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The effect of parental thermal environment on maternal investment and offspring performance

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Abstract

As heat wave phenomena and thermal variance events increase in frequency and intensity, it is important to understand how the effect of exposure to constant elevated temperatures on fitness differs from the one of thermal fluctuations. This study aims to investigate how parental thermal environment affects maternal fitness measured as maternal investment and offspring performance. A wild population of the amphipod *Gammarus chevreuxi* was exposed to constant (15, 20 and 25 °C) or fluctuating (variable between 15 and 25 °C) thermal regimes and allowed to mate. Immediately after fertilization, mothers carrying eggs were transferred to common garden conditions (15 °C), to allow embryo development until hatching. Egg size and hatchling heart rate were measured as proxies for maternal investment and offspring performance respectively. Parental thermal environment did not affect maternal investment but did affect offspring performance. Mothers acclimated to constant, elevated thermal regimes, within or beyond their temperature range, produced offspring with lower heart rate than those acclimated to control conditions. Interestingly, the heart rate of offspring from mothers exposed to fluctuating environments was intermediate between that of offspring from mothers exposed to control and elevated, within range, constant temperatures. This study concludes that aquatic animals which experience thermal fluctuations in their natural environment may be able to adopt mechanisms in response to environmental thermal variance that minimise negative effects on their fitness. Furthermore, it is uncertain whether bradycardia in crustacea hatchlings is adaptive or maladaptive. If it was adaptive, these results would also suggest that *G. chevreuxi* hatchlings displays a higher performance after parental acclimation to constant thermal stress, in comparison to control conditions. If it was maladaptive the opposite would be suggested.

Key words: Ocean warming; thermal fluctuations; maternal investment; transgenerational effects; *Gammarus chevreuxi*.

Introduction

Global temperatures are undergoing an increasing trend at an unprecedented pace (IPCC, 2014). However, the pattern of global warming does not consist in a constant and gradual increase. Heat wave phenomena have been increasing in the past decades and are likely to keep occurring more frequently and to be more extreme in the near future (Frölicher et al., 2018; IPCC, 2014). The way marine organisms respond to and cope with thermal stress in the context of climate change has therefore been a growing concern in the past decades. The short-term responses of individuals to heat stress have been widely studied, one of the main mechanisms of responding to heat shock being the upregulation of heat shock protein synthesis (Tomanek, 2010). However, the mechanisms adopted by organisms to cope with longer exposure to elevated temperatures are less understood (Cloyed et al., 2019). Some examples of long-term heat stress responses of marine organisms include migration (Cattaneo and Peri, 2016), rapid evolutionary processes (O'Connor et al., 2012), phenotypic plasticity (Hillebrand et al., 2018) and acclimation (Lagerspetz, 2006). Particularly, thermal acclimation was found to be an important mechanism to deal with exposure to constant elevated temperatures (Lagerspetz, 2006; Péden et al., 2016). Thermal acclimation is considered a type of phenotypic plasticity (Rohr et al., 2018) and is commonly defined as a physiological change caused by an environmental change in an individual organism, that is usually reversible during its lifetime (Precht et al., 1955). Furthermore, the concepts of capacity acclimation and resistance acclimation were introduced to differentiate the changes in thermal resistance of a function within normal temperature range (capacity) and at thermal extremes (resistance) (Precht et al., 1955).

In the case of exposure to thermal fluctuations, it is still uncertain how the duration and predictability of thermal variations affects a species' potential for acclimation (Angilletta Jr. and Angilletta, 2009). The responses of marine organisms to thermal fluctuations are in fact less understood, especially when such fluctuations reach temperatures beyond the species temperature range. There is a small number of studies recording organisms showing acclimation to fluctuations (da Silva et al., 2019; Terblanche et al., 2010). However, there is also evidence of high thermal variance scenarios preventing typical acclimation responses (Terblanche et al., 2010) and causing a decrease in fitness (Folguera et al., 2011). Furthermore, there is also evidence that extreme thermal variability events can cause mortality, population collapses and loss of populations (Harris et al., 2018).

