

Plasticity of upper thermal limits of Australian *Paratya* spp. (Decapoda, Atyidae) and considerations of climate-change adaptation

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ABSTRACT

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Handling Editor: Richard Marchant

Received: I December 2022 Accepted: 14 February 2023 Published: 13 March 2023

Cite this:

Cox B et al. (2023) Marine and Freshwater Research, **74**(6), 491–499. doi:10.1071/MF22260

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Context. The ability of ectothermic stream invertebrates to adapt to the predicted increases in mean and extreme stream temperatures is crucial to ensuring they continue to exist. Aims. To examine the plasticity of thermal limits of Australian Paratya spp. (Decapoda, Atyidae) from streams in eastern New South Wales (NSW). We hypothesised that the upper lethal temperature (ULT, as indicated by the median lethal temperature, LT_{50} would be higher for warm water-acclimated shrimp individuals than for winter-acclimatised shrimp individuals because of the importance of acclimatisation temperature. Methods. Controlled experiments were undertaken to determine the ULT by using ramping assays for winter field-acclimatised and warm water laboratoryacclimated Paratya spp. Key results. Warm water-acclimated shrimp individuals demonstrated a significantly higher LT_{50} of 36.1°C than did winter-acclimatised shrimp individuals at 34.6°C. Paratya spp. exhibited a limited plasticity for acclimation to warmer temperatures. Conclusions. Results demonstrated the potential vulnerability of ectothermic stream invertebrates to climate change if stream temperatures increase as predicted and thermal thresholds are exceeded. Implications. Understanding the ULT of stream invertebrates helps predict their ability to respond to temperature variability and response to climate change. Increasing resilience through target management of resorting riparian vegetation for shade and securing environmental flows may reduce the impacts of stream warming.

Keywords: acclimatisation, climate change, distribution, macroinvertebrates, plasticity, shrimp, stream temperature, thermal tolerance.

Introduction

Changes to thermal regimes linked to climate change may have severe consequences for the structure of in-stream biotic communities and the functions of stream ecosystems. Thermal changes can affect biodiversity, abundance, species distribution and life-history patterns of stream invertebrates (Cox and Rutherford 2000; Narum et al. 2013; Dallas and Rivers-Moore 2018: Bonacina et al. 2023). Stream invertebrates are ectotherms; as such, they are directly affected by alterations in the thermal regime (Narum et al. 2013; Magozzi and Calosi 2015). Mortality may occur as stream temperatures exceed the critical thermal-tolerance limits of individual invertebrate species (Stewart et al. 2013; Pedreros et al. 2020). When temperatures exceed these lethal limits, the number of individuals of a species in a population is reduced until they become absent from the stream community (Dallas and Rivers-Moore 2018). For example, in a study on freshwater mussels, Archambault et al. (2014) found that increasing stream temperature and reduced stream flow directly affect abundance through mortality. Geographical distribution shifts are a potential effect of mortality because of exceedance of thermal limits of stream invertebrates (Verdelhos et al. 2015). In a review of the effects of climate change and water temperature on stream invertebrates, Bonacina et al. (2023) recommended that community-level physiological responses of individuals or

populations should be studied in more detail, given that their ecological effects are likely to be enhanced by climate warming. Understanding the upper lethal temperature (ULT), plasticity and response of stream invertebrate species and populations to possible future conditions helps forecast the ecological consequences of climate change (Dallas and Rivers-Moore 2018; Morley *et al.* 2019; Hidalgo-Galiana *et al.* 2021).

The seasonal variability of stream thermal regimes has a fundamental influence on the structure of stream invertebrate communities (Pedreros et al. 2020). Examining seasonal variations in thermal thresholds may give some insight into the thermal adaptability of stream invertebrates (Houghton and Shoup 2014). A link between ULT and acclimatisation to seasonal stream temperatures has been studied with varying results. Dallas and Rivers-Moore (2018) showed that the critical thermal limits of two stream invertebrate species significantly differed between late summer and winter; however, those between spring and autumn were less distinct. By contrast, Hidalgo-Galiana et al. (2021) showed that six Coleoptera species had limited acclimation-related plasticity for upper thermal limits and concluded that plasticity of thermal limits is unlikely to buffer the consequences of climate change.

Thermal acclimatisation in response to changing thermal conditions expected under climate change will require organisms to adjust to the changing environmental conditions by plasticity. Physiological plasticity occurs as organisms respond to acclimatisation at a seasonal scale (Gunderson and Stillman 2015). The ability of stream invertebrates to adapt to temperatures outside their current limits is less understood. The impact of climate change on stream invertebrates will depend on the increase in temperature and the rate of increase relative to their adaptive capacity (Palmer et al. 2009). Because climate change leads to increased temperature change, higher average temperatures and more variable temperatures, an ability to adapt will determine the degree of shift of distribution ranges (Verdelhos et al. 2015; Alba-Tercedor et al. 2017; Haase et al. 2019). In eastern Australia this translates specifically to how far the northern limit of specific stream invertebrate species will move south and will be determined by the upper thermal tolerance and plasticity of each species. Because stream invertebrates play a crucial role within aquatic food webs, changes in species' survival rates will influence community composition and structure, significantly affecting entire stream ecosystems. Change is inevitable, but, how much, is uncertain.

