Title

Beat the Heat: Examining Behavioral Trade-offs in the Face of Climate Warming for Intertidal Ectotherms

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Author

McIntire, Lily Clare

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Beat the Heat: Examining Behavioral Trade-offs in the Face of Climate Warming for Intertidal Ectotherms

BY
LILY CLARE MCINTIRE

DISSERTATION

Submitted in partial satisfaction of the requirements for the degree of
DOCTOR OF PHILOSOPHY
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in the
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Approved:

Luke Miller, Chair

Brian Gaylord

Anne Todgham

Committee in Charge

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Abstract

In the age of anthropogenic climate change, ectothermic organisms are at particular risk to elevated temperatures since they rely on access to thermally favorable habitats to moderate their body temperatures. As temperatures continue to increase because of climate change, it is becoming increasingly important to understand how ectotherms interact with their thermal environment, since temperature is one of the driving forces behind species' distributions on both global and local scales. Environmental temperatures affect physiology through metabolic rate changes and the need to mount physiological responses to stress, and ultimately this may, affect how they perform ecologically since they must balance the effects of temperature on their physiology while still foraging for food, accessing mates, and avoiding predation. Not all species are equally affected, however, since the speed with which an animal can move to a safer thermal habitat has been conjectured to affect how well they can respond physiologically to stressful temperatures. Thus, quantifying the tradeoffs species are making both behaviorally and physiologically will help scientists measure the vulnerability of species to climate change.

Terrestrial ecologists have been studying the potential effects of mobility on the evolution of physiological thermal response for decades. Since many terrestrial reptiles can quickly change their position within their habitats, they can maintain a "safe" range of body temperatures regardless of ambient temperatures in their location at large. Since these organisms can select a similar range of body temperatures in warm parts of their range as their counterparts that live in cooler parts of the range, both groups can achieve a similar range of body temperatures during their active period each day. Consequently, the organisms in both populations may have very similar thermal tolerances – this has been termed the Bogert Effect. Since they rarely experience temperatures outside of their stressful range by relying on behavior and availability of environmental refuges, there may be little selection for the ability to acclimatize to extreme

temperatures. For species to cope with climate change, they may need to combine behavioral responses with thermal physiological acclimatization or adaptation in order to offset warming impacts in what were previously suitable thermal microhabitats.

There are four types of data that are needed to understand how species interact with their thermal environment. The first two types are collected in a laboratory setting and used to understand how temperatures are affecting species' thermal performance and physiological limits. First is a thermal performance curve, which is a diagram of species' thermal performance as it initially increases with rising temperature and can benefit species' performance; this will continue to increase until a certain point (termed the optimal temperature). After this peak, performance will decline at warmer temperatures, and the organism will eventually die. The second class of data relates to a species' thermal limits, where measurements of lethal temperatures or critical thermal limits provide an upper (or lower) bound to what body temperature conditions an organism can tolerate for some period of time. In addition to laboratory measurements, field data are also needed; therefore, the third type of data is the body temperatures that the organisms are selecting, which provides insight into how close they are to their thermal limits in nature. Finally, measuring the operative (environmental) temperatures – or the temperatures that animals can select from in their habitat – helps to understand how often species could experience stressful or lethal temperatures in the field. Operative temperatures can be measured using biomimetic models, which are devices that heat up and cool down at the same rate as the live organism, and can be placed throughout habitats to record the temperatures that organisms could be selecting from. These metrics can be combined to calculate the thermal safety margins for species. Positive thermal safety margins indicate that species are not experiencing high risk in their environments, while negative ones indicate that the habitat is thermally stressful and they have to select habitat more carefully or risk dying. All these measures can be combined to understand how species will be affected by continued climatic warming.

The rocky intertidal is a particularly important habitat to measure the effects of elevated temperatures since it is one of the most thermally dynamic habitats on earth as tidal fluctuations expose organisms to potentially thermally stressful air temperatures during low tide. These fluctuations can be as much as 20°C in just a few hours and are already occasionally at or above species' thermal limits in some habitats. This thermal stress is also predicted to become worse as climate change continues, since many species are already living on the cusp of their thermal limits. Additionally, there is a great deal of thermal variation on both a microhabitat and a geographic scale. Within a site, temperatures can differ between sheltered and exposed habitats during one low tide by the same amount as temperatures might differ among sites separated by several degrees of latitude. On a broader scale, tidal timing affects how stressful a low tide could be. For example, in northern California, low tides are most stressful in the spring, when tides occur during midday. Conversely, in southern California low tides in the summer occur at night, so winter tides are counterintuitively more stressful. These variations in temperature stress both spatially and seasonally provide an ideal system for studying thermal stress throughout species ranges and can act as a natural laboratory for understand how climate change will continue to affect marine organisms.

Chapter 1 summary: The role of mobility in how organisms cope with thermal stress has not yet been compared between species that live in the same ecosystem. The rocky shores in California are home to a diversity of organisms that have varying levels of mobility. The goal of this chapter was to compare the responses to temperature of species in four mobility groups: (fast

moving crustaceans such as Pachygrapsus crassipes and Ligia occidentalis; intermediate-speed snails such as Tegula funebralis and Nucella ostrina; slow-moving limpets, Lottia scabra and L. digitalis; and sessile Balanus glandula and Mytilus californianus). In the field we measured body and environmental temperatures using species-specific biomimetic models and in the lab we quantified respiration rates under different air temperatures and upper thermal limits. We then combined these data to calculate thermal safety margins. We predicted that fast and intermediate-speed species would have lower thermal limits and narrower thermal safety margins than slow and sessile animals. However, we found that only the faster species had lower thermal limits and narrower thermal safety margins while the other three mobility classes were more similar to each other. Our findings indicate that mobility is an important characteristic when considering how organisms cope with elevated temperatures and lay the groundwork for understanding how communities may respond to climate change.

Chapter 2 summary: Organisms that exhibit the Bogert Effect are expected to be at higher risk from climate change, since they have not experienced selection for thermal acclimatization. This has yet to be studied in the intertidal zone, where organisms are already at risk of overheating. Pachygrapsus crassipes is a highly mobile intertidal organism that lives on the rocky shores along the western coast of North America. We used the natural variation in temperature that occurs along the coast of California as a natural laboratory to compare crabs from different locations to see if they are exhibiting the Bogert Effect. We compared their body temperatures, environmental temperatures, thermal limits, and thermal safety margins between a thermally stressful part of their range (San Diego, CA) and a cooler part of their range (Bodega Bay, CA). In addition to comparing across latitudes, we also compared their thermal performance curves and thermal limits seasonally at the beginning and end of the summer in Bodega Bay, CA. We found that P. crassipes is not exhibiting the Bogert Effect as they are selecting warmer body temperatures in San Diego on average than in Bodega Bay and have higher thermal tolerances in San Diego. Further, they are also acclimatizing between seasons in Bodega Bay, indicating that they do not only rely on behavior to cope with stressful temperatures. This could be beneficial since organisms that exhibit the Bogert Effect are predicted to be at higher risk to climate warming. However, P. crassipes thermal safety margins are still relatively small in both regions, meaning that climate change still poses a significant threat for this species.