Moreover, not much is known about how the thermal history of a generation will affect maternal fitness in terms of contribution of healthy offspring to the next generation. It has been found that the environmental conditions that parental generations are exposed to can lead to non-genetic transgenerational effects on their offspring (Ho and Burggren, 2010). Specifically, maternal effects represent a case of transgenerational effects (Lee et al., 2020). They consist in an influence of the maternal genotype or phenotype on the offspring's genotype or phenotype (Wolf and Wade, 2009). In the context of exposure to an environmental stressor, the phenotypic or genotypic changes that are induced in a maternal trait can causally induce changes in offspring traits (Wolf and Wade, 2009). Maternal investment is one of the mechanisms that can cause maternal effects (Marshall and Uller, 2007).

This has previously been associated with egg size, with larger eggs usually indicating a higher level of maternal investment and therefore a higher maternal reproductive success (Moran and McAlister, 2009; Thatje and Hall, 2016). High levels of maternal investment have also been shown to lead to increased offspring performance (Räsänen et al., 2005; Xu et al., 2019). In the context of the parental thermal environment, it is currently unknown how exposure to regimes of fluctuating temperatures in comparison to constant elevated temperatures affect maternal investment and offspring performance. Understanding this might give more insight on whether an increase of thermal variations in the wild will affect marine organisms in the long term, over multiple generations.

This study aims to investigate how parental thermal environment affects maternal fitness measured as maternal investment and offspring's performance. The parental generation was exposed to four thermal regimes: control, capacity acclimation, resistance acclimation, and beyond temperature range thermal fluctuations. Mean egg size was used as a proxy for maternal investment, while mean heart rate of the hatchlings was used to indicate offspring performance. It was predicted that the mothers exposed to both the capacity and resistance acclimation treatments, in comparison to the ones exposed to the thermal fluctuations one, will have a higher maternal investment and will produce offspring with a higher performance. This is predicted due to the physiological challenges of responding to rapid and periodical fluctuations in temperature, which may also prevent successful acclimation. *Gammarus chevreuxi* was chosen for this study as it is a good model species to answer questions about maternal effects because of its short reproductive cycle and ease of maintenance and culture (Truebano et al., 2016). Moreover, it is an appropriate organism to study the effect of temperature fluctuations as it is an ectotherm abundantly found in coastal and estuarine waters and therefore used to thermal variations (Macneil et al., 2007; Truebano et al., 2018).

Methodology

Field sampling and thermal regimes

G. chevreuxi specimens were collected from the Plym estuary, Devon, England (50° 23' 24" N, 4° 5' 7" W) in October 2020. The highest temperature the amphipods experience in this environment is of approximately 20 °C (M. Collins, 2021, pers.comm.). The amphipods were returned to the University of Plymouth 10 °C temperature-controlled laboratory and randomly separated into 12 tanks, 3 replicates for treatment, containing diluted sea water (vol.=13 L, salinity=5, O₂=100 % air saturation). All organisms were left to acclimate to laboratory conditions for 24 h before gradually increasing the salinity over two days to 15. After a further 48 h acclimation the control, capacity acclimation and resistance acclimation treatments tanks were gradually moved to temperature-controlled laboratories of 15, 20 and 25 °C respectively. The thermal fluctuations treatment tanks were moved to the 15 °C temperature-controlled laboratory and heat shocked three times a week for 2 weeks by placing them in water baths (Sub Aqua Pro, Grant or DMU19, Fisher Scientific) and gradually increasing the temperature to 25 °C over a time period of 2 h. The tanks were then left at 25 °C for one hour before being moved back to the 15 °C temperature-controlled laboratory. For the duration of the experiment airlines were

used to maintain the 100% oxygen air saturation, the salinity was maintained at 15, the tanks were covered with lids to avoid evaporation and the amphipods were fed carrot *ad libitum*.

Following two weeks of exposure, 20 pre-copula pairs of amphipods for each treatment were isolated in individual tanks with lids containing diluted sea water (vol.=0.1 L, salinity=15, O₂=100 % air saturation, T= 15, 20 or 25 °C). Each individual tank also contained a few pieces of gravel and an airline. Once the pairs had separated, females were inspected and those carrying eggs were randomly divided into two groups: the first group (n= 8, 9, 7, 7 for the control, capacity acclimation, resistance acclimation and thermal fluctuations treatments respectively) was used for egg measurements and the second group (n= 7, 7, 13, 13 for the control, capacity acclimation, resistance acclimation and thermal fluctuations treatments respectively) for hatchling's heart rate measurements.