This study aimed to examine the plasticity of thermal limits of a population of Australian *Paratya* spp. (Decapoda; Atyidae) from streams in eastern New South Wales (NSW). This was achieved through three main objectives. The first was to determine the ULT of winter acclimatised Australian *Paratya* spp. caught in the field. The second was to determine the ULT on the basis of acclimation to summer stream temperatures simulated in the laboratory. Finally, the ULTs of the two treatments were compared to identify any impacts of acclimation temperature. By examining the acclimated specimens' responses, the adaptive capacity of Australian *Paratya* spp. to future warming is considered.

Methods

Study species, collection and acclimatisation

Paratya spp. are the most widespread atyid freshwater shrimp in eastern Australia, found in upland and lowland streams, dams and retention ponds, with distribution from southern Queensland to eastern South Australia (Cook *et al.* 2006; Rahman *et al.* 2020). Prior to a reclassification by Suter *et al.* (2022), it was believed that only a single highly variable Paratya species (Paratya australiensis) occurred in Australia. Since collection and identification of our *P. australiensis* in 2021 for use in this study, Suter *et al* (2022) has redescribed and identified 10 distinct linages of Paratya in Australia. Under this new taxonomic classification, our test specimens were re-identified and found to be a combination of *P. australiensis* and the newly classified species Paratya spinosa sp. nov.

Australian *Paratya* spp., generally, have a life cycle of 2 years, with females breeding in their second summer (Hancock and Bunn 1997; Williams 1977). Temperature is the most critical factor influencing the breeding season of Australian *Paratya* spp., with hydrology a secondary influence (Hancock and Bunn 1997). In contrast to the tropical regions, the breeding season of *Paratya* in temperate and subtropical regions is confined to the warm summer months (Hancock and Bunn 1997; Rahman *et al.* 2020). *Paratya* spp. living within subtropical eastern Australia have not been found any closer than 10 km from the start of saline estuarine conditions and can complete their life history in upland rainforest streams (Hancock and Bunn 1997; Williams 1977; Cook *et al.* 2006).

Specimens of Australian Paratya spp. were collected in July 2021 from a 100-m stretch of Leycester Creek, Barkers Vale (28°33'38.1"S, 153°07'02.7"E), NSW, Australia. This section of the creek is a low-order subtropical stream in the Richmond River catchment. Approximately 520 individuals were collected with a 300-µm sampling net, hand-picked and transported to the laboratory in an aerated bucket. The average stream temperature over the 4 weeks prior to capture was $13^{\circ}C \pm 1.52$ (see Supplementary Fig. S1). Water quality at the time of capture was as follows: temperature was 15°C, pH was 8.1 and dissolved oxygen (DO%) saturation was 92.1%. Specimens transported to the laboratory were split between two 200-L aquarium tanks. Each tank contained ~150 L of preconditioned tap water maintained at 15°C. Tap water was preconditioned with Prime Fresh and Saltwater Conditioner to remove chlorine and chloramine and detoxify ammonia, nitrite, nitrate and any heavy metals in the tap water.

Water was aerated using large air stones, with water being recirculated through the system at a rate of 400 L h⁻¹ using 750 L h⁻¹ pumps (Model: AQUAPROAP750LV). The first tank contained shrimp used for Assay 1 on winter fieldacclimatised shrimp. They were kept at 15°C for 2 days without food before use in Temperature-ramping assay 1. The experiment was conducted 3 days after their collection from the creek.

To examine the ULT of warm water-acclimated shrimp, laboratory acclimation to approximate summer temperatures was required. For Assay 2, ~180 shrimp were laboratory-acclimated to a temperature of 28° C over a 6-week period. The water temperature in the laboratory-acclimation tank was increased from the collection temperature of 15° C at a rate of ~2.7°C week⁻¹ and held at a final temperature of 28° C for 2 weeks. Specimens were fed throughout the acclimation period with algal wafers. Once the acclimation period was complete, the shrimp were transferred to a 200-L holding tank (as above) at 28° C for 2 days without food, before being transferred to experimental apparatuses.

Experimental setup

The apparatus used to examine ULT consisted of four 50-L water baths (Fig. 1). Each water bath contained three small 6.8-L containers suspended in water baths; to avoid any pseudo replication, each small container was filled with preconditioned tap water at a temperature of 15°C for the winter-acclimatised shrimp and 28°C for the warm water-acclimated shrimp and aerated using one large air pump to maintain DO% saturation above 70%. Each small container

held 15 shrimp. Shrimp were not fed during the experiment. Three water baths were used as experimental units (nine replicate containers) and heated using thermal circulators. A pump was placed in each water bath to aid in stirring the water, so as to ensure even water temperature throughout the ramping assay. The fourth water bath was held at the control temperature of 15°C for the winter-acclimatised shrimp and 28°C for the warm water-acclimated shrimp for the entirety of the ramping assay. A control (3 replicates each with 15 shrimp) was used to examine potential mortality from factors other than water temperatures (e.g. container effects, fluctuations in DO, water quality and lack of food) (Dallas and Ketley 2011).

