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Title	Temperature-induced metabolic performance in early life stages of two brachyuran crabs
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Publication date	2025-09-04
Original Citation	van der Walt, K. A., Reddy, S., Knights, A. M., Firth, L. B. and Porri, F. (2025) 'Temperature-induced metabolic performance in early life stages of two brachyuran crabs', Journal of Thermal Biology, 132, 104252 (9pp). https://doi.org/10.1016/j.jtherbio.2025.104252
Type of publication	Article (peer-reviewed)
Link to publisher's version	10.1016/j.jtherbio.2025.104252
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Download date	2026-11-01 14:06:52
Item downloaded from	https://hdl.handle.net/10468/17919



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Temperature-induced metabolic performance in early life stages of two brachyuran crabs

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ABSTRACT

Understanding marine species metabolic responses to short- and long-term temperature variation is critical for predicting the resilience of communities and ecosystems at local and global scales. This study investigated the effect of temperature changes on the routine metabolic rate (RMR) across early life stages (zoea and megalopa) of two brachyuran species, *Hymenosoma orbiculare* and *Pinnotheres* sp. Respirometry results under temperatures ranging from 11 - 25°C revealed stage- and species-specific metabolic responses. In *H. orbiculare*, RMR in megalopa life stage increased steeply and significantly at 22°C and 25°C, whereas the zoea life stage showed no significant change across the temperature range. For *Pinnotheres* sp., the megalopa life stage also exhibited significant RMR increases above 19°C, while the zoea life stage again showed stable RMR. These results demonstrate that megalopae, particularly of *H. orbiculare*, are more metabolically sensitive to acute warming, operating closer to their physiological limits, while zoeae maintain relative stability, but may be constrained by limited plasticity under sustained warming *In situ* monitoring confirmed that present-day water temperatures (14.6 – 24.6°C) already approach the upper experimental limits, with projections indicating a 2.0°C rise by 2100. Species-level differences suggest that *H. orbiculare*, with its higher and more variable RMR, is more vulnerable than *Pinnotheres* sp., whose larval stages maintain comparatively stable metabolism. These findings highlight the importance of

29 resolving life-stage and species-specific thermal responses to better predict larval survival,
30 recruitment, and resilience under future climate warming.

31 **Key words:** routine metabolic rate (RMR); early life stages, brachyuran crabs, respirometry;
32 thermal tolerance; climate change resilience

1. INTRODUCTION

Human-induced climate change, in particular rising air and sea temperatures, is driving major shifts in distribution, abundance and community structure of marine organisms (Lenoir et al., 2020; Pecl et al., 2017; Poloczanska et al., 2016). These thermal changes threaten the fitness and survival of marine species, particularly ectotherms, whose physiology is directly influenced by temperatures (Pörtner 2002, Helmuth et al. 2006, Angilletta 2009). For marine ectotherms, the ability to cope with rapid temperature fluctuations may be more important for ecological adaptation than adjusting to steady and gradual rises in mean values (Harada and Burton, 2019; Scheffler et al., 2019). Understanding their metabolic responses to short- and long-term temperature variation is therefore critical for predicting the resilience of marine communities and ecosystems to climate change events at local and global scales.

Marine ectotherms such as brachyurans, or true crabs, play a vital role in coastal habitats, acting as ecosystem engineers by enhancing nutrient cycling through their burrowing and sediment turnover activities (Chatterjee and Chakraborty, 2014; Lee, 2008). Their sensitivity to environmental changes at different early life stages makes them valuable bio-indicators and ideal model organisms for studying the impacts of change (Torres et al. 2019). Brachyurans have complex life-history strategies involving zoeal and megalopal larval stages, which must successfully metamorphose in coastal environments for adult recruitment (Byrne, 2012; Jirikowski et al., 2015). These early stage processes are vulnerable to climate-induced temperature fluctuations (Magris and Fernandes, 2011), as well as other factors such as light and tidal currents (Epifanio and Cohen, 2016), which can affect larval development and survival (Azra et al., 2020; Kroeker et al., 2013).These impacts can ultimately influence population dynamics, highlighting the need to understand their physiological responses.

Projected ocean warming is expected to increase the functional vulnerability of brachyurans, leading to irreversible changes in individual phenotypes and long-term population fitness (Azra et al., 2020; Burton and Metcalfe, 2014). With rapidly rising water temperatures and variability, brachyuran larvae may miss crucial physical and/or chemical cues, delaying metamorphosis and settlement, ultimately suffering increased mortality (Hadfield et al. 2001, Botello & Krug 2006, Elkin & Marshall 2007, Pinochet et al. 2020). Delays in metamorphosis and prolonged searches for suitable conditions can deplete metabolic energy, reducing resources available for post-settlement growth and compromising adult population size and dynamics (Igulu et al. 2011, Pinochet et al. 2020). Understanding the physiological responses of brachyuran larvae to rapid or fluctuating temperature changes across their life stages is, therefore, critical for assessing their vulnerability and resilience, ultimately informing ecological predictions related to population viability and community structure in the face of climate change.

