The survival and reproductive performance of *Daphniopsis australis* (Cladocera: Daphniidae) in response to temperature changes

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Abstract

The thermal tolerances and reproduction of *Daphniopsis australis* were investigated using a single clone under laboratory conditions. Based on survivorship, measurements of thermal tolerance were conducted using acute exposure within 24, 48 and 72 hours. The upper limit of tolerance was at 28^{o}C, but animals successfully survived until the lowest temperature (4^{o}C) regardless of exposure times. A minimum temperature increment of 6^{o}C above the control temperature (22^{o}C) was detrimental to survival while the optimal temperature of this species was detected from 4 to 26^{o}C. Variation in pattern of reproduction was observed in the range of temperature from 16 to 25^{o}C. The reproductive parameters including age at first reproduction (AFR), clutch number, egg development time (EDT) and total offspring production were significantly affected by temperature changes. Low and high temperature significantly delayed the age for first reproduction and reduced the clutch number. However, EDT and total offspring were negatively related with an increase in temperature. An extreme thermal condition was detected at 25^{o}C where reproductive outputs were adversely affected. Our results suggest that *D. australis* is a eurythermal species, but a rapid increase of temperature could threaten its survival. Reproduction of this species is favourable in the narrow range of temperature with the most optimal temperature is likely at 20^{o}C. This study contributes to the understanding of the impact of global warming on the sustainability of zooplankton fauna in arid temperate regions.

Keywords: temperature – cladoceran – survival – reproduction – tolerance

INTRODUCTION

In the recent decades, the world is threatened with greenhouse gaseous emission resulted with an increasing in environmental temperature. High environmental temperature leads to a scenario of global warming which has been reported severely affected Europe, Asia, Mexico, Africa and Australia (National Climatic Data Center, 2010). This trend of global warming is arising yearly and likely, causes a large scale perturbation to our biosphere with special reference to our biological diversity. Hughes (2000) reported that a loss in biodiversity has expanding at unprecedented rate . A loss in biodiversity means a loss in opportunity for medical discoveries, economic development and consequently reduces the ability to develop a buffer system to new challenges such as manifested under the influence of climatic change (Richardson and Schoeman 2004).

In aquatic food-web, cladoceran populations play a dual role as a secondary consumer which acts as a grazer to producer (phytoplankton) and being a prey to the higher consumers such as fish larvae (Sommer and Stibor 2002). Undesired scenario such as algal bloom has been reported as partly related to the reduced rate of grazing among the grazer species (Buskey et al. 1997). In fact, the loss of grazer population breaks off the ecological link of food web and eventually causes a short food supply to species at higher trophic level (Kairesalo and Seppala 1987). Thus, the existence of cladoceran in natural ecosystem is therefore of great important to buffer extreme fluctuation between a prey-predator relationship.

In specific, the impact of global warming has no exception to cladoceran biodiversity. This impact is manifested by a migration of warm water species to cold northern regions (Lennon et al. 2001), decreasing number of native species from local habitat (Strecker et al. 2004), a change in phenological timing (Walther et al. 2002), alteration in the pattern of life history (Chen and Folt 1996) and finally complete disappearance of cladoceran communities as been reported in Aral Sea (Aladin 1991). Although typically, cladocerans can sustain adverse environments through a switch of reproduction from asexual to sexual mode (De Meester et al. 2004), and that sexual females can produce resistant diapausing eggs, this adaptation is constrained by the huge magnitude of heatwave before the onset of sexual

reproduction (Williams et al. 2008). Thus, survival of cladoceran may depend on the tolerance of species to the degree of thermal changes.

In general, species living in areas experienced seasonal thermal changes develop a high degree of thermal tolerance (Stillman 2002). These species often display a wide range of tolerance enabling them to withstand the fluctuated thermal environments. As an advantage, the wide range of thermal tolerance helps the species to disperse over a diverse habitat away from their original region (Hughes 2000). This is evidenced by the migration of many eurythermal zooplankton species in the ocean during the recent trend of global warming (Shiganova 2008). In contrast, stenothermal species inhabits a stable environment is attributed to a narrow range of tolerance. This attribute is definitely restricts the ability to exploit new habitats and put the animal survivorship at higher risk especially after the dramatic exposure to a climatic change (Chevaldonne and Lejeusne 2003).

