland	15	24 April 07	22.87	10.25	6.08	0.14	0.19	11.67	6.69	0
Holland	16	25 April 07	16.33	9.73	5.75	0.08	0.10	42.33	62.34	1
Dingo	1	4 May 07	18.44	10.71	5.55	0.10	0.14	38.33	302.56	1
Dingo	2	3 May 07	14.35	12.37	5.18	0.18	0.24	43.00	459.36	1
Dingo	4	3 May 07	16.39	11.90	5.60	0.08	0.11	22.33	64.06	0
Dingo	5	3 May 07	16.89	12.27	5.34	0.12	0.16	9.67	16.89	0
Dingo	8	10 May 07	17.34	11.42	5.57	0.21	0.28	24.67	105.83	1
Dingo	9	6 May 07	17.40	9.82	5.11	0.15	0.21	41.67	218.32	1
Wave	5	12 May 07	16.10	8.52	5.21	0.34	0.45	14.00	19.77	1
Wave	6	12 May 07	16.25	9.52	5.70	0.37	0.49	12.67	14.21	1
Wave	8	16 May 07	13.42	13.41	5.18	0.18	0.25	60.00	438.45	1
Wave	9	14 May 07	9.56	13.90	5.80	0.15	0.20	53.33	1041.38	1
Wave	10	14 May 07	10.23	15.15	6.28	0.52	0.68	23.33	95.54	1
Wave	11	13 May 07	16.21	11.11	5.81	0.10	0.14	11.67	18.23	0
Wave	12	15 May 07	13.70	12.62	5.93	0.15	0.20	42.33	217.15	1
Wave	13	13 May 07	15.76	10.63	5.82	0.13	0.17	19.33	57.93	1
Wave	14	12 May 07	16.86	10.05	5.43	0.17	0.23	10.33	8.82	1
Wave	15	15 May 07	14.79	12.38	5.60	0.11	0.15	42.33	217.15	0
Puntapin	6	20 May 07	15.06	12.91	6.41	0.15	0.20	59.67	2609.20	1
Puntapin	8	18 May 07	17.52	10.84	4.99	0.33	0.44	8.00	14.64	1
Puntapin	9	21 May 07	14.42	10.26	5.61	0.21	0.29	34.67	150.43	1
Puntapin	10	18 May 07	16.26	10.89	5.15	0.16	0.21	9.33	21.36	1
Puntapin	11	19 May 07	14.41	11.43	5.23	0.29	0.39	23.00	101.24	1
Puntapin	12	19 May 07	15.03	13.32	5.20	0.52	0.68	12.67	59.85	1
Puntapin	13	20 May 07	14.54	12.89	5.91	0.30	0.41	37.67	398.79	1

Temp, Temperature; DO, Dissolved oxygen; TDS, Total dissolved solids; 0, Juvenile absence; 1, Juvenile presence.