Chapter 3: Urbanization in conjunction with climate change is currently causing major stress for organisms that live in highly urbanized locations. For example, in San Diego, the San Diego Bay was once tidal mudflat habitats; however, in the last century it has become predominantly armored shorelines held up by quarried riprap. In recent decades, land managers have begun to implement “green grey infrastructure” strategies and try to create coastal armoring technologies that protect economically important coastlines, while also increasing biodiversity in heavily trafficked ports. In 2021, the Port of San Diego installed two sections of COASTALOCK, which are large concrete blocks that have large pools of water and crevices that are designed to provide habitat for animals during low tide. It is not yet understood if these units are providing a thermal refuge for intertidal organisms. Our goal was to compare how organisms of differing mobilities (Ligia occidentalis and Pachygrapsus crassipes [fast-moving] and Lottia limatula [slow-moving]) were utilizing thermal habitat in both existing riprap and in the new coastal armoring units. We found that the novel units provided more thermally beneficial habitat for all organisms, particularly P. crassipes, that had negative thermal safety margins in the riprap. Overall, these units have the potential to provide a refuge for animals living in San Diego Bay

because they have more thermally suitable microhabitats available, which may provide a refuge for organisms as climate change continues to progress.

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Chapter 1

The role of mobility in intertidal invertebrates' responses to thermal stress

McIntire, LC and Miller, LP

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Abstract

As climate change progresses, it is important to be able to predict how the effects of elevated temperatures are affected by the ability of ectotherms to seek shelter. Many studies on ectotherms have suggested that mobility is a vital characteristic to understand how species will react to warming. Highly mobile ectotherms are not often exposed to thermally stressful conditions because they can actively select temperatures that are thermally beneficial or benign. Slow-moving or sessile ectotherms, however, are not able to change habitats quickly enough to escape from thermal stress or even death. In order to measure how mobility affected how organisms cope with temperature, we quantified the body temperatures, environmental temperatures (using biomimetic models), and thermal limits using respirometry of eight intertidal ectotherms in four mobility classes: fast, intermediate, slow, and sessile. In addition, we also calculated thermal safety margins (TSMs) for each of our species. While we predicted that fast and intermediately mobile species would have lower thermal limits and narrower TSMs than slow and sessile animals, we found that faster organisms had lower thermal limits and narrower thermal safety margins than the other three mobility classes. Our findings indicate that there is an effect of mobility on how organisms cope with temperatures and lay the groundwork for understanding how communities may respond to climate change.

Introduction

Ectothermic animals are particularly susceptible to elevated temperatures caused by climate change since they rely on their environment to moderate their body temperatures (Jørgensen et al. 2022). On a physiological level, temperature can affect metabolic rates (Sinclair et al. 2016), heat shock protein production (Dong et al. 2022), and other processes. Behaviorally, organisms may select thermally favorable habitats that either shelter them from thermal stress or help them warm their bodies. The way organisms select habitat, however, may be dependent on their mobility – defined as the capacity for movement (Crickenberger et al. 2020). How mobility affects habitat selection could potentially buffer, or exacerbate, the effects of climate change since organisms that are able to primarily rely on selecting a thermally safe habitat quickly are not exposed to selection for increased physiological responses to temperature (Huey et al. 2012). For example, lizards (*Anolis cristatellus*) have been found to have the same body temperatures and physiological thermal limits regardless of ambient temperatures (Huey et al. 2003), because they situate themselves in thermally suitable microsites. However, currently there has been no comprehensive comparison of how relative mobility affects thermoregulatory behavior, though studies have indicated that it is an important metric to understand (Huey and Tewksbury 2009). A comparison of physiology and behavior across species of varying mobility would lay the groundwork for understanding how species and communities could be affected by a warming climate.

Generally, moderate increases in temperature above normal, ambient conditions are not necessarily immediately stressful for ectotherms, since small increases in temperature may increase organismal performance (Huey and Kingsolver 1989). Performance will approach an optimal temperature where the organism functions well, but beyond that point, performance will decline and, eventually, at higher temperatures the organism will die – this rise and fall in performance has been termed a thermal performance curve (TPC, Huey and Kingsolver 1989). For tolerating larger increases in environmental temperatures, the role of avoiding high temperatures via mobility versus tolerating high temperature via physiological mechanisms is particularly important in cases where organisms are experiencing sublethal or lethal stress.

The rocky intertidal zone is a thermally dynamic environment that oscillates between relatively stable ocean temperatures at high tide and variable low-tide temperatures when animals are exposed to air temperatures that can fluctuate up to 20ºC in just a few hours (Helmuth et al. 2011). The habitat complexity of the rocky shore often creates thermal heterogeneity that varies by microhabitat and this small-scale variation can be as great as the variation across many degrees of latitude (Denny et al. 2011; Jurgens and Gaylord 2018). Further, organisms of varying mobility within these habitats react differently to thermal stress during low tide. For example, faster organisms like the shore crab *Hemigrapsus nudus* will shuttle between warm and cool habitats to keep their body temperatures low (McGaw 2003). Conversely, the slower sea star *Pisaster ochraceus* must select cooler habitats to avoid its thermal limits (Monaco et al. 2016). Even slower species, like limpets, will lift their shells off the substrate and “mushroom” which can reduce their body temperatures (Williams et al. 2005). This range of thermal stress provides an ideal system for understanding how organisms of different mobilities will be affected by climate change.

Our study aimed to quantify the thermal niches of eight intertidal species that represent different mobilities: ([fast]: *Pachygrapsus crassipes* and *Ligia occidentalis*; [intermediate]: *Tegula funebralis* and *Nucella ostrina*; [slow]: *Lottia scabra* and *L. digitalis*; and [sessile]: *Balanus glandula* and *Mytilus californianus*). While our study species are not phylogenetically independent, this comparison allows us to quantify thermal niches of co-occurring organisms under current conditions and begin to predict how warming could affect them.

We estimated thermal niches using 1) live animal body temperatures (T_b); 2) operative (or environmental) temperatures (T_e) from species-specific biomimetic models; 3) physiological thermal limits; and 4) thermal safety margins (TSM) calculated from thermal limits and T_es. A TSM, expressed as the difference between a species' thermal tolerance and the extreme operative temperatures of their environment, provides a metric to estimate the vulnerability of organisms to both high and low temperatures within their environment (Sunday et al. 2014). T_es are typically measured with biomimetic models, which mimic the heating and cooling properties of the live organisms (Helmuth et al. 2011). These physical models, in conjunction with laboratory-measured physiological responses to temperature, can help quantify species' TSM and, therefore, potential vulnerability to warming within habitats under climate change (Helmuth et al. 2011). We predicted that 1) fast and intermediate species would be selecting cooler habitats and have lower T_bs than slow and sessile species; 2) fast and intermediate species would have lower physiological thermal limits than slow and sessile organisms; and 3) the TSMs of fast and intermediate organisms would be narrower than those of the slow and sessile species.

Methods

Field sites

We conducted field surveys at two sites on the Bodega Marine Reserve (BMR; Bodega Bay, CA, USA, 38.31°N, 123.07°W). The intertidal zone at BMR is composed of granite benches that face predominantly west. During the summer, it experiences northwesterly waves and semidiurnal mixed tides with the lowest low occurring in the early mornings. We set up two 40-meter transects, one on the north bench and one in Horseshoe Cove, in the upper intertidal zone at shore heights between +1.52 and 2.13 meters above Mean Lower Low Water (MLLW).

Habitat surveys

We quantified the availability of habitat types (vertical surface, horizontal surface, pools, and crevices) within 1 meter of the transect using a 0.25 m^2 quadrat to quantify the percent coverage along each transect (n = 160 quadrats/site).

Body temperature surveys

Surveys were carried out in the late spring to late summer (June – August) from 2021-2024 during daytime low tides lower than +1 m above MLLW that occurred after sunrise (2021 n = 7, 2022 n = 15, 2023 n = 16, and 2024 n =7). We quantified T_bs and habitat selection of our study species within half a meter of the transect within three hours of the low tide.