Experimental procedure

A ramping assay examined ULT for both winter fieldacclimatised and laboratory-acclimated warm-water shrimp. The endpoint criterion was defined as the temperature (°C) that results in the death of an individual (Rezende *et al.* 2014). Following the acclimation period, shrimp were moved to the experimental apparatus and held at the control temperature of 15° C for field-acclimatised and 28° C for laboratory-acclimated shrimp for 1 h. Following the 1-h experimental *in situ* acclimation period, the ramping assay was commenced at a heating rate of 2° C h⁻¹, by using thermal circulating heaters. The heating rate was considered to be slow enough to ensure that the core temperature of the shrimp approximated the ambient temperature, but fast enough to avoid acclimation (Ernst *et al.* 1984; Quinn *et al.* 1994; Dallas and Ketley 2011). This dynamic assay was chosen



Fig. 1. Diagram showing apparatus setup for ramping assay. (a) Top view of the overall apparatus setup; four identical water baths containing three smaller containers holding the shrimp during the ramping essay. (b) A side view of one water bath and water levels maintained during the ramping assay.

not to replicate a specific thermal event, but as a method to examine ULT. Water was heated at this constant rate until the endpoint was observed for all individuals. Throughout the experiment, the temperature was recorded every minute with a data logger (Hobo UA-002-08 temperature- and lightpendant datalogger). Shrimp were continually visually monitored throughout the experiment for mortality. A jet of water from a pipette was used to identify live shrimp from dead shrimp, with lack of agility being the first sign of heat stress. Organisms considered dead were removed and placed in a water tank at the control temperature to confirm mortality. The time of mortality, mortality temperature and size of each shrimp was recorded. Following the ramping assay, organisms were preserved in 70% ethanol and species identification was confirmed. If control survival was above 90%, ULT values were considered valid.

Analysis

To expose the ULT of the shrimp from the two treatments, we estimated median lethal temperature (LT_{50}) and 95% confidence intervals using the PROBIT analysis within IBM SPSS Statistics for Windows (ver. 27.0, IBM Corp., Armonk, NY, USA) by using the total test population response. Outliers were removed from the data; this was only one shrimp per treatment to normalise the data. The resulting regression was used to determine the ULT, which is the temperature that causes mortality of 50% of the test population. Furthermore, to examine thermal thresholds, lethal temperatures for 10 and 90% of the test population (LT_{10} and LT_{90} respectively) values

were estimated using PROBIT analysis (see Supplementary Tables S1–S2). Dose–response curves were created using the PROBIT results, with proportional survival plotted against temperature. To examine and quantify thermal plasticity in response to acclimatisation and identify significant differences between the two treatments, a 95% confidence interval (CI) upper and lower bound overlap was used.

Results

No mortalities occurred in the control population for either treatment. The average mortality temperature for the winter-acclimatised shrimp was 35.4° C (s.d. = 1.58), with 100% mortality occurring at 36.4° C (Fig. 2). The ULT of the winter-acclimatised shrimp by using Ramping-assay 1 had an estimated LT₅₀ value of 34.6° C, and 95% CI (33.9, 35.5) for all individuals tested (Table 1). The calculated window where mortality occurred (LT₁₀–LT₉₀) was 5.2° C (Fig. 2), with most mortality of winter-acclimatised specimens occurring between 32° C and 95% CI (30.5, 32.8) (LT₁₀) and 37.2° C and 95% CI (36.2, 39.3) (LT₉₀). Throughout the experiments, specimens generally remained sedentary, showing limited behavioural changes as temperatures increased. The average size of shrimp tested was 28.03 mm (s.d. = 5.42).

The warm water-acclimated shrimp had an estimated ULT (as indicated by LT_{50}) of 36.1°C, 95% CI (35.7, 37.6) (Fig. 2). The average temperature to cause mortality of the warm water-acclimated shrimp was 37.1°C (s.d. = 0.88), with



Fig. 2. Thermal-response curves from PROBIT (solid lines) and recorded mortality temperature (dots) for each winter field-acclimatised at 15°C and warm-water laboratory-acclimated at 28°C *Paratya* spp. in ramped water-temperature experiment heating at 2°C h⁻¹.

Table I.	Results of PROBIT analysis of winter field-acclimatised
shrimp and	l warm-water laboratory-acclimated with 95% confidence
level upper	and lower bounds.

Treatment	LT ₁₀ (95% CI) (°C)	LT ₅₀ (95% CI) (°C)	LT ₉₀ (95% CI) (°C)
Winter	32.0 (30.5, 32.8)	34.6 (33.9, 35.5)	37.2 (36.2, 39.3)
Warm	35.1 (33.7, 35.4)	36.1 (35.7, 37.6)	37.1 (36.6, 41.0)

100% mortality occurring at 37.8°C. The LT_{10} was 35.1°C, 95% CI (33.7, 35.4), and the LT_{90} was 37.1°C, 95% CI (36.6, 41.0). The range between LT_{10} and LT_{90} , where the highest mortality occurred, was 2°C (Fig. 2), being considerably narrower than for the winter-acclimatised shrimp (5.2°C). The average size of warm water-acclimated shrimp tested was 24.76 mm (s.d. = 4.03). Again, specimens generally remained sedentary, showing little behavioural changes as temperatures increased. The ULT of the warm water-acclimated shrimp was 1.5°C higher than that of the winter field-acclimatised shrimp.

In response to acclimatisation, the ULT of warm water-acclimated shrimp was significantly higher (36.1°C, 95% CI (35.7, 37.6)) than that of winter-acclimatised shrimp (34.6°C, 95% CI (33.9, 35.5)). The confidence intervals from the PROBIT analysis had no overlap (Fig. 3) and showed significant differences in the LT_{50} and LT_{10} values between warm water-acclimated and winter-acclimatised shrimp specimens. By contrast, the results of the estimated

 LT_{90} values were not significantly different between assays shown by the overlap of the confidence intervals. The LT_{90} for winter-acclimatised shrimp (37.2°C (36.2, 39.3)) is almost identical, being only 0.1°C higher than those of the warm water-acclimated shrimp (37.1°C (36.6, 41.0)).