It is widely acknowledged that temperature enhances the physiological processes regarding to growth, development and reproduction (Kingsolver and Huey 2008). In small poikilotherms such as cladocerans, warm temperature increases metabolism of these animals and leads to accelerated growth and development (Vijverberg 2006). In response to warm temperatures, cladocerans mature at an early age and reproductive activities start earlier than their congeners that live in cold, temperate regions (Sarma et al. 2005). Also, cladocerans can reproduce through parthenogenesis with iterative reproduction and thereby, warm temperature shortens the generation time by accelerating the embryonic development (Goss and Bunting 1983). The eggs hatch in a short time while a new clutch of eggs can be produced soon after the neonates are released from the brood chamber. With an increased rate in reproductive activities, animals reach the senescene stage quickly. As a result, the life history of cladocerans in a warm environment is relatively shorter than species that live in a cold environment.

As the issue of global warming has not reach the ultimate endpoint, study on the species tolerance may partly contribute to the understanding of animals' survivorship. It is believed that a great impact from global warming can reach beyond the species tolerance and animals will simply die on the arrival of unfavourable warming conditions. In this study, we choose *Daphniopsis australis*, a euryhaline cladoceran species found in ephemeral salt lakes in southeastern Australia (Sergeev and Williams 1985). Lakes in these regions experience great temperature fluctuation due to dry and hot weather and high evaporation during summer (Timms 2007). The occurrence of *D. australis* is somehow, highly seasonal, with high and low abundances respectively observed in spring and winter, and becomes undetectable during summer and autumn (Campbell 1994). This suggests that there is an adaptive life strategy of this species in response to the seasonality of temperature in southeastern Australia. Therefore, in this study, we aimed to explore the impact of temperature on the survival and reproductive performance of euryhaline cladocerans, *D. australis*. On this basis, the knowledge of species tolerance is of great important to provide useful information to deliver a guideline for monitoring system and bioconservation in future.

MATERIALS AND METHODS

Experimental Procedure

Culture condition of stock animals

Experimental animals were collected from a temporal saline pond near Coorong National Park, South Australia in 2005. The laboratory population was established in the Animal House of Flinders University as a stock culture with a total number of animals <100 individuals in a 10 L plastic container. Standard rearing temperature at 22^{o}C and salinity at 22 PSU were employed which were similar to where the animals were collected in the field. Stock cultures were exposed to the 12 h dark: 12 h light regime provided by cool fluorescent white lights (1800 lux). Food regime was given at every 2-3 days using a green alga, *Tetraselmis* at 10^5 - 10^6 cells/mL, an optimal food level for most cladoceran species (Delbare et al. (1996). The animal density was controlled below 1,000 ind/L to minimize water quality problem and overcrowding. This was employed by flushing half volume (5 L) of the culture water and replaced it with the same volume of fresh culture medium at approximately 3 times per month.

Prior to investigation on the species tolerance, an allozyme analysis was conducted on the laboratory population to test the possibility of genetic variation. The result proved that the entire population was represented by a single clone. Therefore, during experimental period, animals were randomly selected among parthenogenetic adults at the age between 10-12 days.

Acute temperature tolerance

Temperature tolerance was measured to estimate the upper and lower limit of *Daphniopsis australis*. The temperature regime was divided into two phases: an increase of temperature to reach the upper limit of tolerance and a decrease of temperature to obtain the lower limit of tolerance. A reference temperature of 22^{o}C was used as a control because the animals were collected at this temperature in the field.

Media were prepared using filtered seawater and diluted with demineralised water to obtain the desired salinity (22 PSU). Adult parthenogenetic animals were inoculated into each culture medium with a total volume of 500 mL in plastic containers. Each plastic container comprised of 10 individuals, and five replicates were allocated for each set of treatment. The conditions of feeding, salinity and

photoperiod were the same as their parental culture. All the containers were incubated in temperature controlled light cabinets.

To estimate the upper thermal limit, the incubating temperature started to increase from 22°C. The temperature regime was designed by a 2°C incremental until the value of the lethal level was reached, i.e., 50% of population was killed. At each test temperature, a new batch of animals was used to test the acute temperature response. At each test temperature, animals were exposed for a maximum of 72 hours and the mortality was observed every 24 hours. All experiments were replicated 5 times. Animals were considered dead if there was no response of the animal to any physical touch or stimulation. Dead individuals and newly hatched neonates were recorded and removed immediately. Similarly, the experimental protocols and death criteria were applied to the lower tolerance limit. However, the lower end of temperature was retained at 4°C considering that the minimum ambient temperature was approximately 4°C in salt lakes of South Australia.