While understanding how larval life stages respond to changes in environmental temperature is crucial, most research has thus far focused on the effects of physical changes on major life history events, such as development, growth and survival, with less emphasis on stage-specific metabolic responses (Alter et al., 2015; Leiva et al., 2018; Paschke et al., 2010; Schiffer et al., 2014; Small et al., 2015). Existing studies on sesarmid and other mangrove-associated crabs have primarily explored physiological responses such as salinity stress tolerance and osmoregulatory capabilities, largely through respirometry investigations on embryonic stages (Anger & Charmantier 2000, Diele & Simith 2006, Simoni et al. 2013, Simith et al. 2014). These investigations have however not examined metabolic sensitivity to thermal variation in post-embryonic stages, leaving a gap in our understanding of how temperature fluctuations affect later larval stages. Recent research in mangrove ecosystems has demonstrated that acute temperature fluctuations impose physiological stress on spawning females and embryos, manifesting as developmental delays and reduced larval quality, thereby affecting subsequent

recruitment success (Vorsatz et al., 2021). Additionally, zoea and megalopa life-stages in tropical and temperate microhabitats have revealed thermally induced changes in metabolic demands and survival thresholds (Vorsatz et al., 2021), providing a comparative framework for understanding stage-specific thermal vulnerability. A substantial knowledge gap, however, persists in understanding how brachyuran larvae respond to short- and long-term temperature changes. This lack of understanding hinders the ability to predict which early life stage may be more vulnerable or resilient to persistent climate anomalies, and how this might ultimately affect larval supply, recruitment success, and the maintenance of functional crab populations and coastal community dynamics. This risk is especially concerning for semi-enclosed coastal settings, which experience increasing and variable surface water temperatures.

Here, we assessed the extent to which natural rapid increases in water temperature affect the metabolic (respirometric) performance of zoea and megalopa life stages of two brachyuran species, the crown crab *Hymenosoma orbiculare* and the pea crab *Pinnotheres* sp. These species were selected because they represent contrasting ecological niches and life history strategies within the same habitat, allowing for valuable comparative insights into thermal sensitivity. It is important to note that while both zoea and megalopa larvae are planktonic and share the water column, the differences in the adult forms of these species provide a framework for exploring potential divergences in their physiological responses. *Hymenosoma orbiculare* is a small, slow-moving species often found inhabiting sheltered benthic areas, characterised by its limited dispersal and site fidelity (Emmerson, 2016). In contrast, *Pinnotheres* sp. exhibits a strictly commensal lifestyle, residing exclusively within the mantle cavities of invertebrate hosts such as bivalves (e.g. *Mytilus* spp.) (Emmerson 2016,Becker & Türkay 2017, Pérez-Miguel et al. 2019, de Gier & Becker 2020, Nicolau et al. 2023). During settlement, larvae must enter and remain within hosts, exposing it to a more sheltered microhabitat, likely buffering thermal variability and potentially providing thermal refugia. Understanding how

106 these contrasting adult life strategies influence their larval metabolic responses to temperature
107 fluctuations can provide broader ecological implications for benthic community dynamics and
108 species resilience. We hypothesised that short-term increases in temperature would
109 significantly elevate the metabolic rates of both crab species and both larval stages; and zoeae
110 to exhibit a higher sensitivity (i.e., increased routine metabolic rate – RMR) to temperature
111 changes compared to megalopae. Addressing these hypotheses, will increase our understanding
112 of how thermal stress affects the early life stages of brachyuran crabs and it will help identify
113 the resiliency of specific life stages to extreme temperatures likely to be experiences in these
114 coastal habitats in the near future.

2. MATERIALS AND METHODS

2.1. Study area and sampling sites

Zoea and megalopa life stages of the crown crab (*Hymenosoma orbiculare*) and the pea crab (*Pinnotheres* sp.) were collected from two jetties (Jetty A, Jetty B) within the urban Port Alfred Marina (33.59305556, 26.89500000), situated in the warm-temperate south-east coast of South Africa (Figure 1). Sampling was conducted throughout the reproductive season of both species (Emmerson, 2016), during the austral spring (September – November 2021), summer (December 2021; January, February 2022) and autumn (March and April 2022).

2.2. Environmental data

Between September 2021 and April 2022, hourly *in situ* water temperature data were collected at both jetties using EnvLoggers (ElectricBlue) (Figure 1). We supplemented these data with hourly water temperatures collected at the same sampling sites between September 2019 to February 2020 (Reddy 2022). This combined dataset provided a robust understanding of temperature variability at the sites and informed the experimental test temperatures used in the oxygen consumption trials based on the minimum = 15°C, average = 19°C and maximum temperature = 25°C (see Supplementary Material, Figure 1). For each sampling trip, salinity was recorded using a handheld seawater refractometer (RedSea), with salinity readings being full seawater (32 – 36 ppt; see Table S1).

2.3. Animal Collection

Brachyuran early life stages were collected using up to four modified small light traps per sampling site during each sampling period (after Chan et al. 2016). The traps, attracting positively phototactic taxa, used passive, non-invasive and non-destructive sampling techniques (Hickford and Schiel, 1999). The light traps were deployed for approximately 12

hours from sunset to dawn, coinciding with new spring tides. After retrieval, specimens were transported to the laboratory in eight aerated 5 L containers filled with water collected at the sampling site. To maintain ambient water temperature, the containers were placed into a sealable cooler box, with ice packs added whenever necessary. On arrival at the laboratory (within 1 hour), samples were sifted through a 65 μm mesh sieve and placed into separate 500 ml beakers filled with aerated, filtered seawater. They were acclimated for at least 1 hour in two external programmable water baths (GP 200, Grant Instruments) set to the collection temperature (see Table S1). After acclimation, samples were quickly sorted by species and life stage (zoea and megalopa) under a dissecting microscope to minimise stress from handling, then placed into species-specific beakers and returned to the water baths at the set collection temperature.