Discussion

Predicting the consequences of increasing mean and extreme stream water temperatures on the survival and distribution of stream invertebrates is key to understanding the impacts of climate change on stream biota and riverine ecosystems (Stewart et al. 2013; Kim et al. 2017; Bonacina et al. 2023). The ability to acclimatise to changing thermal conditions is expected to be a primary factor that dictates the robustness of stream invertebrates to increasing stream temperatures (Palmer et al. 2009; Rohr et al. 2018). The thermal acclimation potential of Paratya spp. was identified, with the warm water-acclimated shrimp having a higher ULT (+1.52°C) than that of the winter-acclimated shrimp, on the basis of the acclimatisation temperatures of 15 and 28°C respectively, and a rate of temperature increase of 2°C h⁻¹. Gradual temperature ramping was used because it is expected to provide a better ecologically relevant estimate of the impacts of cumulative stream temperature change than is shock (Overgaard et al. 2012; Jørgensen et al. 2019). Because



Fig. 3. Overlap of 95% confidence intervals (CI) for warm water-acclimated (red) and winter-acclimatised (blue) shrimp. Showing the lack of a difference in LT_{90} (winter-acclimatised shrimp = 36.2, 39.3, warm water-acclimated shrimp = 36.6, 41.0) between the two assays is represented by CI overlap; the lack of overlapping CI for both the LT_{50} (winter-acclimatised shrimp = 33.9, 35.5, warm water-acclimated shrimp = 35.7, 36.1) and the LT_{10} (winter-acclimatised shrimp = 30.5, 32.8, warm water-acclimated shrimp = 33.7, 35.4) suggested that there is a significant difference between the groups for these critical values.

warming leads to mortality, generating thermal tolerance data is vital for understanding how ectothermic stream invertebrates will tolerate increasing average and extreme water temperatures.

The warm water-acclimation temperature mimics the peak summer stream temperatures experienced during hot, dry summers that are becoming more common in eastern NSW (Chessman 2009). Paratya spp. showed some capacity for physiological plasticity to survive higher temperatures in summer. This capacity for physiological plasticity is essential to understanding the impact of climate change and stream warming (Palmer et al. 2009; Morley et al. 2019). Our results highlighted a potential critical temperature of ~37°C for this population of Australian Paratya spp., as demonstrated by the similar LT₉₀ values of 37.2 and 37.1°C, in winteracclimatised and warm water-acclimated shrimp. An assay using shrimp caught in summer's height would further clarify extreme upper thermal-tolerance limits. The examination of temperature differences in other Paratya spp. over latitudinal and elevation gradients would also provide insights to physiological plasticity within this genus, with the inclusion of evolutionary responses.

Biological and physiological processes affect thermal tolerance. One of the most critical factors affecting ULT is respiration/metabolic rate. Because metabolic rate increases as temperature rises, which raises biological oxygen demand and therefore requires greater oxygen concentrations to sustain normal bodily functions (Verberk and Calosi 2012; Verberk et al. 2020; Bonacina et al. 2023). We aerated the containers used in the ramping assay, which may have reduced low-oxygen stress in the experiment; however, this might not occur in the natural environment. Once oxygen demand reaches a point where it exceeds the supply, mortality eventuates (Verberk and Calosi 2012). During the assays, as temperature increased, the behaviour of the shrimp was affected, with the initial effects being reduced locomotion, soon followed by death. The size of the shrimp had no bearing on ULT. Similar studies of thermal limits indicated that oxygen limitations may be occurring and are linked to stream invertebrates' upper thermal tolerance (Magozzi and Calosi 2015; Verberk et al. 2016). Other studies have shown that stream temperature profoundly influences aspects of stream invertebrates' biology (metabolic rate), physiology and behaviour (Ward and Stanford 1982; Sweeney et al. 1992; Isaak et al. 2012; Semsar-kazerouni and Verberk 2018). Examining oxygen limitation in the form of availability (i.e. dissolved oxygen saturation) rather than the inability of invertebrates to take in enough oxygen to meet biological oxygen demand needs to be further investigated.

Comparisons of the ULT obtained in our study with similar studies of stream invertebrate ULT showed that Australian *Paratya* spp. have a high tolerance to increased temperatures (Fig. 4). In a review of upper thermal tolerances of stream invertebrates, Stewart *et al.* (2013) found that upper limits



Fig. 4. Range of mean upper thermal tolerances for major taxonomic groups adapted from Stewart *et al.* (2013) and including our results.

for the major taxonomic groups of stream invertebrates ranged from 22.3°C for Ephemeroptera to 43.4°C for Coleoptera. Compared with this dataset, our Australian *Paratya* spp. had a higher tolerance to elevated temperatures than most other stream invertebrates except for Odonata and Coleoptera taxa. However, these outcomes are determined from limited data sets, highlighting the urgent need to undertake work in finding the ULT for stream invertebrates.