For mobile mollusc species, we measured T_bs within randomly placed 0.25 m^2 quadrats by inserting a thermocouple wire gently between their shell and mantle. For barnacles and mussels, valves were gently parted, and the thermocouple wire was inserted inside. For the faster species, we did T_b surveys immediately upon arrival at the site as an area search within 1 meter of the transect since their habitat selection would change in the researcher's presence. *Li. occidentalis* was measured by gently placing a thermocouple wire on the top of the carapace, verified by initial comparisons of temperatures taken internally versus externally (see Supplemental 1). *P. crassipes* would retreat deep into crevices if disturbed, so we used a thermal imaging camera (FLIR Model TG267, Goleta, CA, USA; emissivity = 0.97) with a 2x lens so we could measure crab T_bs from a distance, after making pilot comparisons of internal body temperature versus external temperatures (Supplement S1).

Biomimetic models (Tes)

We created species-specific biomimetic models of all eight species to quantify the range of T_es in the field. All biomimetic models were created using resin epoxy and shells of live organisms. They were on average within 1-2°C of live organisms (for methodological details see Supplement 2). The mimics were placed haphazardly throughout the intertidal zone in sun-exposed and sheltered habitats for the duration of the low tide and temperatures were recorded on a thermocouple data logger every 5 seconds.

Respiration rate measurements

In the laboratory, we quantified respiration rates in air for *P. crassipes, Li. occidentalis*, *T. funebralis* and *N. ostrina* with closed chamber respirometry. Aerial respiration rates for the remaining four species were taken from the literature. Organisms were captured from the field and placed in a flow-through aquarium held at 12°C (monitored with HOBO TidbiT Temperature Logger, USA) for at least 1 hour before being tested to give them time to recover from handling stress. All organisms were tested within 72 hours of capture.

The respiration chambers were aluminum containers (volume = 52.3mL) with a paper towel (4 cm^2) soaked with 2mL of seawater to keep humidity near 100%. For smaller organisms, we used resin blocks to reduce the volume of air in the chamber so they would be able to measurably reduce oxygen in the chambers (volume = 8 – 35mL). We submerged the respiration chambers in water baths (ThermoFisher Scientific, Waltham, USA) at 14.5°C that were then heated at a rate of 8°C hour^{-1} to the treatment temperature. Chambers had ports that were left open during the ramping period to allow air exchange and closed once the treatment temperature was reached, followed by a one-hour sampling period where oxygen sensor spots (Pt3, PreSens, Regensburg, Germany) placed inside the chamber were sampled using fiber optic cables attached to a data logger (oxy-4, PreSens). Twelve individuals per species were exposed to each temperature treatment (~14.5, 26, 32°C), and each individual was only used in one trial. Temperatures were selected starting with the average air temperatures at BMR during summertime morning low tides (14.5°C, McIntire unpublished) and increased to be below previously published limits for either closely related species or their thermal limits in water (Hayford et al. 2018; McGaw 2003; Eberl et al. 2013; Gleason and Burton 2013). An empty chamber was included in each trial to serve as a control for potential sensor drift, and sensors were calibrated using a two-point calibration process at 0% O_2 using nitrogen gas, and water-saturated air for normoxia.

LT_{50}s and TSMs

We monitored mortality during respirometry trials to determine the temperature at which 50% mortality (LT_{50}) was achieved. Organisms would be removed from the chambers and observed for 30 minutes, and if no response was elicited by gentle probing the organism was considered dead. If 100% mortality was not achieved, we then would increase the temperature treatment until complete mortality occurred ([*P. crassipes*: 35.0, 36.9, 37.4°C]; [*Li. occidentalis*: 36.7 and 38.6°C]; [*T. funebralis:* 40.6 and 44°C]; and [*N. ostrina*: 37.1 and 39.1°C]). We used published LT_{50} values for *L. digitalis* (Dong and Somero 2009), *M. californianus* (Jurgens and Gaylord 2016), and *B. glandula* (Gilman et al. 2015). While *L. scabra* LT_{50} measurements were unavailable in the literature, Miller et al. (2015) measured the critical maximum temperature (39.6 °C, CT_{max}) as the temperature where locomotor function was lost (Orsted et al. 2022).

We calculated the TSMs by subtracting the 99th percentile of T_es value observed for biomimics of each species and that species' thermal limits (LT_{50} or CT_{max}). This allowed us to encompass the most stressful conditions during a typical northern California summer. Negative numbers indicate that a habitat is not thermally safe for organisms, and they may need to avoid stressful T_bs, while positive values indicate that temperatures typically do not exceed species' thermal limits (Sunday et al. 2014).

Data analysis

We calculated the frequency at which T_b and T_e values were within a range of stressful temperatures and at/above the thermal limits in the field. Stressful temperatures were defined based on optimal temperatures from thermal performance curves (see below). Differences in T_bs between species were tested using ANOVA and post hoc Tukey test. To compare T_bs across mobility groups, we used a hierarchical model with species as a random factor.

Respiration rates were calculated using the slopes of the best fit least squares regression line between elapsed time and oxygen concentration, and rates were compared within species using ANOVA. The data violated the assumption of homogeneity of variances, so we used the nlme package to weigh each average proportional to its variance (Pinheiro et al. 2025) in R (version 4.1.2, R Core Team 2021). Post hoc Tukey comparisons were made using the multcomp package (Hothorn et al. 2008). Optimal temperatures were determined by fitting a thermal performance curve to the respiration data (Sharpe-Schoolfield; Smith et al. 2019) using the package rTPC (Padfield et al. 2025). For literature sources, we used ImageJ (Schneider et al.

2012) to estimate the peak of their respiration rates. LT_{50} values were calculated by fitting a curve to the mortality data in the MASS package (Venables and Ripley 2002).

Results

Respirometry and LT50

Among the fast-moving pair of species, *Li. occidentalis* and *P. crassipes,* there were no significant differences in respiration rate between temperature treatments. For *Li. occidentalis,* respiration rates were low at 14.5°C and their respiration rates peaked at 36.6°C, while at higher temperatures (39.1°C) their respiration rates declined, and they began to die (Fig. 1; LT_{50} = 36.8°C, non-significant ANOVA results are shown in Supplement 3). *P. crassipes* consumed less oxygen between 14.5 and 20.1°C but peaked at 35.8°C (Fig. 1) and had a LT_{50} = 33.5°C (Fig. 1). Their respiration peaked about their LT_{50} since they died over a wide range of temperatures.

For the intermediate pairing, *T. funebralis* respiration rates peaked at 40.6°C (Fig. 1; LT_{50} = 40°C), though temperature treatments were not significantly different from each other (Supplemental 3). *N. ostrina* respiration rates were statistically different from each other between lower and higher temperatures (Fig. 1; Supplemental 3; ANOVA; $F_{4, 61} = 6.12$; $P < 0.01$). At 14.5 and 26.1°C their respiration rates were similar (Tukey; $Z_{4, 11} = 0.43$; $P = 0.99$), but respiration rates increased significantly at higher temperatures between 32.5 and 34.2°C, peaking at 36.1°C (Fig. 1; LT_{50} = 35.3°C).

We took slow species respiration and thermal limits from the literature. *L. scabra* respiration rates peaked at 35°C and their CT_{max} was 39.6°C (Fig. 1; Miller et al. 2015). *L.*

digitalis respiration rates peaked at 35°C (Bjelde & Todgham 2013) and their LT_{50} was measured at 38.4°C (Fig. 1; Dong and Somero 2009).