2.4. Experimental setup and oxygen consumption measurements

Individual water bath temperatures were adjusted to the target experimental test temperature at a rate of 1°C every 15 minutes to mimic the rapid water temperature fluctuations typical of intertidal environments (Reddy 2022, Kelley et al. 2011). This adjustment was made from the acclimation/collection temperature for both sampling sites (see Table S1). The experimental test temperatures comprised of five temperatures: 11, 15, 19, 22 and 25°C reflecting minimum (15°C), average (19°C) and maximum (25°C) *in situ* temperatures recorded previously (2019–2020, Reddy 2022). Individuals were exposed to either a down-ramp (from acclimation temperature to 15°C and 11°C) or an up-ramp (from acclimation temperature to 19°C, 22°C and 25°C). Once the target temperature was reached and stabilised, specimens were allowed to acclimatise for an additional hour within the external water baths.

After this period, mass-specific aquatic oxygen consumption ($\dot{V}O_2$) was measured as a proxy for RMR (McMahon, 1988), defined as standard metabolic rate plus any extra metabolism

spent due to spontaneous activity and stress (Arnott et al. 2006). $\dot{V}O_2$ was measured at each test temperature using an optical fluorescence-based oxygen meter (Sensor dish reader-SDR2, PreSens, Germany) in a static respirometry system. This system comprised a 24-well glass microplate (Loligo Systems, Denmark) placed into a temperature controlled chamber which recirculated water from an external water bath. Depending on species and life stage, up to four individuals (four zoea for *Pinnotheres* sp., two zoea for *H. orbiculare*; or one megalopa for both species; Vorsatz et al. 2021b) were haphazardly placed into 80 μl (zoea) or 200 μl (megalopa) wells containing filtered seawater. The number of zoeae per well, determined from preliminary trials, ensured a measurable oxygen decrease. Of the 24 wells, 18 contained specimens, while the remaining six served as controls with filtered seawater to account for background oxygen consumption. The microplate was sealed with parafilm and a silicone pad, and placed into the temperature controlled water chamber. The sensor dish reader (SDR) system, connected to a laptop running the SDR software (v4.0.0, PreSens, Germany), recorded oxygen levels from non-invasive sensor spots affixed to the bottom of each well every minute, for approximately 60 minutes, to determine RMR. During $\dot{V}O_2$ trials, individuals were unfed and kept in darkness by covering the chamber with aluminium foil (Vorsatz et al., 2021). $\dot{V}O_2$ was calculated as the linear decrease in oxygen concentration over time, using 80% pO_2 saturation as the cut-off to minimise the effects of stress and hypoxia on oxygen consumption (Vorsatz et al. 2021b). After each trial, specimens were preserved in 90% ethanol in Eppendorf tubes for later biovolume measurements. Three replicate trials per temperature were conducted for each species and developmental stage (n = 60) and repeated for each sampling site.

2.5. Biovolume measurements

Each individual was photographed using a high-powered stereo microscope (Olympus SZX2-ILLB) to obtain morphometric measurements for the calculation of its biovolume estimate

using geometric shapes to correct for the volume of each experimental well and calculate mean mass-specific oxygen consumption (Hillebrand et al., 1999). The biovolume of *Pinnotheres* sp. zoeae was estimated from the volume (*V*) of a sphere (Vorsatz et al. 2021b), using the formula:

$$V = \frac{4}{3}\pi r^3$$

where *r* represents the radius measured individually. The biovolume of *H. orbiculare* zoeae was estimated from the volume (*V*) of a cone + sphere + cone geometric shapes. Cone geometric shape was calculated using the formula:

$$V = (\pi r^2 h)/3$$

where *r* represents the radius and *h* represents the height. The biovolume of megalopae for both species was estimated from the volume (*V*) of a rectangular prism using the formula:

$$(V = l*w*h)$$

where *l* represents the maximum length, *w* the maximum width and *h* the maximum height of each individual. Carapace lengths were then measured and converted to dry weight (kg) (Espinoza and Bertrand, 2008) using the formula:

$$DW = 3.946\ TL^{2.436}$$

Mean dry weight of individuals in each well was then used to calculate the mass corrected MO_2 and expressed as μmol O_2 min^{-1} g^{-1}.

2.6. Data analysis

The respirometry data were filtered by removing measurements taken in the first 10 minutes of recordings. A quality threshold, $R^2 > 0.95$, was implemented to filter the linear decline in oxygen. Individual well respirometry measurements were corrected for biovolume and mass

corrected MO_2 (Glazier, 2006) and analysed using the R package "RespR" (Harianto et al. 2019) in R (v4.3.1; R Core Team, 2024) to calculate RMR of MO_2 using 90% of the data. The MO_2 for blank wells were averaged and subtracted from the individual well measurements to account for background respiration and expressed as μmol O_2 min^{-1} g^{-1}.

2.7. Statistical analyses

To evaluate the effects of temperature, life stage and species on RMR estimates, linear mixed effects models (LMEs) using the "nlme" package(Pinheiro & Bates 2024) were fitted. Prior to modelling, RMR estimates were square-root [sqrt (x + a)] transformed to meet the assumptions of normality and homoscedascity for both species. An integrated model was implemented across both *H. orbiculare* and *Pinnotheres* sp., with species, life stage (zoea and megalopa), temperature and their interaction specified as fixed effects. Temperature was further modelled as a random intercept to account for repeated measures and hierarchical structure. Temperature was fitted using second-order orthogonal polynomials to capture the curvilinear nature of the temperature-RMR relationship and to minimise multicollinearity among polynomial terms. Model selection was guided using Akaike information criterion (AIC) and Bayesian information criterion (AIC) scores, and the best-supported model included the three-way interaction: *Species* x *Stage* x *poly (Temp, 2)*. This combined model provided a statistically robust framework to assess differences in thermal performance across developmental stages and between species.