Interactions between warming and plasticity

Stream invertebrates are sensitive to water temperature and the thermal regimes of the stream (Ross-Gillespie 2014). To survive changing thermal conditions, stream invertebrates need the ability to adapt through metabolic or behavioural adjustments (Magozzi and Calosi 2015; Pallarés et al. 2021). Stream invertebrates have some physiological plasticity, vital to surviving the range of temperatures experienced over different timescales (González et al. 2010). Although some plasticity in ULT is evident for Australian Paratya spp. from our results, this may not be adequate to keep in step with the increase in mean and extreme stream temperatures predicted under climate-change scenarios. According to CSIRO and Bureau of Meteorology (2020) predictions, by 2040, it is expected that in Australia, mean temperatures will increase to +2.8°C above the pre-industrial temperatures, along with changes in regional patterns of rainfall and increased drought frequency and duration. The lack of any significant difference in LT₉₀ values suggests a limit to the capacity for adaptation to higher stream temperatures. Although some change in ULT is shown in response to acclimatisation, plasticity may be unable to buffer Australian Paratya spp. sufficiently from changing thermal conditions in streams. The lack of buffering indicates that Australian Paratya spp. could be at risk of higher mortality rates associated with an increase in the frequency of extreme events such as heatwaves, low flow events, the rise of the occurrence of high-severity wildfires and the increase in mean temperatures with climate change (Dudgeon 2019; CSIRO and Bureau of Meteorology 2020; Arias Font et al. 2021;

Seyedhashemi *et al.* 2022). Knowledge of thermal limits can be used to delineate guidelines and create trigger points for management action (Gomez Isaza *et al.* 2022). Species with broad plasticity are more likely to adjust to climate shifts (Pallarés *et al.* 2021).

The range where increasing water temperatures affect organisms is linked to their ability to survive future warming. The consequences expected will be more intense in tropical and subtropical streams as generally, stream invertebrates in these streams live closer to their physiological thermal limits (Egea-Serrano *et al.* 2022). We observed a 2°C difference between LT₁₀ and LT₉₀ for warm water-acclimated shrimp and a 5.2°C difference for winter-acclimatised shrimp. Even though mortality of warm-water shrimp occurred at a higher temperature, once temperature exceeded the thermal limits, mortality will occur irrespective of thermal acclimation.

Results from Gunderson and Stillman (2015) indicated that physiological plasticity might not be sufficient to buffer stream invertebrates from increasing stream water temperatures under predicted climate-change conditions. Survival may therefore require an evolutionary response to increasing stream temperatures. Given that plasticity is a trait that can evolve, this may be an adaptive mechanism for stream invertebrates to avoid the impacts of increasing stream temperatures. However, Gunderson and Stillman's (2015) investigations also suggest that plasticity in thermal tolerance may be evolutionarily constrained. Examining acclimatisation potential and changes in plasticity over multiple generations may give further insights. Our results and research showed that stream invertebrate species with high UTLs will fare best under a warming climate (Palmer et al. 2009).

Ecological consequences

Thermal alteration is associated with an ecological change in freshwater stream ecosystems (Fenoglio et al. 2010; Rivers-Moore et al. 2013; Bruno et al. 2019). Stream temperature alteration may force thermally sensitive species to change their geographical distribution range, negatively affecting stream communities, biodiversity and ecosystems (Fenoglio et al. 2010; Alba-Tercedor et al. 2017; Amundrud and Srivastava 2020). While examining the response of stream invertebrates to changing thermal regimes in South America, Pedreros et al. (2020) suggested that changes in stream temperature could lead to the displacement in altitude and latitude of some stream invertebrates. The distribution range of some Australian Paratya spp. may change and their distribution may be reduced or shifted southward as a response to increasing stream temperatures that exceed their ULT. This may mean a loss of biodiversity if some species of Australian Paratya are restricted to high elevations (Rahman et al. 2020). Field examinations could assess species distribution and predict distribution limits (Chessman 2018; Terblanche and Hoffmann 2020).

As filter feeders and grazers, shrimp play a key role in stream communities (Moulton et al. 2012: Suter et al. 2022). They are essential in controlling periphyton biomass (Moulton et al. 2012) and are a major food source for streamdwelling fishes such as Mogurnda adspersa and Tandanus tandanus; they are also preved on by Ornithorhynchus anatinus (platypus) (Bain et al. 2016; Rahman et al. 2020). Their loss may also have stream health impacts because they are consumers of periphyton and, hence, important for ecosystem functioning (Moulton et al. 2012). The loss of this important component from the food web may lead to changes in predator-prev dynamics, disturbing population dynamics of other species with which they interact (Ferris and Wilson 2012). Climate change-associated stream warming disrupts biological communities and severs ecological linkages. Despite this, there are significant gaps in our knowledge of the environmental tolerances, including the ULT of this ecologically significant group (Bonacina et al. 2023).

Maximum stream temperatures are decreased by shading (Johnson 2004; Fuller *et al.* 2022). Developing resilience in the landscape to reduce in-stream impacts may be important. Thermal impacts could be moderately mitigated through increasing shading by riparian vegetation and ensuring natural environmental flows. Restoring riparian vegetation in inadequately shaded streams may counteract some of the influence of projected warming and drying under climate change (Trimmel *et al.* 2018; Fuller *et al.* 2022). However, air temperatures will continue to increase and affect currently well-shaded streams (Fuller *et al.* 2022).

Conclusions

This study provides new data on winter and summer ULT and the plasticity of Australian Paratya spp. in Australian streams. As hypothesised, the ULT (as indicated by LT₅₀) of warm water-acclimated shrimp was higher than that of winteracclimatised shrimp. However, the population of Australian Paratya spp. examined in this study had limited plasticity of thermal limits and may be unable to buffer against the influences of climate change on stream temperatures. Australian Paratya spp. showed a vulnerability to rising stream water temperatures under future climate warming, given the limited adaptive response of their UTLs. Climate change-associated stream warming may significantly affect stream invertebrate populations through the contraction of suitable habitat ranges. Furthermore, stream water temperatures influence the growth, feeding, reproduction and, ultimately, survival of ectothermic stream invertebrates. Increasing resilience through target management of resorting riparian vegetation for shade and securing environmental flows may reduce the impacts of stream warming.