Sessile species' thermal performances were also taken from the literature. *M. californianus* respiration rates peaked at 27°C (Monaco et al. 2016) and their LT_{50} was 38°C (Fig. 1; Jurgens and Gaylord 2016). For *B. glandula* respiration rates were highest at 30°C (Ober et al. 2019) and their LT_{50} was 40.5°C (Fig. 1; Gilman et al. 2015).

T_bs and T_es

All species were found to non-randomly selected habitat (Supplement 4). T_bs in the field did not vary significantly between mobility classes (ANOVA; $F_{3, 2278} = 4.2$; $P = 0.10$), but there was still a trend towards faster species being cooler than the other mobility classes (Fig. 2). There were also differences between species within the mobility classes (Fig. 2; ANOVA; $F_{7, 2274} = 22.05$; $P << 0.01$). Further, all species were predominately found in cooler, non-stressful temperatures (~12-20°C; Fig. 3). However, T_bs of the fast species, *Li. occidentalis* and *P. crassipes,* were never above their thermal limits and individuals were rarely found within thermally stressful ranges (Fig. 3a, b). In the typical summer conditions at our sites, their T_es were also rarely above their thermal limits (Fig. 3a, b). Similarly, the intermediately mobile *T. funebralis* were never above their thermal limits or within their stressful range (Fig. 3c). *N. ostrina*, however, was within a stressful temperature range 6% of the sampling period, but never above their lethal limits (Fig. 3d). The slow-moving species, *L. scabra* and *L. digitalis,* were never in their stressful range (Fig. 3e, f). Similarly, their T_es were never above their thermal limits or within their stressful range (Fig. 3e, f). The sessile species, *B. glandula* and *M. californianus* were never found above their thermal limits, but their T_bs were within their stressful range 6% and 10% of the time and the biomimic T_es were within their stressful range 1% and 10% of the time respectively (Fig. 3g, h).

TSMs were smallest for *P. crassipes,* and *Li. occidentalis* and *N. ostrina* both had small TSMs (Fig. 4). While *T. funebralis* has a higher capacity for movement, it has a comparatively high thermal limit (Fig. 1) and TSM (Fig. 4). *L. scabra, L. digitalis, M. californianus,* and *B. glandula* all had relatively larger positive TSMs because of their high thermal limits; therefore, they experience fewer risky days than their faster counterparts during a typical Northern California summer (Fig. 4).

Discussion

Overall, thermal limits and TSMs for fast species were lower than those of intermediate, slow, and sessile species, except for *N. ostrina*. We had predicted that fast and intermediate species would be similar but found that *T. funebralis* was more similar to slow and sessile species. Slow and sessile species' wider thermal niches are potentially a consequence of their reliance on cellular-level and organ-system-level physiological responses rather than behavior, while faster species are avoiding thermal stress, resulting in a narrow thermal tolerance niche (Buckley et al. 2015). Like our fast-moving crustacean species, highly mobile crabs in the genus *Petrolisthes* that live in cooler microhabitats than our study species also have narrow TSMs (Stillman and Somero 2000). Consequently, less-mobile organisms are potentially less susceptible to increased temperatures since they have higher thermal limits. Conversely, highly mobile organisms may be at higher risk under climate warming since they are unable to physiologically cope with elevated temperatures if thermal refuges are unavailable (Buckley et al. 2015). Our data was collected under typical northern California summer conditions, but TSMs could be narrower under extreme heatwave events that can occur in northern California, particularly in the spring when the lowest tides are during midday (Harley 2008). Further, the effects of a mosaic of microhabitat warming could also be a factor (Woods et al. 2015). For example, crevices may warm less than horizontal surfaces; however, for species like our fast species, even a few degrees of warming could be detrimental and could relegate them to only cooler microhabitats.

It is important to acknowledge the study species we chose necessarily involved a phylogenetic confound, as the fast-moving species are both crustaceans, while the intermediate and slow-moving species are all gastropods. This leads to morphological differences that are important for thermal relations (i.e. warming from contact with substrate by molluscan foot vs crustacean legs or the energy expense of molluscs creating a mucus layer to move). Our study design is driven by the existence of these co-occurring species as members of a present-day ecological community that experience the same set of site-level weather conditions, while potentially experiencing different species-specific thermal histories driven by their mobility or physiological tolerance.

For example, *Li. occidentalis* and *P. crassipes* can move fast enough to make instantaneous decisions to find shelter from elevated temperatures, but molluscs, even the intermediate species like *T. funebralis* and *N. ostrina,* cannot. Slow-moving organisms like *L. scabra* and *L. digitalis* also cannot move quickly enough to protect themselves from stressful temperatures during a single low tide – which could prove lethal (Dong et al. 2009, Dong et al. 2008). For these species, making a “mistake” when selecting habitat at the start of a low tide period, or even over the course of days or weeks, is potentially more detrimental (Hui et al. 2022). Sessile animals like *B. glandula* and *M. californianus* experience heavy selection for thermal tolerance after settlement due to thermal stress (Ober et al. 2019, Logan et al. 2012, respectively). These consequences could result in selection for less-mobile animals having higher thermal limits than faster species since fast animals rely on behavior at the expense of physiological responses (Huey et al. 2012).

The variation in thermal limits (Fig. 1) and TSMs (Fig 4) between mobility classes may not be solely due to their ability to quickly move in direct response to thermal stress, but instead due to their behavior during high tide. For example, *N. ostrina* has been documented to have a circatidal rhythm by which they will change their position on the shore each day before the low tide throughout the two-week tidal cycle (Hayford et al. 2018). Therefore, while *N. ostrina* was classified in this study as an organism with intermediate mobility, it is selecting thermally benign habitats during the high tides (Hayford et al. 2018). This has also been demonstrated in other slow-moving species, like *Pisaster ochraceus*, which will increase its internal water volume and move lower on the shore after thermally stressful low tides, which allows them to increase their thermal inertia (Pincebourde et al. 2009). This type of behavior has been termed "bet hedging" and has been documented in many slow-moving intertidal ectotherms (McIntire & Bourdeau 2020, Pincebourde et al. 2009).

Like the difference in TSM observed between *T. funebralis* and *N. ostrina* that may be linked to their temperature stress avoidance strategy, the slow-moving limpets *L. scabra* and *L. digitalis* also differ in their TSM and movement patterns. The homing behavior of *L. scabra* limits its location on the shore, because it must be able to forage and return to its home scar before the tide falls again, meaning that it is effectively less mobile than some of its congeners (Wolcott 1973). Conversely, *L. digitalis* exhibits an aggregating behavior that allows it to seek out habitat more opportunistically and will shift their aggregations away from "hot spots" (Frank 1964). This difference in behavior has been hypothesized to be the reason why these organisms have different thermal tolerances (Dong et al. 2008, Wolcott 1973). It is worth noting that it is generally well documented that *L. scabra* has a higher thermal limit than *L. digitalis* (Dong et al. 2008, Wolcott 1973); however, in our study we did find that they were on average cooler than *L. digitalis*. This is likely due to the nature of the temperature sampling, particularly in the early morning when some substrates were not yet exposed to the sun. Overall, for slower-moving organisms like molluscs it is important to consider not only instantaneous behavior, but also behavior that is taking place during non-stressful high tides.

Further, some species may be selecting habitats for other reasons, such as access to food and mates, or avoiding predators. For example, fiddler crabs will traverse hot, dry habitats to access mates (Allen and Levinton 2014), and geckos will choose to avoid predators over accessing thermally beneficial habitats (Downes and Shine 1998). Additional studies measuring how individuals select thermal habitat when exposed to predators or to find food are needed to understand the tradeoffs organisms are making when selecting habitat.