Hourly *in situ* water temperature data were collected between September and December 2021, and January – April 2022 at two jetties. A Mann-Whitney U test revealed no significant difference in temperature between jetties such that data were pooled for subsequent analysis. To explore the relationship between current *in situ* temperature and RMR across species and life stages, linear mixed-effects models were constructed separately for each species - life stage

combination using the lmer () function in the lme4 package. Models incorporated temperature as a second-degree orthogonal polynomial to account for potential non-linear responses, with experimental date treated as a random intercept to account for repeated measures and inter-trial variation. The best-fit models were selected based on AIC criteria. To project RMR under field conditions, coefficients from the fitted models were used to predict square-root transformed RMR across the empirical range of hourly *in situ* temperature values. Although models were fitted using the scaled orthogonal polynomials, predictions were generated using raw temperature values to enhance biological interpretability of the resulting trends. To normalise residuals, RMR data were square-root transformed. All statistical analysis was conducted using R (v4.3.1; R Core Team, 2024) with the RStudio interface (v23.3.0). The significance level used for all statistical analysis was $p < 0.05$.

3. RESULTS

Routine metabolic rate (RMR) showed significant difference across species, life stages and temperature treatments, with key interaction effects detected (Table 1, Figure 2). For *Hymenosoma orbiculare*, RMR significantly increased with temperature in the megalopa life stage, particularly at 22°C and 25°C, reflecting a steep, non-linear metabolic response (Figure 2A, Table 1). In contrast, the zoea stage exhibited a more modest and statistically non-significant change in RMR across the temperature range (Figure 2A, Table 1). For *Pinnotheres* sp., a similar but less pronounced pattern was observed: RMR in the megalopa stage increased significantly with temperature, especially beyond 19°C, whereas the zoea stage showed no significant temperature-related effect (Figure 2B, Table 1). Significant three-way interactions (Species x Stage x Temperature) and two –way interactions (Stage x Temperature, Species x Stage) indicate that RMR responses to temperature are both species-specific and stage-specific. No consistent main effect of temperature was observed across all stages and species.

Hourly *in situ* water temperatures for the 2021 – 2022 sampling period showed no significant differences between sampling sites (Mann-Whitney Y-test; $W = 29937$, $p = 0.670$), allowing data to be pooled (Figure 3). The recorded temperatures averaged of 19.0°C, with a minimum of 14.6°C (2 February 2022) and a maximum of 24.6°C (24 February 2022), closely aligning with data collected from September 2019 to February 2020 (Reddy, 2022) (Figure 3). Greater variability in water temperature was observed during the summer months (December- February 2022) compared to spring (September-November 2022) and autumn (March-April 2022) (Figure 3). Projected increases of 2.0°C by the end of the century, as predicted by the IPCC (2014, 2019), suggest an average temperature of 21.0°C, with a minimum temperature of 16.6°C and a maximum temperature of 26.6°C. When comparing current hourly *in situ* water temperature data and predicted RMR values over time, megalopa exhibited larger RMR fluctuations, particularly for *H. orbiculare*, compared to zoea, where the RMR changes for both *H. orbiculare* and *Pinnotheres* sp. are more subdued - flat (Figure 3).

4. DISCUSSION

Thermal sensitivity during early development is a key determinant of ectotherm survival and recruitment success under climate change (Pörtner & Farrell 2008, Sinclair et al. 2016). In the present study, routine metabolic rate (RMR) increased with temperature across the two brachyuran species and life stages, though the magnitude and variability of this response differed markedly between them. Contrary to the initial hypothesis that the zoea life stage would be more sensitive to warming, findings indicate that megalopa, especially *Hymenosoma orbiculare*, exhibited greater metabolic responsiveness to temperature changes than zoea, with elevated and more variable RMR at higher temperatures. These patterns suggests that ontogenetic stage plays a critical role in shaping thermal performance and highlight potential stage-specific vulnerabilities to short-term thermal stress. Such differential responses

underscores the importance of resolving life-stage specific physiological mechanisms to better predict recruitment outcomes under climate variability.

To interpret these outcomes within a physiological framework, we define "resilience" as metabolic stability along a thermal gradient – that is, the ability to maintain a relatively constant RMR despite rising temperature. This concept aligns with existing literature on thermal performance and metabolic compensation (Seebacher et al., 2015; Stillman, 2003). In this context, the zoea life stage of both crab species exhibited relatively stable metabolic responses across the temperature range tested, suggesting a capacity for partial metabolic compensation or even metabolic suppression. This well-documented stress response strategy allows organisms to supress their metabolism as a ration to their resting metabolic rate to conserve energy under stress (Guppy et al., 1994; Guppy and Withers, 1999). Such a strategy could be beneficial in reducing energetic costs during transient warming events or acute stress, potentially increasing resilience and enhancing survival. Metabolic stability could however also reflect limited plasticity, suggesting zoea may lack the physiological flexibility to adjust to sustained warming. Due to their small size and being the earliest developmental stage, zoeae may have reduced physiological reserve to cope with prolonged stress. Their underdeveloped respiratory systems may also restrict their ability to increase metabolism, potentially limiting performance under prolonged elevated temperatures (Leiva et al., 2018). Long-term, under the projected temperature increase of 2.0°C by the end of the century, if the marginal downward trend in RMR estimates at higher temperatures continues (Figure 2, 3), zoea may be unable to respond to increased temperatures, leading to mismatch in energy dynamics between life stages, ultimately affecting population viability and ecosystem balance.