Reproductive performance

Based from the survival tolerance, three temperatures (16, 20, 25°C) were selected to measure the reproductive performance of this species. In prior to reproductive experiment, a single parthenogenetic female was isolated and reared in a jar containing 50 mL medium similar to the stock culture condition. Starting from the first generation, newborn neonates were individually introduced to experimental temperature 16, 20, 25°C respectively. Media were renewed daily and only the third-generation animals (age < 24 h) were used for experimental animals in the reproductive experiment. This procedure was taken as a precaution to offset phenotypic plasticity and maternal effect as suggested by Lynch and Ennis (1983).

In the reproductive experiment, the culture medium was prepared using filtered seawater diluted with demineralized water to reach desired salinities (22 PSU). Algal suspension was added at the density of 10^6 *Tetraselmis suecica*/ml. The algae were harvested at the exponential growth phase and the density was quantified using a haemocytometer under a light microscope (400×). Each experimental animal of less than 24 hours/old was individually inoculated in the 50 mL culture medium at respective temperature treatments; 16, 20, 25°C. Each temperature treatment was replicated for 25 times. In order to avoid contamination of media from animal waste metabolite and dead microalgae, the media were renewed on daily basis. To secure the range of temperature, the animal cohorts were kept in a temperature controlled cabinet at each desired temperature. The photoperiod and salinity were maintained the same as in the parental culture.

Experimental animals were daily observed for age at first maturation (day), total clutches (no. female^{-1}), egg development time (day) and total offspring (no. female^{-1}). Any newborn neonates during the study period were enumerated and then removed soon after birth.

Statistical analysis

To obtain the optimal range of survival, the impacts of temperature regimes were analysed using pooled data. Normality and homogeneity of variances were inferred using SPSS (ver 15.0). Since skewness and kurtosis statistics were significant at the 5% level, nonparametric tests were employed. Pooled data on the mean percentage mortality were analysed by Kruskal-Wallis test. Comparisons between groups were examined using the two-tailed Mann-Whitney U-test.

All data for reproductive variables exhibited normality and parametric analysis was conducted using a one-way ANOVA. Post-hoc test was employed by using Tukey HSD for comparison between experimental temperatures. During the analysis, all the significant level was set up at $P < 0.05$.

Results

Range of temperature tolerance

The mortality result showed a distinct pattern of two zones (Figure 1), i.e., optimal zone and lethal zone. The optimal zone was between 4 and 28°C. The population did not reach 50% mortality between 4 and 28°C even after 72 h exposure. Within this range, almost no mortality occurred between 4 and 22°C and the exposure times did not significantly impact mortality from 4 to 26°C (Kruskal-Wallis; $P > 0.05$; Table 1). The threshold temperature was detected at 28°C and the exposure times significantly affected the mortality at this temperature (Kruskal-Wallis; $P < 0.05$; Table 1). Above 28°C was the lethal zone where the mortality exceeded 50% in all exposure times.

Reproductive performance

a) Age at first reproduction

Temperature significantly affected the age at first reproduction in population of *D. australis* (One-way ANOVA; $P < 0.01$; Table 2). Animals incubated at 20°C started the first reproduction significantly earlier than animals incubated at either 25 or 16°C (Tukey HSD; $P < 0.01$; Figure 2A). At 16°C, the reproduction was significantly delayed in comparison to other temperature treatments ($P < 0.01$).

b) Egg development time

Temperature significantly affected the egg development time in *D. australis* (One-way ANOVA; $P < 0.01$; Table 2). The fastest eggs development was significantly attained by animals incubated at 25°C (Tukey HSD; $P < 0.01$; Figure 2B). Subsequently, the fast egg development was observed in animals incubated at 20°C. The slowest egg development was significantly displayed by animals incubated at 16°C ($P < 0.01$).

c) Clutch number

The number of clutch was significantly altered by temperature changes (One-way ANOVA; $P < 0.01$; Table 2). Animals produced the greatest number of clutch at 20°C followed by animals at 16°C. At 25°C, the clutch number was the smallest in comparison to the other temperature treatments (Tukey HSD; $P < 0.01$; Figure 2C).

d) Total offspring

The total offspring production was significantly affected by temperature (One-way ANOVA; $P < 0.01$; Table 2). At 16°C, the production of offspring was the highest but did not differ significantly with the total production of offspring at 20°C (Tukey HSD; P > 0.01; Figure 2D). The lowest offspring production was significantly displayed when animals were incubated under 25°C ($P < 0.01$).