Our methods for determining thermal limits in the laboratory removed other abiotic factors like humidity, wind, and solar radiation. Consequently, the thermal limits in our study are likely higher than what an organism would be able to handle in the wild since they may often be dealing with desiccation stress in addition to thermal stress (Iacarella & Helmuth 2011). Additionally, we determined mortality within 30 minutes of temperature exposure, so our LT_{50}s may be slightly less conservative than the other studies cited for thermal limits of our slow and sessile species (Kingsolver and Woods 2016). Studies that evaluate survival after longer periods (hours to days) may find mortality at slightly lower peak temperatures, which would decrease our species TSMs further, thus creating the same pattern of fast species having lower thermal limits than the other species in our study.

Understanding how mobility affects the susceptibility of organisms to climate change is vital for understanding the ecological consequences of elevated temperatures. In our study, highly mobile organisms had narrower TSMs, which are likely to be exacerbated by climate change. Additionally, slower and sessile organisms may have reduced TSMs in the future. Not only are they going to be potentially experiencing more frequent lethal stress events, but sessile organisms are experiencing higher temperatures, which could result in higher levels of energetic need during low tides. There is also the possibility that these organisms will no longer be able to rely on their movement behaviors to avoid thermal stress as temperatures continue to increase and thermal refuges become less available, and so quantifying operative environmental temperatures and thermal safety margins now will help give insight into how these communities may respond to climate change.

Chapter 1 Figures

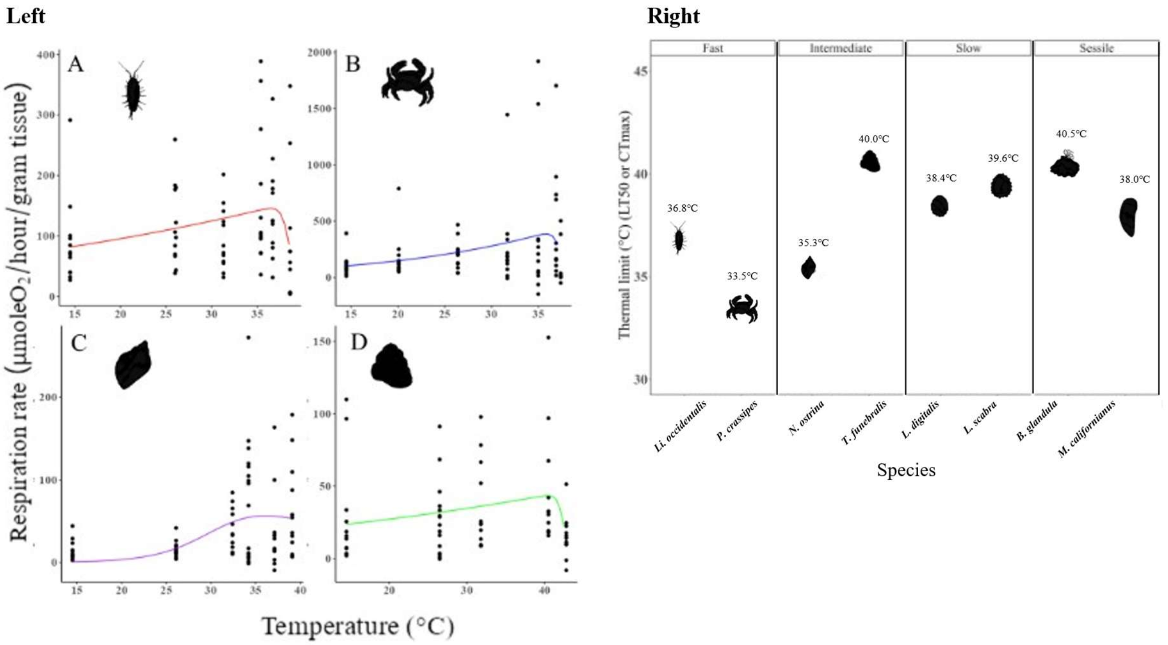

Figure 1: Left panel: Mass-adjusted mean respiration thermal performance curves for A) *Li. occidentalis,* B) *P. crassipes,* C) *N. ostrina,* and D) *T. funebralis.* Right panel: Thermal limits (LT_{50}, CT_{max}) of all species (*Li. occidentalis; P. crassipes; T. funebralis; N. ostrina* (all LT_{50}s, this study); *L. scabra* (CT_{max}, Miller et al. 2015)*; L. digitalis* (LT_{50}, Dong and Somero 2009)*; B. glandula* (LT_{50}, Ober et al. 2019); *M. californianus* (LT_{50}, Monaco et al. 2015).

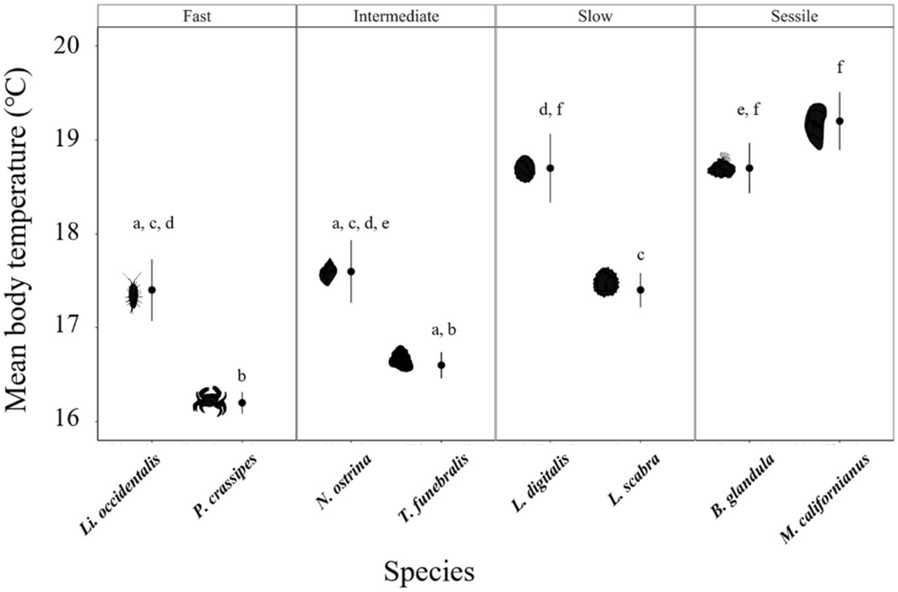

Figure 2: Average T_bs of species from field surveys during low tide. There was no statistical difference between the mobility classes (ANOVA; $F_{3,\,2278} = 4.2$; $P = 0.10$), but there was a difference between species within those classes (ANOVA; $F_{7,\,2274} = 22.05$; $P << 0.01$). Letters represent statistical similarity. Bars represent standard errors.