In contrast, megalopae under the current thermal regime demonstrated significantly higher RMR absolute values and variability at higher temperatures compared to zoea, especially for

303 *H. orbiculare* (Figures 2, 3). This heightened metabolic sensitivity is likely due to increased
304 energetic demands during the later developmental stage (i.e., increased size, more activity), as
305 megalopae prepare for settlement and metamorphosis (Alter et al., 2015; Giménez, 2010; Leiva
306 et al., 2018; Small et al., 2015). Greater variance in RMR at higher temperatures in megalopae
307 of both species may either show increased physiological stress or a compensatory response to
308 temperature fluctuations, supporting emerging views on trait variability under environmental
309 stress (Noble et al., 2025) where increased trait variance can indicate either adaptive capacity
310 or impending performance limits. Notably, even though an upper critical thermal limit (CT_{max})
311 was not directly measured in this study, if the trend of increasing metabolic rate under
312 increasing temperature continues, and if temperatures were to increase beyond our highest test
313 temperature (25°C), metabolic capacity might become constrained. The observed increase in
314 RMR, without reaching a clear plateau within our experimental range (Figure 2), could indicate
315 that these megalopae are operating closer to their physiological limits. While such plasticity
316 could suggest some capacity for thermal acclimation, it seems to rather indicate increased
317 susceptibility to future warming, particularly during short-term events such as marine
318 heatwaves which are already occurring in the study region (van der Walt et al., 2021) and are
319 projected to become more frequent and intense (Schlegel et al., 2017).This increased metabolic
320 demand in megalopae could indeed translate in increased predation risk or reduced foraging
321 efficiency, ultimately impacting their survival and recruitment success (Leiva et al. 2018).
322 Thus, while increased RMR may indicate short-term compensatory capacity, we do not
323 consider this equivalent to resilience as defined here, since it reflects greater energetic costs
324 and potential vulnerability under sustained warming.

325 If future temperatures exceed thermal tolerance, metabolic stress or increased mortality may
326 occur, especially in extreme conditions. The capacity for persistence may also depend on the
327 availability of suitable habitats for settlement, as megalopae rely on specific temperature cues

for successful moulting and settlement (Epifanio and Cohen, 2016; Forward et al., 2001). Despite their ability to upregulate metabolism under warming, if megalopae cannot find a suitable (thermal) substrate to settle on (Pinochet et al., 2020), they cannot delay metamorphosis indefinitely and have a temporal threshold beyond which settlement must occur without habitat cues (Forward et al., 2001). Nevertheless, if their upper temperature tolerance is close to the local maximum temperature, and adaptation does not keep pace with rising temperatures, *H. orbiculare* megalopae may face declines or local extinctions as a result of an ontogenetic bottleneck (Storch et al., 2011; Walther et al., 2010). In this context, the greater metabolic stability of zoeae may play an important population-level role, helping to buffer againtst high natural losses from dispersal, predation, and thinning, thereby ensuring that sufficient numbers survive to reach the more energetically costly and vulnerable megalopa stage. These risks are further compounded by interactions with other environmental stressors, including habitat degradation and reduced water flow. While enclosed urban systems such as marinas may reduce energetic costs due to calmer hydrodynamics, they may also create thermally stressful microhabitats (e.g., Firth et al. 2024a), acting as ecological traps that negatively affect larval recruitment and survival (Komyakova et al. 2022, Firth et al. 2024b). Overall, the megalopa life stage is likely more vulnerable compared to the zoea life stage for both species under both current and future temperature regimes due to higher baseline metabolic demands, greater susceptibility to extreme temperature fluctuations and the compounding effect of prolonged heat stress which could push them closer to physiological thresholds.

Species-level difference in metabolic responses further elucidate the differential resilience of *H. orbiculare* and *Pinnotheres* sp. to environmental variability. *Hymenosoma orbiculare* exhibited consistently higher and more variable RMR values than *Pinnotheres* sp., particularly at the megalopa stage, indicating a greater energetic cost of living and potential physiological

353 stress under warming (Figure 2). In contrast, *Pinnotheres* sp. maintained relatively stable RMR
354 values across both life stages, reflecting a potentially broader thermal tolerance and reduced
355 sensitivity to environmental fluctuations. Although we initially speculated that adult habitat
356 stability may influence larval thermal sensitivity, we recognised that this assumption lacks
357 direct empirical support. An alternative hypothesis – that early life stages may inherit greater
358 resilience from adults inhabiting more variable environments – is also plausible and supported
359 by ecological theory (Murren et al., 2015; Scheffler et al., 2019). *Hymenosoma orbiculare*,
360 which occupies more dynamic coastal habitats as an adult (Emmerson 2016), may therefore
361 have evolved a more flexible or energetically responsive larval physiology to cope with
362 environmental variability. In contrast, *Pinnotheres* sp., which commonly inhabit the internal
363 cavities of bivalves (Becker and Türkay, 2017; de Gier and Becker, 2020; Nicolau et al., 2023;
364 Pérez-Miguel et al., 2019), might benefit from more buffered microhabitats, contributing to
365 reduced energetic demands in larvae. Direct comparisons of adult thermal regimes and
366 metabolic rates would however be required to validate these proposed adult-larval
367 physiological linkages. Overall, *H. orbiculare* is likely the more vulnerable species because its
368 higher metabolic demands mean it will experience greater energy stress as water temperatures
369 increase. Its sensitivity to environments changes, as evidenced by the sharp RMR fluctuations
370 in megalopa (Figures 2, 3), makes it less adaptable to temperature extremes short-term and
371 likely long-term. These species-specific differences in metabolic plasticity likely play a key
372 role in structuring crab communities and influencing ecological processes in coastal
373 ecosystems.