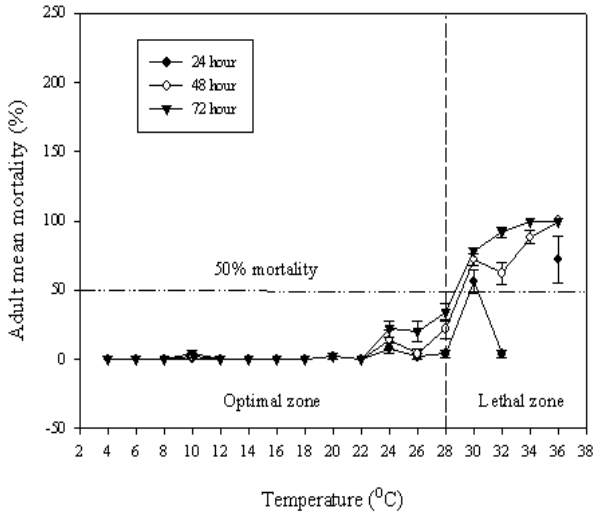
Table 1 Statistical comparison using Kruskal-Wallis of mean mortality (%) under a temperature regime with different exposure times.

Temperature (°C)	df	χ^2	*P*
4	2	0.001	0.999
6	2	0.001	0.999
8	2	0.001	0.999
10	2	2.333	0.311
12	2	0.001	0.999
14	2	0.001	0.999
16	2	0.001	0.999
18	2	0.001	0.999
20	2	0.001	0.999
22	2	0.001	0.999
24	2	3.210	0.201
26	2	5.568	0.062
28	2	7.627	0.022*
30	2	5.129	0.077
32	2	12.261	0.002*
34	2	5.714	0.017*
36	2	4.286	0.117

*significant at $P < 0.05$

Figure 1 Pooled data of mean mortality + SE (%) of *D. australis* under different temperatures and exposure times.

Discussion



Temperature Tolerance

The results showed that population of *D. australis* could survive when the temperature was below 28°C for 72 hours. However, regardless of exposure time, 50% of the population was killed when the temperature increased above 28°C. Apparently, a minimum increase of 6°C from the reference temperature was sufficient to initiate a lethal effect by killing 50% of the population even within short exposure (24 h). Conversely, there was no lethality effect when the temperature dropped by 18°C from the reference temperature regardless of exposure times. As temperature decreased, animals became moving slow and stayed on the bottom, which is similar to the response of *Daphnia magna*, *Daphnia pulex* and *Daphnia laevis* such as reported by Gerritsen (1982). Interestingly, without acclimation to each tested temperatures these animals still tolerated a wide range of temperature from 4 to 28°C regardless of exposure times. These attributes indicate that this species is eurythermal with preference to a colder environment.

Most studies on thermal tolerance have revealed the variability of thermal limits although the same species was used under investigation (Kivivuori and Lahdes, 1996). The reason is due to different experimental protocols and conditions, which makes the comparison between studies difficult. In studies where a shock-recovery method was used, animals were shortly exposed to a series of temperatures and then returned to their acclimation temperature (Bradley, 1978; MacIsaac et al., 1985). The result revealed that acclimated animals showed a positive correlation between exposure time and the degree of tolerance.

Table 2 Results from One-way ANOVA for reproductive variables treated at different temperatures.

ANOVA	df	F	Sig.
AFR			
Between group	2	57.33	0.01
Within group	65		
Total	67		
Clutch number			
Between group	2	66.81	0.01
Within group	72		
Total	74		
EDT			
Between group	2	304.28	0.01
Within group	61		
Total	63		
Total offspring			
Between group	2	85.66	0.01
Within group	72		
Total	74		

summer. The upper limit of tolerance displayed by the population of *D. australis* at ≥28°C was similar to other populations that experienced acclimation such as *Daphnia hyaline* (Van Urk, 1979), *Moina salina* (Gordo et al., 1994), *Simocephalus vetulus* (Sharma and Pant, 1982), *Daphnia catawba* (Chen and Folt, 1996) and *Daphnia lumholtzi* (Lennon et al., 2001). These findings suggest that temperatures above 28°C are ultimately lethal to most cladoceran populations regardless of acclimation procedure.