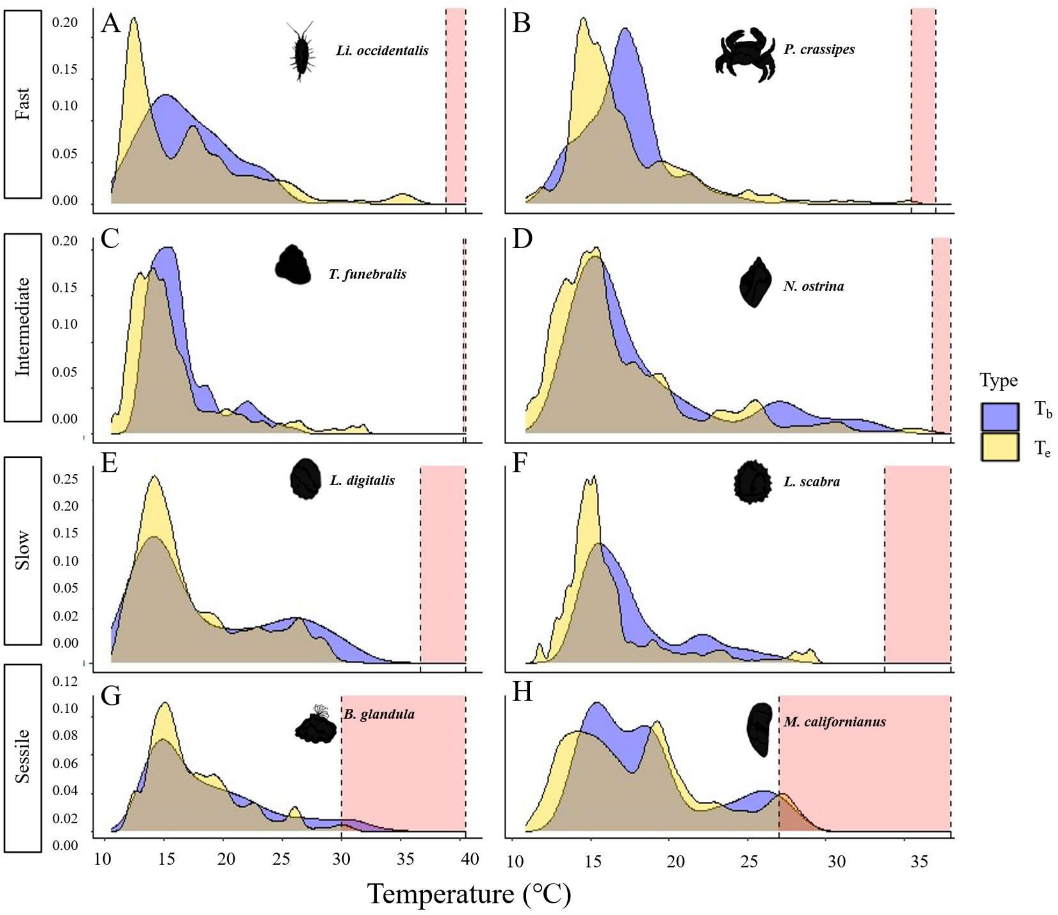

Figure 3: Densities of animal body temperatures (T_b) and operative temperatures of biomimics (T_e) based on field measurements during daytime low tides. The left edge of each shaded region is the temperature at which the species' respiration rate peaked, while the right edge denotes the species' thermal limits from this study or the indicated reference: A) *Li. occidentalis; B) P. crassipes; C) T. funebralis; D) N. ostrina; E) L. scabra* (CT_{max}, Miller et al. 2015)*; F) L. digitalis* (LT_{50}, Dong and Somero 2009)*; G) B. glandula* (LT_{50}, Ober et al. 2019); *H) M. californianus* (LT_{50}, Monaco et al. 2015).

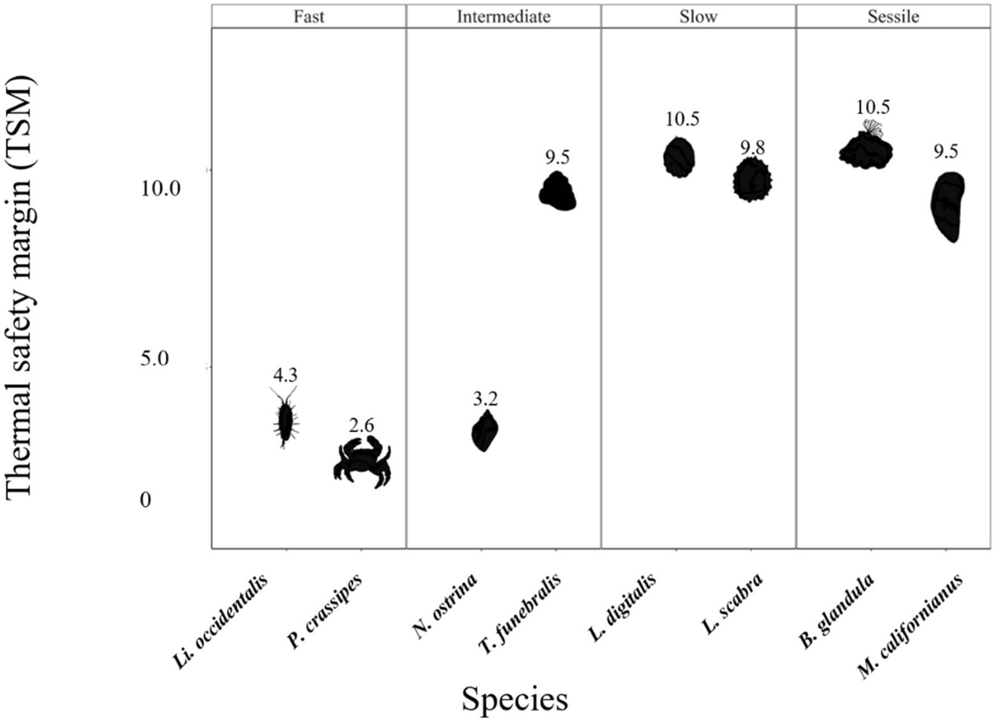

Figure 4. TSMs for each species, calculated by subtracting their thermal limits (CT_{max} or LT_{50}) from the 99th percentile of T_es in the field (*Li. occidentalis; P. crassipes; T. funebralis; N. ostrina* (all LT_{50}s, this study); *L. scabra* (CT_{max}, Miller et al. 2015)*; L. digitalis* (LT_{50}, Dong and Somero 2009)*; B. glandula* (LT_{50}, Ober et al. 2019); *M. californianus* (LT_{50}, Monaco et al. 2015).

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Supplemental material for McIntire LC & Miller LP. The role of mobility in intertidal invertebrates' responses to thermal stress

Supplement 1: Comparison of the internal and external body temperatures of fast species

Since we could not insert wires non-lethally into the body cavities of the isopod *Li. occidentals* and *P. crassipes* we did an initial comparison of their internal body temperatures and external carapace temperatures by inserting a thermocouple wire into their body cavity and gluing (Loctite™, Westlake, OH, USA) a thermocouple wire (type K, 36 gauge attached to an Omega HH508, Norwalk, CT, USA) to their carapace in the field (n = 8/species; *Li. occidentalis* mean difference: 0.47 ± 0.02°C; *P. crassipes* mean difference: 0.85 ± 0.22°C).

Supplement 2: Mimic building and validation

We used resin as it is a common filler for biomimetic models since it has similar thermal characteristics to organismal tissue (Hayford et al. 2021; PuDuo Resin, USA). *Li. occidentalis* mimics were made from black resin casts of the real animals. *P. crassipes* biomimetic models were a carapace filled with resin with a water filled sponge placed on top of a resin cast of a crab to allow for evaporative cooling. *P. crassipes* size impacted how quickly thermal transfer occurred, so smaller crabs were made from black resin and larger ones were made from clear resin. All other biomimetic models were constructed from the shells of the animal and filled with resin. For the gastropod mimics, we applied a thin layer of glycerol (glycerine and hydroxyethylcellulose, KY, NY, USA) between the rock and their resin "foot" to mimic the mucus layer of a live mollusc.

All biomimetic models were validated by comparing them to live organism temperatures (see figures below). We placed live animals side-by-side with biomimetics in the laboratory and in the field with thermocouple wires inserted in each. In the laboratory, we used reptile heat lamps to capture a wide temperature range (from 12-35℃, except for *P. crassipes*, which died at 35℃, those trials stopped at 30℃). In the field we deployed biomimics and live animals for three hours after low tide and recorded temperature readings of the animals and biomimetic models every minute (n=8 /species).