Supplementary material

Supplementary material is available online.

References

- Alba-Tercedor J, Sáinz-Bariáin M, Poquet JM, Rodríguez-López R (2017) Predicting river macroinvertebrate communities distributional shifts under future global change scenarios in the Spanish mediterranean area. *PLoS ONE* **12**(1), e0167904, doi:10.1371/journal.pone.0167904
- Amundrud SL, Srivastava DS (2020) Thermal tolerances and species interactions determine the elevational distributions of insects. *Global Ecology and Biogeography* **29**(8), 1315–1327. doi:10.1111/geb.13106
- Archambault JM, Cope WG, Kwak TJ (2014) Survival and behaviour of juvenile unionid mussels exposed to thermal stress and dewatering in the presence of a sediment temperature gradient. *Freshwater Biology* 59(3), 601–613. doi:10.1111/fwb.12290
- Arias Font R, Khamis K, Milner AM, Sambrook Smith GH, Ledger ME (2021) Low flow and heatwaves alter ecosystem functioning in a stream mesocosm experiment. *Science of The Total Environment* 777, 146067. doi:10.1016/j.scitotenv.2021.146067
- Bain PA, Gregg AL, Kumar A (2016) De novo assembly and analysis of changes in the protein-coding transcriptome of the freshwater shrimp *Paratya australiensis* (Decapoda: Atyidae) in response to acid sulfate drainage water. *BMC Genomics* 17(1), 890. doi:10.1186/ s12864-016-3208-y
- Bonacina L, Fasano F, Mezzanotte V, Fornaroli R (2023) Effects of water temperature on freshwater macroinvertebrates: a systematic review. *Biological Reviews* **98**(1), 191–221. doi:10.1111/brv.12903
- Bruno D, Belmar O, Maire A, Morel A, Dumont B, Datry T (2019) Structural and functional responses of invertebrate communities to climate change and flow regulation in alpine catchments. *Global Change Biology* **25**(5), 1612–1628. doi:10.1111/gcb.14581
- Chessman BC (2009) Climatic changes and 13-year trends in stream macroinvertebrate assemblages in New South Wales, Australia. *Global Change Biology* **15**(11), 2791–2802. doi:10.1111/j.1365-2486.2008.01840.x
- Chessman BC (2018) Dissolved-oxygen, current and temperature preferences of stream invertebrates estimated from field distributions: application to assemblage responses to drought. *Hydrobiologia* **809**(1), 141–153. doi:10.1007/s10750-017-3455-1
- Cook BD, Baker AM, Page TJ, Grant SC, Fawcett JH, Hurwood DA, Hughes JM (2006) Biogeographic history of an Australian freshwater shrimp, *Paratya australiensis* (Atyidae): the role life history transition in phylogeographic diversification. *Molecular Ecology* **15**(4), 1083–1093. doi:10.1111/j.1365-294X.2006.02852.x
- Cox TJ, Rutherford JC (2000) Predicting the effects of time-varying temperatures on stream invertebrate mortality. New Zealand Journal of Marine and Freshwater Research 34(2), 209–215. doi:10.1080/ 00288330.2000.9516927
- CSIRO and Bureau of Meteorology (2020) State of the climate 2022. (Australian Government: Canberra, ACT, Australia) Available at http://www.bom.gov.au/state-of-the-climate/2022/documents/2022-state-of-the-climate-web.pdf
- Dallas HF, Ketley ZA (2011) Upper thermal limits of aquatic macroinvertebrates: comparing critical thermal maxima with 96-LT₅₀ values. *Journal of Thermal Biology* **36**(6), 322–327. doi:10.1016/ j.jtherbio.2011.06.001
- Dallas HF, Rivers-Moore NA (2018) Temporal thermal refugia and seasonal variation in upper thermal limits of two species of riverine invertebrates: the amphipod, *Paramelita nigroculus*, and the mayfly, *Lestagella penicillata. Aquatic Ecology* **52**(4), 333–349. doi:10.1007/s10452-018-9667-2
- Dudgeon D (2019) Multiple threats imperil freshwater biodiversity in the anthropocene. *Current Biology* **29**(19), R960–R967. doi:10.1016/j.cub.2019.08.002
- Egea-Serrano A, Alves MC, Solé M, Tejedo M (2022) Upper thermal tolerances and vulnerability to global warming in a Brazilian Caatinga fish *Astyanax bimaculatus* (Linnaeus, 1758) population. *Austral Ecology* **47**(6), 1157–1161. doi:10.1111/aec.13207