Thermal tolerance has long been recognized as a determinant factor influencing seasonal succession and global distribution (Brown, 1929). Temperature is a powerful climatic factor for classifying geographical locations (Parkins, 1926) and substantially affects animal distribution (Clarke, 1996). Conventionally, above 18-20°C, the region is classified as tropical, between 10-18°C as temperate (Poore, 1995) and below 10°C as the polar region (Tupper et al., 1998). In this study, 50% of the *Daphniopsis* population was killed within 72 hours with an increase of nearly 6°C from the reference temperature indicating that a relatively low tolerance to an episode of hot

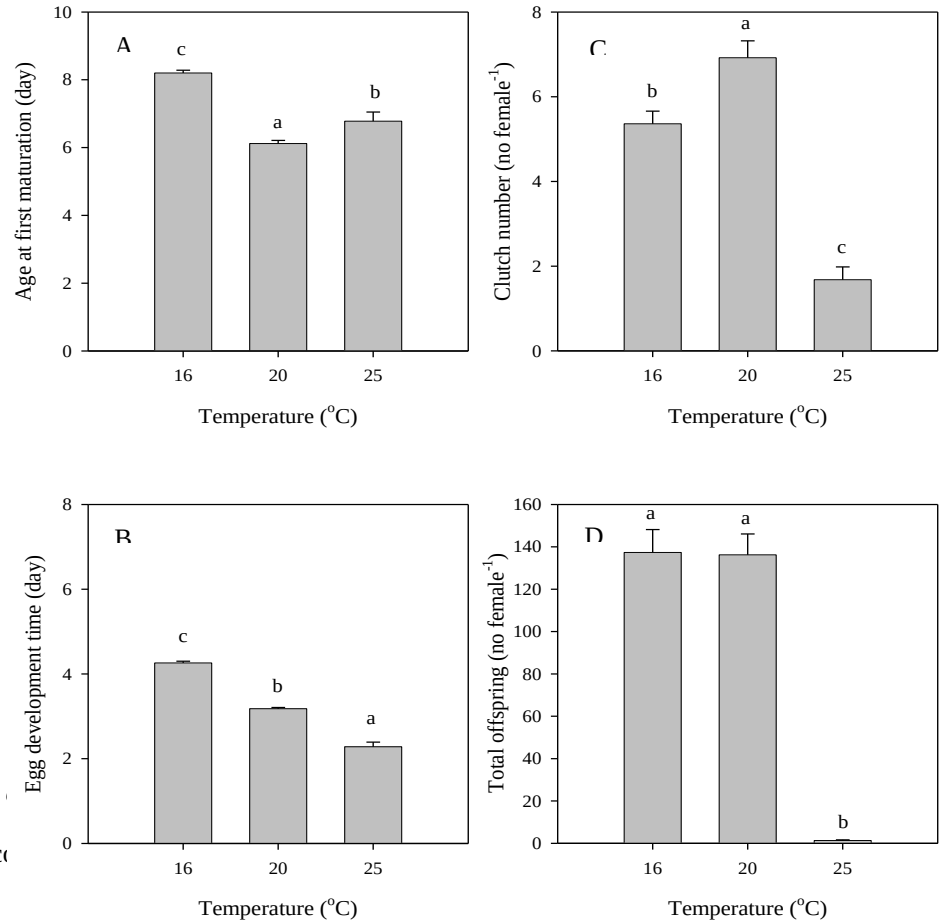


Figure 2 Age at first reproduction (A), Egg development time (B), Clutch number (C) and Total offspring (D) of *D. australis* treated with different temperatures. Bar represent standard error.

In comparison to the present study, *D.* acclimated to each testing temperature, was employed because the climatic c Australia can change dramatically,

whereas tropical regions of more than 28°C are lethal to their survival. Global warming may threaten the survival of *Daphniopsis* population and its distribution may move from temperate to much colder regions.