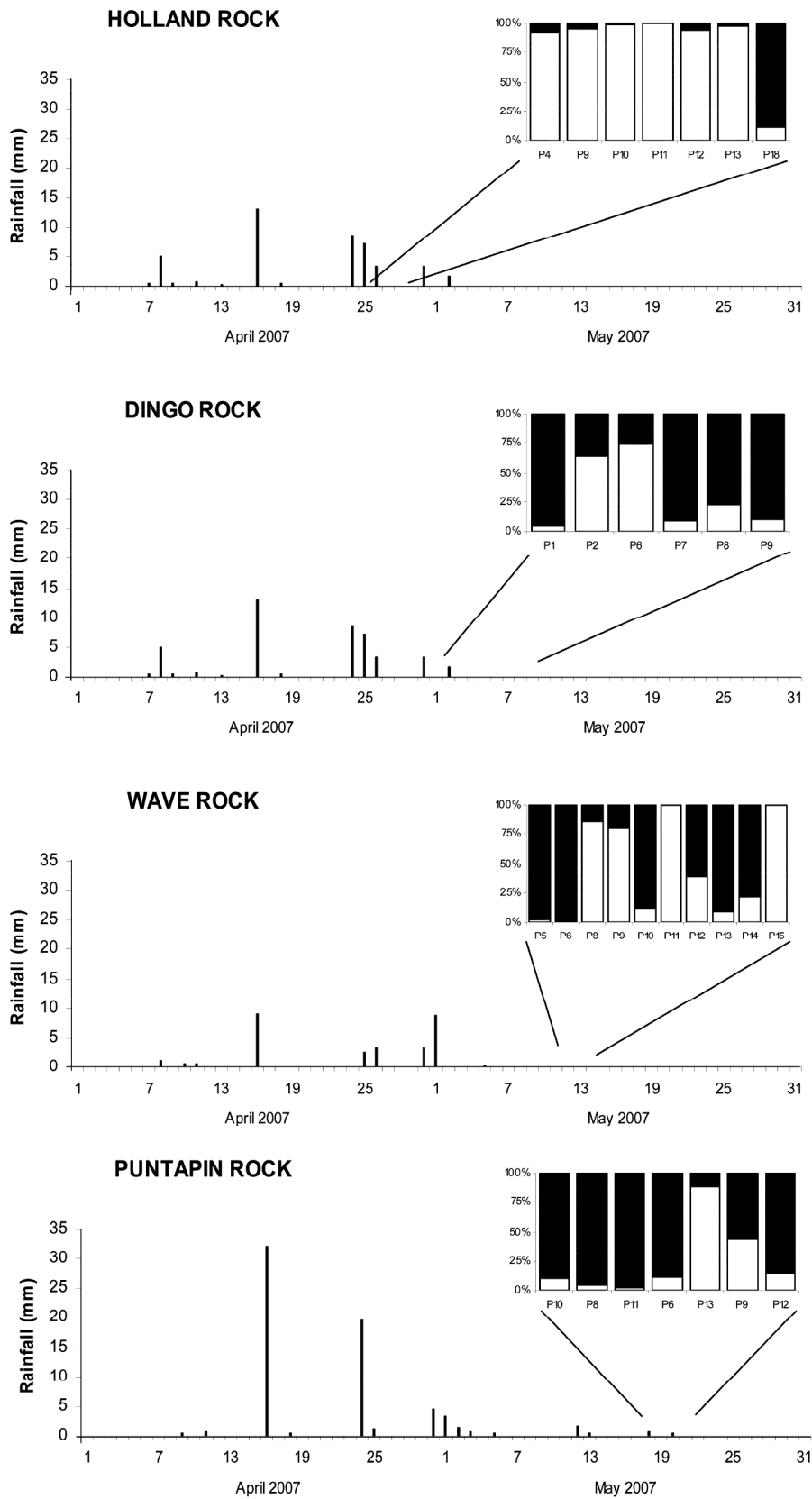
**Table 2.** Principal component analysis on physio-chemical parameters across the rock outcrops

Principal component	PC1	PC2
Eigenvalue	2.8854	1.1004
Per cent variation	57.7082	22.0085
Cumulative % variation	57.7082	79.7167
Eigenvectors		
Temp. (°C)	-0.45521	0.44236
DO concentration (mg/l)	0.39704	-0.35658
pH	-0.36140	0.43003
Salinity (ppt)	0.50231	0.49600
TDS (ppt)	0.50222	0.49621

hatching, a multi-nominal logistic regression was performed using PC1 (after log-transformation) and PC2 (whole model:  $R^2 = 0.1799$ ,  $n = 35$ ,  $P = 0.0231$ ). The analysis showed a significant influence of PC1 ( $P = 0.0337$ ). The

first principal axis is highly correlated with low temperature, high dissolved oxygen, low pH, and high salinity and total dissolved solids (but still freshwater) (Table 2;  $P < 0.0001$ ). However, no single variable can account for secondary hatching events.

Juveniles and adults of *L. badia* co-occurred in 25 of the 35 ponds, indicating at least two hatching events (Figure 2). In the remaining 10 pools, three had only adult *L. badia* (Holland Rock: pool 11; Wave Rock: pools 11 and 15) and seven had no clam shrimp (Dingo Rock: pools 4 and 5; Holland Rock: pools 1, 3, 7, 14 and 15). We observed great variation in hatching success in pools (measured as the number of juveniles present): juveniles in pools varied from 0 to 709, and densities varied from 0 to 12.5 juveniles/dm<sup>3</sup>. Figure 2 illustrates the frequency of adults vs juveniles in each pool on the days sampled. Males and females presented a marked size difference ( $t$ -test:  $P = 0.000187$ ). In Dingo Rock, males ranged from



**Figure 2.** Rainfall data for April–May 2007 on the four granite rock outcrops sampled in southwestern Western Australia. Bar graphs represent the proportion of juveniles (black columns) and adults (white columns) in multiple pools for each outcrop, in the window of the sampling time (refer to text for more details). Pools are listed in chronological order (sampling day, see Table 1).