Egg measurements

Within 24 h of the separation of the pair, the eggs were removed from the mother by delicately scraping the brood pouch from below the head towards the tail. A picture of the eggs removed from each mother was captured using an inverted CCD camera (QImaging R6 Retiga, Teledyne) equipped with a zoom lens (Zoom 70XL, OPTEM), using the program Micro-Manager (Edelstein et al., 2014). A graticule was used to set the scale for image analysis. The area of each egg was measured by analysing the images with the package 'Fiji' of the image processing programme ImageJ (Schindelin et al., 2012). The mothers were weighed after egg removal to the nearest microgram with a laboratory balance (Cubis, Sartorius).

Hatchlings' heart rate measurement

Within 24 h of separation of the pair, fertilized females for all treatments were moved to the 15 °C temperature-controlled laboratory in their individual tanks, to allow embryo development under common garden conditions. Each tank was checked for hatchlings daily. The hatchlings' resting heart rate was measured within 48 h of hatching. This was done by keeping the organisms still between a glass slide and a flexible plastic cover and filming their dorsal portion, where the heartbeat is visible. As previously described, the same method used for capturing egg pictures was used to record 2-minute videos for each hatchling. The videos were subsequently slowed down for analysis with the package 'Fiji' of the image processing programme ImageJ (Schindelin et al., 2012). For each video, the heart beats were counted for three 15 seconds intervals. From these three measurements mean heart beats per minute (bpm) was calculated. The mothers were weighed after the eggs hatched with a laboratory balance (Cubis, Sartorius).

Statistical Analysis

All statistical analyses were performed utilizing RStudio, v. 4.0.3 (R Core Team 2020). Two linear mixed-effects (LME) analyses were performed to analyse the effect of the parental thermal regime on mean egg size (mm²) and mean hatchling heart rate (bpm). For each LME analysis mother and mother mass were included as random factors. Before running the analysis, diagnostic plots were visually inspected

to ensure that the residuals were unbiased, homoscedastic and normally distributed. Model simplification was carried out by comparing models and selecting the one with the lowest Akaike's Information Criterion (AIC) value. The models were fitted using the nlme package (Pinheiro et al., 2015). This resulted in one model including egg size as a fixed factor and mother as a random factor, and one including only heart rate as a fixed factor. An ANCOVA test was run for each chosen model to analyse the effect of treatment on egg size and heart rate. A post Hoc Tukey HSD was then run for each model to analyse the differences between mean hatchlings' heart rate and mean egg size within treatments.

Results

The thermal regime experienced by the parents had no significant effect on mean egg size ($P > 0.05$; Fig. 1a). Yet, parental thermal regime had a significant effect on hatchlings' heart rate ($F_{3,121} = 9.712$, $P < 0.001$). The heart rate of the hatchlings from mothers exposed to control conditions (15 °C) was significantly higher, by 9.8 % and 14.5 % respectively, than that of the hatchlings from parents exposed to the capacity (20 °C, $P < 0.05$) and resistance (25 °C, $P < 0.001$) acclimation treatments. At the same time, mean heart rate of offspring from parents exposed to the capacity and resistance acclimation treatments were not significantly different from each other ($P > 0.05$). Interestingly, mean heart rate of hatchlings from parents exposed to thermal fluctuations was intermediate to that of hatchlings from parents exposed to control conditions (15 °C, $P > 0.05$) and to capacity acclimation (20 °C, $P > 0.05$). It was however significantly higher, by 10%, than the heart rate of hatchlings from parents exposed to the resistance acclimation treatment (25 °C, $P < 0.001$; Fig. 1b).