374 Importantly, we do not interpret reduced RMR response as a universal marker of superior
375 performance. In some contexts, high metabolic rates may confer ecological advantages (e.g.,
376 faster development or greater activity), while in others, metabolic suppression may enhance
377 energy conservation and survival. These outcomes depend on ecological context, energy

budgets and the balance between metabolic demand and environmental supply. Our results highlight the need for a nuanced understanding of how metabolic responses, taking into account life-history strategy, behavioural ecology and environmental predictability.

5. CONCLUSION

This study reveals that acute water temperature increases have significant and differential impacts on the metabolic performance of two brachyuran crab species during their early life stages, highlighting the complexity of thermal stress responses across different developmental stages and species belonging to the same infraorder. Our findings reveal that developmental stage plays a critical role in determining vulnerability, with the megalopae stage of both species, particularly in *Hymenosoma orbiculare*, being more sensitive to acute temperature changes than the zoeae stage. The heightened RMR rates in megalopae at higher temperatures suggest increased energy expenditure which may lead to faster depletion of energy reserves, especially in environments where food availability is limited. As a result, the observed differences in metabolic responses between life stages could have cascading ecological effects, influencing larval dispersal, settlement success and ultimately, population dynamics and ecosystem stability. Future research should prioritise the megalopa life stage, while also investigating adaptive capacity, intra-cohort variability, and the critical upper thermal limits of both species. Observed species-specific differences further highlight that *H. orbiculare* is more vulnerable to both current and future warming compared to *Pinnotheres* sp., which exhibited more stable metabolic performance across temperatures and life stages. While this pattern may be linked to their association with buffered habitats (e.g. bivalve hosts), further validation is needed This contrast underscores the importance of considering species-specific ecological niches and life history strategies when predicting the impacts of environmental change. Furthermore, future research for both species should focus on the interactive effect of multiple

stressors, including temperature, hypoxia and food availability to better predict the cumulative impacts of climate change on larval fitness and survival. Although survival was not systematically recorded during the experimental trials, observational data noted some mortality in *H. orbiculare* megalopae at 25°C, with deceased individuals removed from the analysis. Such mortality aligns with the elevated RMR trends observed, reinforcing the need for explicit survival assays to link to metabolic performance with fitness outcomes. Future studies should incorporate standardised survival assessments across temperatures and life stages to more robustly link metabolic sensitivity to organismal fitness and environmental resilience. Overall, the combination of higher metabolic demands and greater sensitivity to environmental variability makes *H. orbiculare*, particularly in the megalopa life stage, more susceptible to the impacts of climate change. These findings emphasise the need to understand how species-specific metabolic adaptations and life history strategies influence the resilience of marine invertebrate populations in the face of changing environmental conditions.

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7. TABLES

Table 1. Fixed effects from the best-fit linear mixed-effects model testing the effect of species, life stage, temperature (as orthogonal polynomials) and their interactions on the square-root transformed routine metabolic rate (RMR) of *Hymenosoma orbiculare* and *Pinnotheres sp.* A linear mixed-effects model (REML) was fitted with temperature as a random effect grouping factor (n = 1065 observations; 5 temperature groups).. Akaike information criterion (AIC),Bayesian information criterion (BIC) and log-likelihood (LogLik) are reported. Significant values ($p < 0.05$) are highlighted in bold.

Metabolic rate	Fixed Effect Term	Estimate	Std. Error	DF	t-value	*p*-value
RMR	(Intercept)	4.841	0.065	1049	74.42	<0.0001
AIC = 3443.53	Species (Pinnotheres sp.)	-1.4	0.097	1049	-14.48	<0.0001
BIC = 3512.97	Stage (zoea)	-1.372	0.106	1049	-12.92	<0.0001
LogLik = -1707.77	poly(Temp, 2)[1]	31.129	2.143	1049	14.53	<0.0001
	poly(Temp, 2)[2]	17.047	2.082	1049	8.19	<0.0001
	Species × Stage	1.38	0.154	1049	8.94	<0.0001
	Species × poly(Temp, 2)[1]	-12.239	3.143	1049	-3.89	0.0001
	Species × poly(Temp, 2)[2]	-14.456	3.166	1049	-4.57	<0.0001
	Stage × poly(Temp, 2)[1]	-27.139	3.421	1049	-7.93	<0.0001
	Stage × poly(Temp, 2)[2]	-21.143	3.457	1049	-6.12	<0.0001
	Species × Stage × poly(Temp, 2)[1]	13.881	5.101	1049	2.72	0.0066
	Species × Stage × poly(Temp, 2)[2]	13.981	5.079	1049	2.75	0.006