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- Ernst MR, Beitinger TL, Stewart KW (1984) Critical thermal maxima of nymphs of three Plecoptera species from an Ozark foothill stream. *Freshwater Invertebrate Biology* **3**(2), 80–85. doi:10.2307/1467096
- Fenoglio S, Bo T, Cucco M, Mercalli L, Malacarne G (2010) Effects of global climate change on freshwater biota: a review with special emphasis on the Italian situation. *Italian Journal of Zoology* 77(4), 374–383. doi:10.1080/11250000903176497
- Ferris R, Wilson RS (2012) The physiological arms race: exploring thermal acclimation among interacting species. *Journal of Thermal Biology* **37**(3), 236–242. doi:10.1016/j.jtherbio.2012.01.006
- Fuller MR, Leinenbach P, Detenbeck NE, Labiosa R, Isaak DJ (2022) Riparian vegetation shade restoration and loss effects on recent and future stream temperatures. *Restoration Ecology* **30**(7), e13626. doi:10.1111/rec.13626
- Gomez Isaza DF, Cramp RL, Franklin CE (2022) Fire and rain: a systematic review of the impacts of wildfire and associated runoff on aquatic fauna. *Global Change Biology* **28**(8), 2578–2595. doi:10.1111/gcb. 16088
- González RA, Díaz F, Licea A, Denisse Re A, Noemí Sánchez L, García-Esquivel Z (2010) Thermal preference, tolerance and oxygen consumption of adult white shrimp *Litopenaeus vannamei* (Boone) exposed to different acclimation temperatures. *Journal of Thermal Biology* **35**(5), 218–224. doi:10.1016/j.jtherbio.2010.05.004
- Gunderson AR, Stillman JH (2015) Plasticity in thermal tolerance has limited potential to buffer ectotherms from global warming. *Proceedings of the Royal Society of London – B. Biological Sciences* 282(1808), 20150401.
- Haase P, Pilotto F, Li F, Sundermann A, Lorenz AW, Tonkin JD, Stoll S (2019) Moderate warming over the past 25 years has already reorganized stream invertebrate communities. *Science of The Total Environment* 658, 1531–1538. doi:10.1016/j.scitotenv.2018.12.234
- Hancock MA, Bunn SE (1997) Population dynamics and life history of Paratya australiensis Kemp, 1917 (Decapoda: Atyidae) in upland rainforest streams, south-eastern Queensland, Australia. Marine and Freshwater Research 48(4), 361. doi:10.1071/MF97003
- Hidalgo-Galiana A, Ribera I, Terblanche JS (2021) Geographic variation in acclimation responses of thermal tolerance in South African diving beetles (Dytiscidae: Coleoptera). *Comparative Biochemistry* and Physiology – A. Molecular & Integrative Physiology 257, 110955. doi:10.1016/j.cbpa.2021.110955
- Houghton DC, Shoup L (2014) Seasonal changes in the critical thermal maxima of four species of aquatic insects (Ephemeroptera, Trichoptera). *Environmental Entomology* 43, 1059–1066. doi:10.1603/EN13344
- Isaak DJ, Wollrab S, Horan D, Chandler G (2012) Climate change effects on stream and river temperatures across the northwest US. From 1980–2009 and implications for salmonid fishes. *Climatic Change* **113**(2), 499–524. doi:10.1007/s10584-011-0326-z
- Johnson SL (2004) Factors influencing stream temperatures in small streams: substrate effects and a shading experiment. *Canadian Journal* of Fisheries and Aquatic Sciences **61**(6), 913–923. doi:10.1139/f04-040
- Jørgensen LB, Malte H, Overgaard J (2019) How to asses Drosophila heat tolerance: unifying static and dynamic tolerance assays to predict heat distribution limits. Functional Ecology 33(4), 629–642. doi:10.1111/ 1365-2435.13279
- Kim KS, Chou H, Funk DH, Jackson JK, Sweeney BW, Buchwalter DB (2017) Physiological responses to short-term thermal stress in mayfly (*Neocloeon triangulifer*) larvae in relation to upper thermal limits. *Journal of Experimental Biology* 220(14), 2598–2605. doi:10.1242/ jeb.156919
- Magozzi S, Calosi P (2015) Integrating metabolic performance, thermal tolerance, and plasticity enables for more accurate predictions on species vulnerability to acute and chronic effects of global warming. *Global Change Biology* **21**(1), 181–194. doi:10.1111/gcb.12695
- Morley SA, Peck LS, Sunday JM, Heiser S, Bates AE (2019) Physiological acclimation and persistence of ectothermic species under extreme heat events. *Global Ecology and Biogeography* **28**(7), 1018–1037. doi:10.1111/geb.12911
- Moulton TP, Souza ML, Brito EF, Braga MRA, Bunn SE (2012) Strong interactions of *Paratya australiensis* (Decapoda: Atyidae) on periphyton in an Australian subtropical stream. *Marine and Freshwater Research* 63(9), 834. doi:10.1071/MF12063