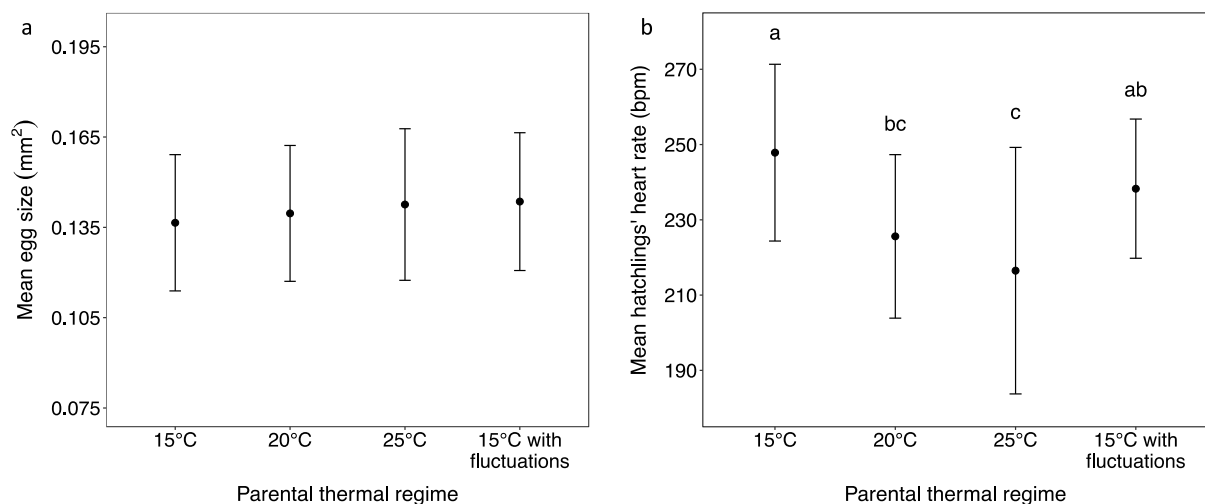


Figure 1: The physiological effects of *G. chevreuxi* parental exposure for two weeks to constant 15 °C (control), 20 °C (capacity acclimation) and 25 °C (resistance acclimation), as well as 15 °C with regular 25 °C fluctuations (thermal fluctuations). (a) mean (+/-SD) egg size (mm²; n=57, 77, 48, 54 respectively) (b) mean (+/- SD) hatchlings' heart rate (bpm; n= 27, 15, 36, 47 respectively). Letters by error bars indicate significant difference between heart rate within treatments.

Discussion

This study aimed to investigate the effects of *G. chevreuxi*'s parental thermal environment on maternal fitness measured as maternal investment and offspring performance. It was found that the parental thermal regime did not significantly affect egg size. This indicates that maternal investment is not influenced by either constant elevated or fluctuating temperatures. However, parental thermal regime had a significant effect on the heart rate of the hatchlings. It can be concluded that offspring performance differs in relation to the thermal stress its parents experience. It was found that the heart rate of the hatchlings from the mothers of the control treatment was significantly higher in comparison to the heart rate of the hatchlings from mothers of both the capacity and resistance acclimation treatments. Bradycardia in crustacea hatchlings has previously not been associated with either adaptive or maladaptive effects, therefore it is difficult to interpret this study's results with certainty. There is evidence of acclimation to constant regimes leading to positive effects on organism's fitness (Geister and Fischer, 2007; Seebacher and Wilson, 2006). If this was true for all organisms and stressors, the bradycardia of the hatchlings as a result of parental acclimation should be adaptive. However, there are multiple exceptions of acclimation leading to fitness benefits (Cao et al., 2018; Gibert et al., 2001; Huey et al., 1999; Leroi et al., 1994). On the other hand, elevated cardiac activity during early life stages, in comparison to adult stages, is found in many species (Aubret, 2013; Pearson et al., 1999; Polhill and Dimock, 1996; Zehendner et al., 2013). This is suggested to be partly responsible for the sustainment of the fast metabolism of organisms during their early development (Pearson et al., 1999). Particularly, heart rate in crustacea hatchlings has been shown to undergo an increasing trend before starting to decrease when maturity is reached (Reiber, 1997; Reiber and Harper, 2001; Spicer, 2001). Therefore, the low heart rate in the hatchlings from capacity and resistance acclimated mothers might not be high enough to sustain the hatchlings' fast metabolic rate and could be interpreted as a delay in normal cardiac development.

Moreover, these results imply that both capacity and resistance parental acclimation to constant elevated thermal regimes lead to similar effects on hatchling performance. If bradycardia was adaptive such results would demonstrate that both capacity and resistance acclimation to thermal stress of *G. chevreuxi* can lead to an increase in maternal fitness through the production of high performing hatchlings. On the other hand, if bradycardia was maladaptive the results would suggest that an exposure to constant heat stress is equally detrimental on maternal fitness independently on whether such elevated temperature is within or beyond temperature range.