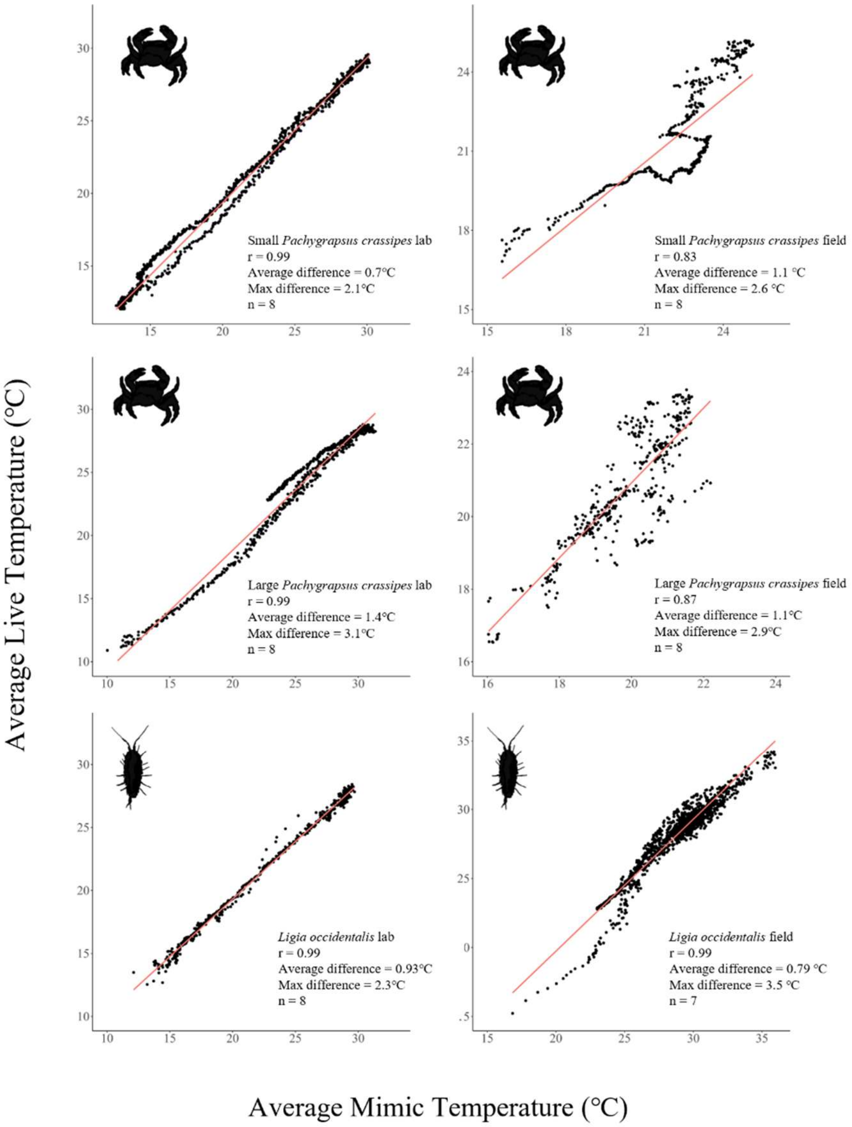

Figure S2A: The relationship between biomimic temperatures and live animal temperatures from both indoor heat lamp trials (left column) and outdoor field trials (right column) is shown for the two fast-moving species. Eight live animals and 8 mimics were placed together either in the laboratory or in the field with thermocouple wires embedded in both. Temperatures were taken every 5 seconds over the course of 2 hours in the lab and 1 hour in the field. Points represent the average temperature of 8 mimics and 8 live animals at a given time point. The red line indicates a 1:1 relationship, so points falling below the line indicate that the biomimic was cooler than the live animal.

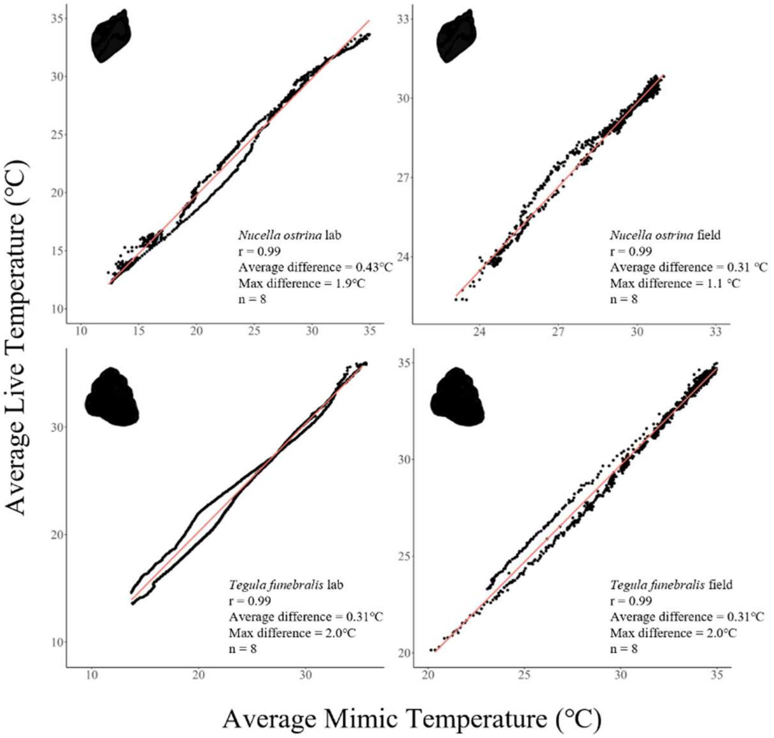

Figure S2B: The relationship between biomimic temperatures and live animal temperatures from both indoor heat lamp trials (left column) and outdoor field trials (right column) is shown for the two intermediate species. Eight live animals and 8 mimics were placed together either in the laboratory or in the field with thermocouple wires embedded in both. Temperatures were taken every 5 seconds over the course of 2 hours in the lab and 1 hour in the field. Points represent the average temperature of 8 mimics and 8 live animals at a given time point. The red line indicates a 1:1 relationship, so points falling below the line indicate that the biomimic was cooler than the live animal.