- Narum SR, Campbell NR, Meyer KA, Miller MR, Hardy RW (2013) Thermal adaptation and acclimation of ectotherms from differing aquatic climates. *Molecular Ecology* 22(11), 3090–3097. doi:10.1111/ mec.12240
- Overgaard J, Kristensen TN, Sørensen JG (2012) Validity of thermal ramping assays used to assess thermal tolerance in arthropods. *PLoS ONE* 7(3), e32758. doi:10.1371/journal.pone.0032758
- Pallarés S, Verberk WCEP, Bilton DT (2021) Plasticity of thermal performance curves in a narrow range endemic water beetle. *Journal* of *Thermal Biology* **102**, 103113. doi:10.1016/j.jtherbio.2021.103113
- Palmer MA, Lettenmaier DP, Poff NL, Postel SL, Richter B, Warner R (2009) Climate change and river ecosystems: protection and adaptation options. *Environmental Management* 44(6), 1053–1068. doi:10.1007/ s00267-009-9329-1
- Pedreros P, Guevara-Mora M, Stehr A, Araneda A, Urrutia R (2020) Response of macroinvertebrate communities to thermal regime in small Mediterranean streams (southern South America): implications of global warming. *Limnologica* **81**, 125763. doi:10.1016/j.limno. 2020.125763
- Quinn JM, Steele GL, Hickey CW, Vickers ML (1994) Upper thermal tolerances of twelve New Zealand stream invertebrate species. *New Zealand Journal of Marine and Freshwater Research* **28**(4), 391–397. doi:10.1080/00288330.1994.9516629
- Rahman S, Schmidt D, Hughes JM (2020) Genetic structure of Australian glass shrimp, *Paratya australiensis*, in relation to altitude. *PeerJ* 8, e8139–e8139. doi:10.7717/peerj.8139
- Rezende EL, Castañeda LE, Santos M (2014) Tolerance landscapes in thermal ecology. *Functional Ecology* 28(4), 799–809. doi:10.1111/ 1365-2435.12268
- Rivers-Moore NA, Dallas HF, Ross-Gillespie V (2013) Life history does matter in assessing potential ecological impacts of thermal changes on aquatic macroinvertebrates. *River Research and Applications* 29(9), 1100–1109. doi:10.1002/rra.2600
- Rohr JR, Civitello DJ, Cohen JM, Roznik EA, Sinervo B, Dell AI (2018) The complex drivers of thermal acclimation and breadth in ectotherms. *Ecology Letters* **21**(9), 1425–1439. doi:10.1111/ele.13107
- Ross-Gillespie V (2014) Effects of water temperature on life-history traits of selected South African aquatic insects. PhD thesis, University of Cape Town, Cape Town, South Africa.
- Semsar-kazerouni M, Verberk WCEP (2018) It's about time: linkages between heat tolerance, thermal acclimation and metabolic rate at different temporal scales in the freshwater amphipod *Gammarus fossarum* Koch, 1836. *Journal of Thermal Biology* **75**, 31–37. doi:10.1016/j.jtherbio.2018.04.016
- Seyedhashemi H, Vidal J-P, Diamond JS, Thiéry D, Monteil C, Hendrickx F, Maire A, Moatar F (2022) Regional, multi-decadal analysis on the

Loire River Basin reveals that stream temperature increases faster than air temperature. *Hydrology and Earth System Sciences* **26**(9), 2583–2603. doi:10.5194/hess-26-2583-2022

- Stewart BA, Close PG, Cook PA, Davies PM (2013) Upper thermal tolerances of key taxonomic groups of stream invertebrates. *Hydrobiologia* **718**(1), 131–140. doi:10.1007/s10750-013-1611-9
- Suter PJ, Mynott JH, Crump M (2022) New species of Paratya (Decapoda: Atyidae) from Australian inland waters – linking morphological characters with molecular lineages. *Memoirs of Museum Victoria* 81, 55–122. doi:10.24199/j.mmv.2022.81.04
- Sweeney BW, Jackson JK, Newbold JD, Funk DH (1992) Climate change and the life histories and biogeography of aquatic insects in eastern North America. In 'Global climate change and freshwater ecosystems'. (Eds P Firth, SG Fisher) pp. 143–176. (Springer)
- Terblanche JS, Hoffmann AA (2020) Validating measurements of acclimation for climate change adaptation. *Current Opinion in Insect Science* 41, 7–16. doi:10.1016/j.cois.2020.04.005
- Trimmel H, Weihs P, Leidinger D, Formayer H, Kalny G, Melcher A (2018) Can riparian vegetation shade mitigate the expected rise in stream temperatures due to climate change during heat waves in a humanimpacted pre-alpine river? *Hydrology and Earth System Sciences* 22(1), 437–461. doi:10.5194/hess-22-437-2018
- Verberk WCEP, Calosi P (2012) Oxygen limits heat tolerance and drives heat hardening in the aquatic nymphs of the gill breathing damselfly *Calopteryx virgo* (Linnaeus, 1758). *Journal of Thermal Biology* **37**(3), 224–229. doi:10.1016/j.jtherbio.2012.01.004
- Verberk WCEP, Overgaard J, Ern R, Bayley M, Wang T, Boardman L, Terblanche JS (2016) Does oxygen limit thermal tolerance in arthropods? A critical review of current evidence. *Comparative Biochemistry and Physiology – A. Molecular & Integrative Physiology* 192, 64–78. doi:10.1016/j.cbpa.2015.10.020
- Verberk WCEP, Buchwalter DB, Kefford BJ (2020) Energetics as a lens to understanding aquatic insect's responses to changing temperature, dissolved oxygen and salinity regimes. *Current Opinion in Insect Science* 41, 46–53. doi:10.1016/j.cois.2020.06.001
- Verdelhos T, Marques JC, Anastácio P (2015) Behavioral and mortality responses of the bivalves *Scrobicularia plana* and *Cerastoderma edule* to temperature, as indicator of climate change's potential impacts. *Ecological Indicators* 58, 95–103. doi:10.1016/j.ecolind.2015.05.042
- Ward JV, Stanford JA (1982) Thermal responses in the evolutionary ecology of aquatic insects. *Annual review of entomology* 27(1), 97–117. doi:10.1146/annurev.en.27.010182.000525
- Williams W (1977) Some aspects of the ecology of *Paratya australiensis* (Crustacea: Decapoda: Atyidae). *Marine and Freshwater Research* **28**(4), 403–415. doi:10.1071/MF9770403

Data availability. The data that support this study will be shared upon reasonable request to the corresponding author.

Conflicts of interest. There is no conflicts of interest relating to this article.

Declaration of funding. This research did not receive any specific funding.

Acknowledgements. A huge thanks go to Dr Sue Oeding for assisting with collecting and hand-picking all the shrimp on a cold July day.

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