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**Table 3.** Mean values of water parameters for the four outcrops sampled. Data are expressed as average  $\pm$  standard deviation

Rock outcrop	<i>n</i>	Temp. (°C) $\pm$ SD	DO (mg/l) $\pm$ SD	pH $\pm$ SD	Salinity (ppt) $\pm$ SD	TDS (ppt) $\pm$ SD
Holland	12	20.74 $\pm$ 2.74	9.34 $\pm$ 1.32	6.50 $\pm$ 0.39	0.12 $\pm$ 0.05	0.16 $\pm$ 0.07
Dingo	6	16.80 $\pm$ 1.38	11.42 $\pm$ 0.99	5.39 $\pm$ 0.21	0.14 $\pm$ 0.05	0.19 $\pm$ 0.06
Wave	10	14.29 $\pm$ 2.58	11.73 $\pm$ 2.11	5.68 $\pm$ 0.34	0.22 $\pm$ 0.14	0.29 $\pm$ 0.18
Puntapin	7	15.32 $\pm$ 1.16	11.79 $\pm$ 1.22	5.50 $\pm$ 0.51	0.28 $\pm$ 0.13	0.37 $\pm$ 0.17

6 to 8.1 mm, carapace length (mean: 7.32 mm,  $n = 39$ ) and females ranged from 5.6 to 7.9 mm (mean: 6.88 mm,  $n = 39$ ). Juveniles ranged from 1.8 to 4.4 mm (mean: 3.15 mm,  $n = 20$ ).

### Discussion

#### *Multiple hatchings within a single wet period as a secondary bet-hedging strategy?*

A bet-hedging strategy relies on asynchrony of hatching in the same clutch of eggs and thus asynchrony of hatching of the overall egg bank. This strategy helps cope with highly unpredictable environments<sup>4,6,7</sup>: if the favourable climate subsists for a period shorter than that required to reach sexual maturity, all hatched individuals will die prior to reproduction. The fitness advantage of differential hatching is evident (i.e. spreading the risk temporally), but less evident is the mechanism by which differential hatching occurs. Many researchers have investigated the hatching requirements in various crustaceans and have hypothesized that temperature and photoperiod are the primary cues in stimulating hatching<sup>2,14,15</sup>; yet not all cysts respond at the same time.

We found no significant differences in the physiochemical parameters measured, between the 25 pools with multiple hatching events from the ten exhibiting only one or no initial hatching. However, we took our measurements a few days after the hatching events (we always observed juveniles, but we did not see nauplii) and it is possible that we missed the differences in cues between pools that had a second hatching vs those that did not. Further, the scale at which we measured the different abiotic parameters might not be indicative of the microcosm at which the cysts experience them in the sediment of the pool. For instance, cysts may be partially or totally covered with sediment and might not be exposed to the mean value of these cues in the pool. Thus, the delayed hatch might have emerged from cysts dropped in previous generations that are not exposed to these hatching cues initially, but through new episodes of rain or strong winds, may be exposed later to effective hatching cues when the sediment is disturbed.

Alternatively, cysts contributing to the second hatch may be newly laid offspring from the first hatched individuals. This has been shown to occur in laboratory experiments in the fairy shrimp, *Streptocephalus proboscideus*

(Frauenfeld, 1873)<sup>10</sup> and indicates that a period of dormancy is not necessarily required. Unfortunately, due to the timing of our sampling and our field/experimental constraints, we cannot distinguish the source of the secondary hatching. Yet, regardless of whether the secondarily hatched juveniles come from the established egg bank or newly laid cysts, it is evident that they are responding together to one or several strong cues, resulting in a distinct cohort. We never observed a continuous hatching progression that would result in the co-presence of nauplii, juveniles, young adults and older adults.

We did observe, however, different hatching rates (no juveniles vs hundreds of juveniles) in adjacent pools on each outcrop, and this could be attributed to spatial variation between each pool. While we did not find significant differences in our measured parameters between pools on each outcrop, we hypothesize that variability in hatching could be influenced by differences in the micro-environment of the pools, such as the depth of the substrate, protection from or exposure to wind, and modes of filling (e.g. direct rain or intake of water washed from the top of the outcrop). These parameters might be responsible for major changes, spatially and temporally localized, potentially acting as a sudden and strong cue that could trigger specific hatching events.

These findings suggest that delayed hatching may not be a secondary bet-hedging strategy so much as a response to cues which the cysts were not exposed to in the original hydration of the pond.

#### *Implications for mate-guarding behaviour*

Male clam shrimp guard their mate by clasping the edge of the female's carapace for a prolonged period of time, waiting until copulation can occur. As in many other crustaceans, females can be inseminated for a brief period only after the moult<sup>16</sup>. Precopulatory mate guarding is a complex behaviour. In order to optimize their reproductive success, males need to decide which females to guard, when to start the guarding phase, and how long to guard instead of searching for new mates<sup>17</sup>. Optimality models suggest that males are most likely to be successful by choosing to guard females that are closest to the moult and therefore most likely to be receptive to mating<sup>17-20</sup>.