8. FIGURES

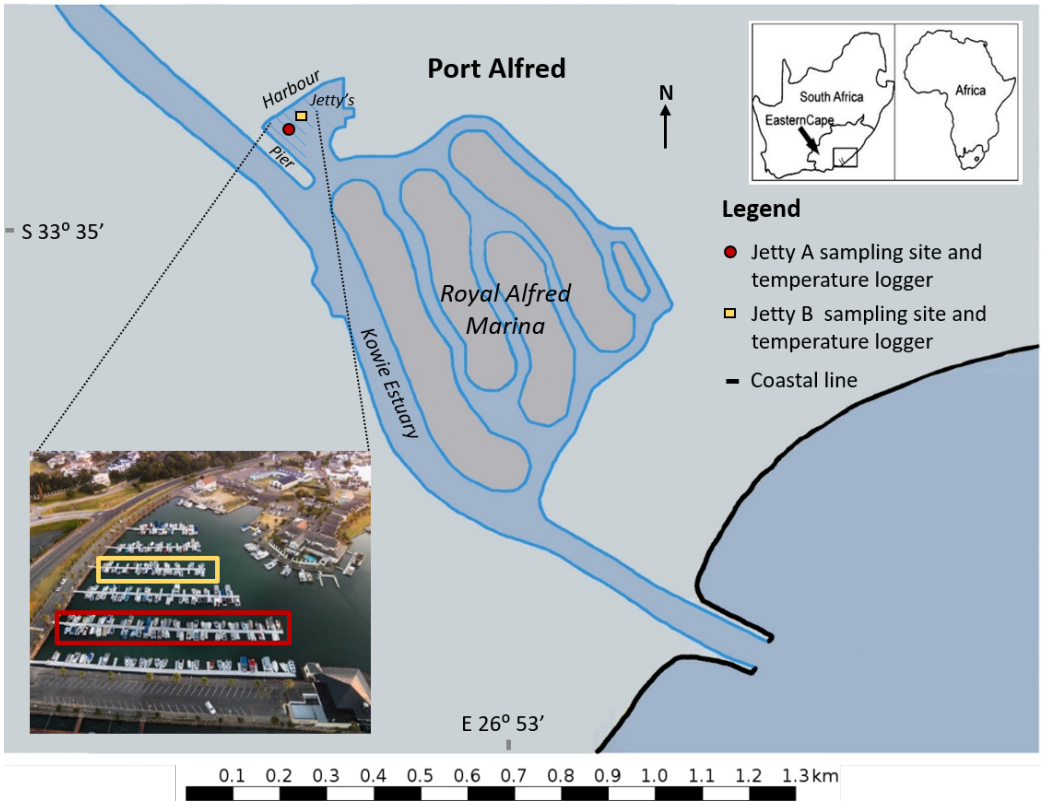


Figure 1. Map of Port Alfred, Eastern Cape, South Africa showing the Royal Alfred Marina and the jetty sampling sites, A (red circle) and B (yellow square) outlined by the Google Earth map image in the Port Alfred Marina. The site icons also correspond to the position of deployment of the loggers measuring *in situ* water temperatures.