Interestingly, mothers exposed to thermal fluctuations produced hatchlings with intermediate heart rate between mothers exposed to control and capacity acclimation conditions. The similarity of hatchling heart rate from mothers exposed to control and thermal fluctuation treatments, independently on whether hatchling bradycardia is adaptive or not, suggests that *G. chevreuxi* does not experience strong effects on fitness as a result of exposure to thermal fluctuations. These results contradict the initial hypothesis. The lack of effect of thermal fluctuations on fitness could be explained by the fact that environmental fluctuations may allow time for

damage repair between exposure to the temperature increases (Boardman et al., 2013; Foucreau et al., 2016). Such damage repair has been found to involve the upregulation of heat shock protein synthesis (Folguera et al., 2011). Alternatively, organisms that experience regularly occurring stress are suggested to experience greater selection for reversible plastic traits (Gabriel et al., 2005), in the case of ectotherms exposed to reoccurring thermal stress the plastic traits are suggested to be a result of thermal acclimation, a form of phenotypic plasticity (Rohr et al., 2018). Therefore, it could be proposed that *G. chevreuxi* did not experience an effect on maternal fitness because it was able to physiologically acclimate to the thermal fluctuation treatment.

The fact that parental beyond temperature range thermal fluctuations and within range constant thermal regime have similar effects on hatchling performance suggests that, although not significant, there is a decreasing trend in hatchling heart rate after parental exposure to thermal fluctuations in comparison to control conditions. At the same time, comparing resistance acclimation, that consisted of exposure to constant 25 °C, with the thermal fluctuation treatment, which fluctuations reached the same temperature, hatchling heart rate is significantly lower. This considered, it could be suggested that a thermal regime of thermal fluctuations that reach a certain temperature, in comparison to one of constant exposure to that same temperature, would have a lesser effect, whether adaptive or maladaptive, on offspring performance. It would be interesting to investigate in future studies whether a similar thermal regime comparison using a different temperature would yield the same results.

In contrary to the initial hypothesis, treatment had no effect on egg size. This contradicts previous studies that show a correlation between increasing temperature and decreasing egg size (Blanckenhorn, 2000; Ernsting and Isaaks, 1997; Fischer et al., 2003). It could be suggested that such correlation was not observed in this study because the *G. chevreuxi* organisms were exposed to the treatments for a shorter amount of time (2 weeks) in comparison to lifespan exposure (Blanckenhorn, 2000) or multiple months exposure (Ernsting and Isaaks, 1997). However, Fischer et al. (2003)'s study found that eggs in butterflies were smaller in size after only a few days of maternal exposure to elevated temperatures, in comparison to control conditions. Alternatively, it could be suggested that *G. chevreuxi* might adopt different strategies from maternal investment to increase their fitness through production of viable offspring. The lack of effect of parental thermal regime on maternal investment may in fact suggests that the differences in offspring heart rate must have been caused by another process. Potentially this could involve epigenetic mechanisms (Ho and Burggren, 2010) as it has been previously observed that they can be responsible for parental effects on offspring performance (Chen et al., 2019; Curley et al., 2011); this would be interesting to investigate in future studies.

Conclusions

In conclusion, further research about the cardiac physiology of crustacea hatchlings, specifically on the role of heart rate in early development, is needed to interpret these results with certainty. If hatchling bradycardia was adaptive, it could be concluded that *G. chevreuxi* is an organism capable of coping with heat stress both

under a constant and a fluctuating thermal regime. However, it could also be concluded that parental acclimation of *G. chevreuxi* to constant thermal regimes leads to stronger adaptive offspring traits in comparison to exposure to thermal fluctuations. On the other hand, if bradycardia was maladaptive, this study would provide evidence that *G. chevreuxi* is better able to respond and cope with a regime of thermal fluctuations that reach temperatures beyond normal thermal range, in comparison to an exposure to constant, beyond temperature range elevated temperatures. In the ecological context of *G. chevreuxi*, a species which commonly experiences thermal variance, especially when inhabiting estuaries, it seems logically advantageous for organisms to adopt a strategy that helps them deal with fluctuations rather than with constant heat stress. Either way, it is very interesting that mothers exposed to the thermal fluctuations produced hatchlings with similar performance to the ones hatched from mothers exposed to control conditions. It could be proposed that ectotherms that experience thermal variance may be able to adopt mechanisms that minimise negative effects on their fitness, even when thermal fluctuations are extreme. In the context of climate change, this might translate to a higher survival through heat wave events or extreme thermal fluctuations of *G. chevreuxi* or similar ectotherms; but might also mean that such ectotherms might not be able to cope with a sudden thermal increase, if not quickly followed by a temperature decrease.

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