Additionally, our finding provides the optimal range of temperature for *D. australis* survival. Less than 50% mortality was observed below 28°C for adults. However, small percentage of mortality has started at 24°C for adults indicating that at this temperature, a stress was readily imposed. Thus, the most optimum temperature for survival of this population is likely below 22°C which is still in the optimal range of the other temperate species such as *Daphnia* spp. (Chen and Folt, 1996; Moore et al., 1996) and *Moina* spp. (Gordo et al., 1994; Benider et al., 2002). This optimum range should be suitable to predict for the maximum performance for growth and reproduction of *D. australis*. Therefore, the current results on survival would be a baseline to investigate the range of optimal growth and reproduction in the future.

Reproductive performance

Although *D. australis* can survive within 4 to 28°C, result from reproductive performance clearly showed that there was a variable pattern of reproduction as temperature fluctuated between 16 to 25°C.

Temperature is a dominant factor in regulating the AFR and EDT in many zooplankton species (Venkataraman and Job 1980; Goss and Bunting 1983). As such, in *D. australis*, the AFR decreased in response to an increase of temperature from 16 to 20°C. Interestingly, AFR increased again at high temperature of 25°C. This finding is in contrast with previous studies that observed a decrease in AFR with an increase of temperature from 4-21°C, 15 to 30°C and 15 to 30°C in *Daphnia carinata* (Hall and Burns 2002), *Daphnia lumholtzi* (Lennon et al. 2001) and *Moina salina* (Gordo et al. 1994) respectively. According to Sarma et al (2005), low temperature is principally associated with slow development and high temperature may lead to a physiological impairment for some species. However, physiological impairment due to temperature constraint depends on the tolerance of the species. For example, tropical species such as *Moina salina* may display a higher physiological tolerance and therefore continuous acceleration in AFR is observed even temperature is increased up to 30°C. However, cold temperate species such as most of *Daphnia* spp. experience physiological intolerance that affected the development and maturation at temperature as low as 25°C (Moore et al. 1996). Considering that *D. australis* is a temperate species, the pattern of AFR is regulated in the range of 16 and 25°C with the suitable temperature for first reproduction must be less than 25°C.

In contrast to AFR, the EDT of *D. australis* is negatively related with an increase in temperature from 16 to 25°C. This pattern is commonly found in most of zooplankton species regardless of their environmental backgrounds. The EDT of brackish water copepod, *Sinocalanus tenellus* (Kimoto et al. 1986) decreased with increasing temperature from 6 to 31°C while in freshwater cladoceran, the EDT of *Leptodora kindtii* decreased from 5.9 to 2.6 days in response to temperature increment from 15 to 25°C. The quickest egg development of eurythermal, *D. australis* was within 2-3 days at 25°C. In comparison, another eurythermal cladoceran species, *Moina mongolica*, develops much faster than *D. australis* at the same temperature where the complete egg development is observed at 1-2 days (He et al. 2001). Although both species are eurythermal, temperature retards the egg development of *D. australis* more than that of *M. mongolica*, indicating the significance of temperature in regulating egg development in cladocerans.

Although the increase of temperature could enhance the egg development of *D. australis*, signs of egg degeneration were observed at 25°C during egg development. In a previous study, egg degeneration was also observed in the euryhaline cladoceran, *Moina salina* but it occurred at 15°C and 20°C (Gordo et al. 1994). The eggs of the freshwater cladoceran, *Daphnia pulex* start to degenerate at 20°C (Gulbrandsen and Johnsen 1990) while *D. catawba* aborts its eggs at 30°C (Chen and Folt 2002). The unsuccessful egg development in *D. australis*, *Moina salina*, *D. pulex* and *D. catawba* seems to be exclusively due to temperature elevation.

Temperature had a significant impact on the number of total egg clutch and offspring production in *D. australis*. The highest clutch number was observed at 20°C but the total offspring production was similar from 16 to 20°C. Similarly, the maximum reproductive output of *Moina mongolica* occurs at 20°C (He et al. 2001) while *M. salina* seems to be adapted with a maximum reproduction at higher temperature of 30°C (Gordo et al. 1994). The difference between these species is that both *D. australis* and *M. mongolica* are naturally distributed in temperate and cold environments while *M. salina* is adapted with tropical warm environments. In other studies, the temperature of 25°C was considered the upper threshold limiting the fecundity amongst temperate *Daphnia* spp. (Goss and Bunting 1983; Moore et al. 1996). Therefore, the low egg production, egg degeneration and the low offspring production in temperate species such as *D. australis* is not uncommon as temperature reaching to 25°C and above.

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