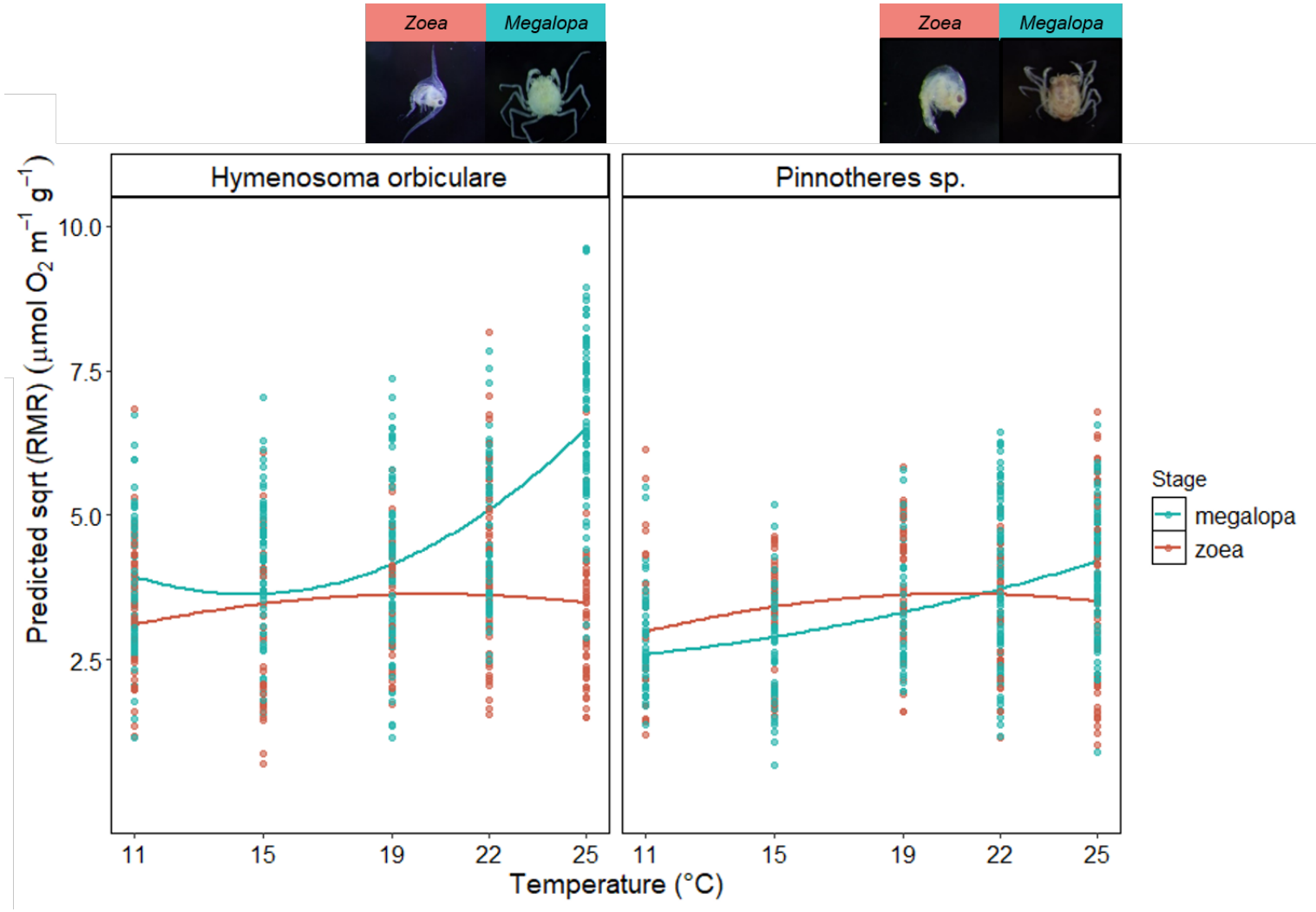


Figure 2. Predicted square root $_{(x + a)}$ transformed routine metabolic rate (RMR) responses of *Hymenosoma orbiculare* (A) and *Pinnotheres* sp. (B) brachyuran zoea (blue) and megalopa (red) life stages under five experimental temperatures (11, 15, 19, 22 and 25°C). Predictions (lines) were derived from the best-fit linear mixed-effects model using a second order polynomial term for temperature. Individual data are presented as points.

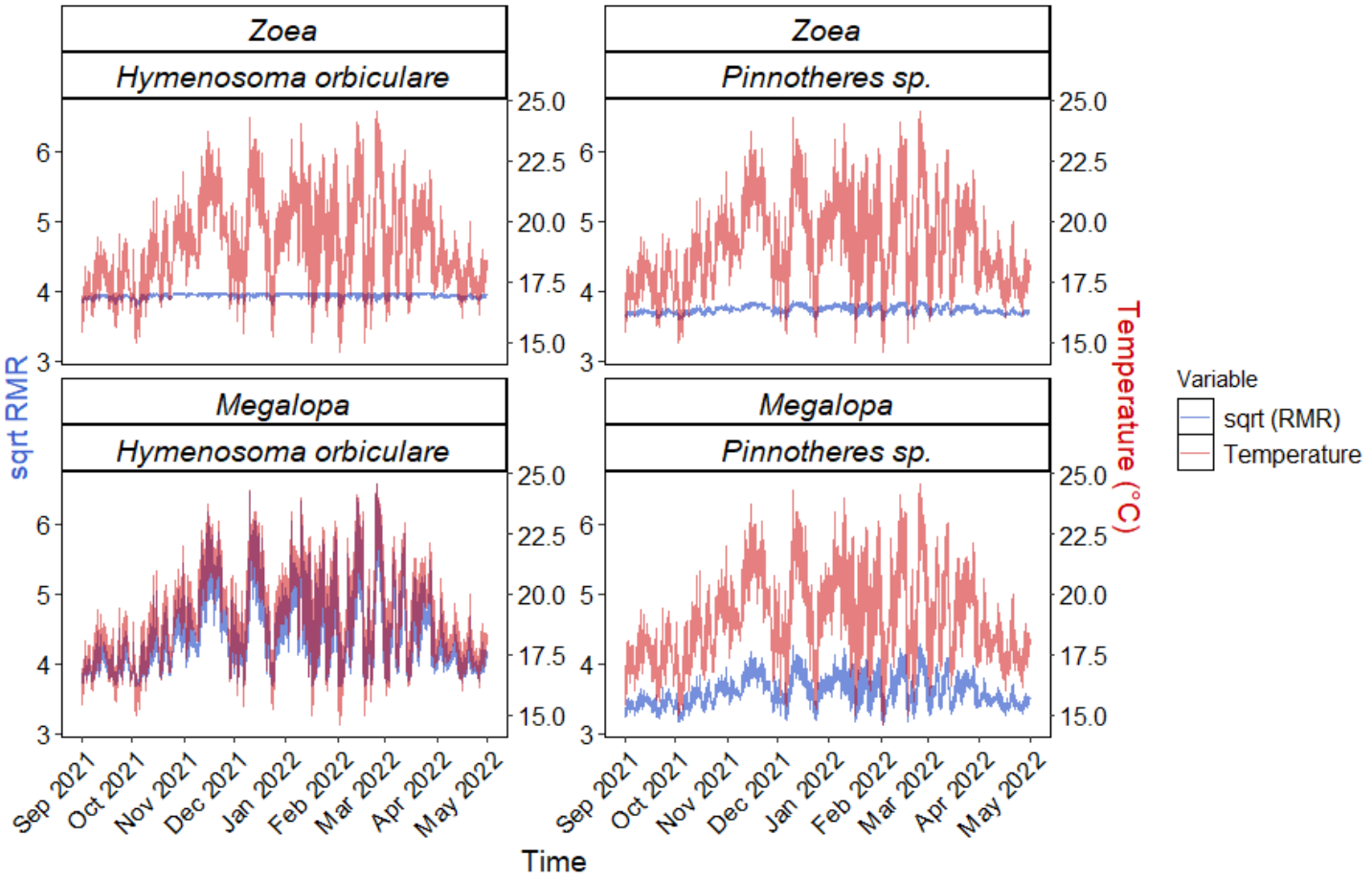


Figure 3. Time series plots showing predicted square root-transformed RMR rates (μmol.O_2.m^{-1}.g^{-1}, blue) overlaid on current *in situ* hourly temperature data (°C, red) recorded from September 2021 to May 2022. Projections are shown separately for the zoea and megalopa stages of *Hymenosoma orbiculare* (left panels) and *Pinnotheres* sp. (right panels). Square-root RMR values were generated using the best-fit second-order polynomial mixed-effects model for each life stage combination. Although the model was statistically fitted using orthogonal polynomials of scaled temperature, predictions were re-expressed using untransformed empirical temperature data to ensure biological interpretability.

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