Although how males 'decide' when to guard is not clear, the assessment of a mate's receptivity in clam shrimp occurs after physical contact<sup>21</sup>, and we predict

that the farther an individual is away from moulting, the less likely the male would guard.

During this field study we observed adult males clasping juveniles on a number of occasions, despite the presence of mature females. This could only occur in pools where overlapping cohorts were present due to multiple hatching events.

Clasping of immature conspecifics has been reported as an adaptive strategy in symbiotic marine isopods, where virgin females are highly valuable and juvenile stages can be inseminated long before they become sexually mature<sup>22,23</sup>. However, we know of no evidence that this is the case in clam shrimp. Juveniles at this stage can take days to become sexually mature, and this time largely exceeds the mean mate-guarding time of the population in the field (around 3 h, ranging from a few minutes to almost 12 h; C.B., pers. obs.). Also, the adult–juvenile pairs observed broke up before a successful mating was possible. Thus we do not consider this to be an adaptive strategy for clam shrimp.

Alternatively, some species of harpacticoid copepods are known to clasp juveniles when there are few available adult females<sup>24</sup>. In several pools we sampled, abundant juveniles were found together with fewer mature adults (Figure 2). It is possible that males most often encountered juveniles and ‘chose’ to guard a juvenile after never encountering a mature female. It is also possible that this behaviour is not adaptive, but is triggered by the ‘wrong cue’. *Eulimnadia texana* (Packard, 1871) males preferentially guard their mates in the time-frame between dropping a batch of eggs and movement of the next one to the brood chamber<sup>21</sup>, which coincides approximately with the time of moulting. If the moulting hormone is a possible cue (still debated)<sup>25,26</sup>, then juveniles (which moult more frequently than adults) could send the wrong signal to males. This ‘mistake’ would not be too detrimental, considering the low probability of encountering many juveniles, if multiple hatchings are not common (despite results from the current study), or typically do not overlap.

What are the implications of forming adult–juvenile pairs? There is likely a decrease in fitness of individual males because of missed mating opportunities with receptive females. Also, if males are spending time with immature conspecifics instead of searching for receptive females, the operational sex ratio can change in the population, since a lower number of males are involved in successful reproduction. This will affect the overall mating rate in the population.

### *Implications for community ecology*

Overlapping cohorts of clam shrimp most certainly interact and impact the ephemeral pool community in ways that single cohorts do not (or do so to a lesser degree). Individuals that emerge later during a single hydroperiod

are potentially at higher risk from habitat desiccation, depleted nutrients, and greater exposure to predators. Resource availability is a key factor to the success of consecutive cohorts, since trophic-level dynamics may shift with the growing populations. Clam shrimp are largely filter feeders and their increased population may reduce the abundances of planktonic food sources.

While a delayed hatching cohort may experience fewer resources, they may themselves be a new resource from the community perspective. Newly hatched nauplii may provide an additional food source for the initial cohort of clam shrimp. Cannibalism of this kind has been reported in anostracans<sup>10</sup>, leading to higher fecundity in the initial cohort. It would be relevant to elucidate whether this could occur in clam shrimp. Further, these younger clam shrimp could experience higher predation pressure, since natural predators (e.g. tadpoles, notostracans, and dytiscid larvae)<sup>27,28</sup> may switch to the easier prey, i.e. the abundant juveniles. Predation may be heavier on later-emerging cohorts than the initial hatching, because the predators will have attained larger sizes. Additionally, some predators are not present in the pool immediately after hydration, but will be established via migration as later cohorts emerge<sup>29</sup>. While these situations may benefit the initial cohort, overall increased prey biomass may lead to increased predator biomass in pools and could affect clam shrimp population as a whole.

Finally, as the community changes through time, an unexpected consequence to later emerging individuals is the reduced ability to find a mate. At late stages in the life of the pool, algal mats could become so dense as to entangle the clam shrimp and completely restrict movement. Algal growth varied across pools (A.C., pers. obs.), and it is possible that individuals in pools with heavy growth will experience some relief from predation, as predators too will be restricted.

Overall, the phenomenon of multiple emergences in the large branchiopods adds new dimensions to understanding the role of hatching cues. Rather than being a secondary bet-hedging strategy, the emergence of a new cohort of clam shrimp may result from a renewed exposure of cysts to the hatch-triggering environmental cues. There is still much to be explored regarding the implications of delayed hatching in extended hydroperiods for mating behaviour, population dynamics and community ecology of temporary pools.

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