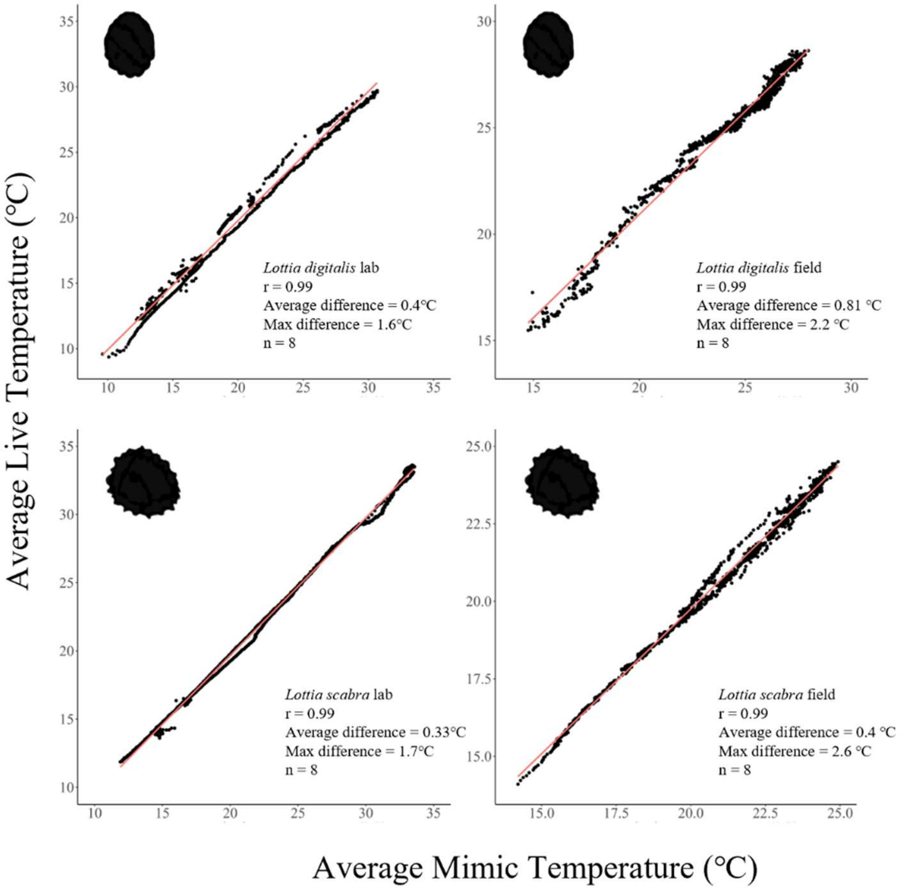

Figure S2C: The relationship between biomimic temperatures and live animal temperatures from both indoor heat lamp trials (left column) and outdoor field trials (right column) is shown for the two slow-moving species. Eight live animals and 8 mimics were placed together either in the laboratory or in the field with thermocouple wires embedded in both. Temperatures were taken every 5 seconds over the course of 2 hours in the lab and 1 hour in the field. Points represent the average temperature of 8 mimics and 8 live animals at a given time point. The red line indicates a 1:1 relationship, so points falling below the line indicate that the biomimic was cooler than the live animal.

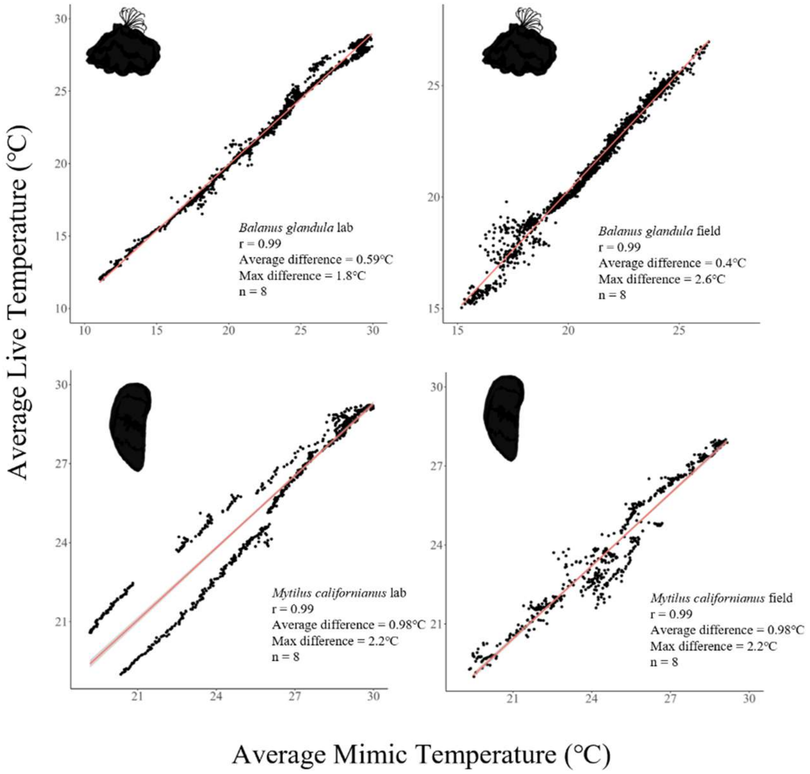

Figure S2D: The relationship between biomimic temperatures and live animal temperatures from both indoor heat lamp trials (left column) and outdoor field trials (right column) is shown for the two sessile species. Eight live animals and 8 mimics were placed together either in the laboratory or in the field with thermocouple wires embedded in both. Temperatures were taken every 5 seconds over the course of 2 hours in the lab and 1 hour in the field. Points represent the average temperature of 8 mimics and 8 live animals at a given time point. The red line indicates a 1:1 relationship, so points falling below the line indicate that the biomimic was cooler than the live animal.

Supplement 3: Results for respiration trials by species. Asterisks symbolize significance α < 0.05.

Li. occidentalis Tukey pairwise comparison results

Temperature comparison	**Estimate**	**Std. Error**	**df**	**z value**	**Pr(>|z|)**
14.5 - 26.1C	21.72	124.57	11	168.02	0.99
14.5 - 31.3C	6.43	97.01	11	109.88	1.00
14.5 - 35.4C	70.87	32.58	11	174.31	0.31
14.5 - 38.6C	0.68	104.12	11	102.77	1.00
26.1 - 31.3C	15.29	161.58	11	131.01	1.00
26.1 - 35.4C	49.15	97.15	11	195.44	0.87
26.1 - 38.6C	22.40	168.69	11	123.90	0.99
33.3 -35.4C	64.44	39.01	11	167.88	0.40
31.3 - 38.6C	7.11	110.55	11	96.34	1.00
35.4 - 38.6 C	71.54	174.99	11	31.90	0.30

P. crassipes Tukey pairwise comparison results

Temperature comparison	**Estimate**	**Std. Error**	**df**	**z value**	**Pr(>|z|)**
14.5-20.1C	66.4	64.29	11	1.03	0.93
14.5 -26.4C	86.09	46.8	11	1.84	0.47
14.5 - 31.7C	160.47	115.04	11	1.40	0.77
14.5 - 35C	276.29	189.54	11	1.46	0.73
14.5 - 36.9C	324.52	145.02	11	2.24	0.24
14.5 - 37.4C	-30.64	57.01	11	-0.54	1.00
20.1 - 26.4C	19.69	69.1	11	0.29	1.00
20.1-31.7C	94.07	125.78	11	0.75	0.99
20.1 - 35C	209.89	196.24	11	1.07	0.92
20.1-36.9C	258.13	153.67	11	1.68	0.58
20.1 -37.4C	-97.03	76.39	11	-1.27	0.84
26.4-31.7C	74.38	117.8	11	0.63	1.00
26.1-35C	190.2	191.23	11	1.00	0.94
26.1-36.9C	238.43	147.22	11	1.62	0.62
26.1-37.4C	-116.72	62.39	11	-1.87	0.45
31.7-35C	115.82	218.21	11	0.53	1.00
31.7-36.9C	164.05	180.88	11	0.91	0.96
31.7-37.4C	-191.11	122.22	11	-1.56	0.66
35 - 36.9C	48.24	235.39	11	0.21	1.00
35 - 37.4C	-306.92	193.98	11	-1.58	0.65
36.9 - 37.4C	-355.16	150.77	11	-2.36	0.18

N. ostrina Tukey pairwise comparison results

Temperature comparison	Estimate	Std. Error	df	z value	Pr(>|z|)
14.5 - 26.1C	1.98	4.55	11	0.43	0.99
14.5 - 32.4C	24.90	8.31	11	3.00	0.02*
14.5 - 34.2C	53.41	18.01	11	2.96	0.02*
14.5 - 39.1C	48.34	16.85	11	2.87	0.03*
26.1 - 32.4C	22.94	8.07	11	2.84	0.03*
26.1 - 34.2C	51.43	17.91	11	2.87	0.03*
26.1 - 39.1C	46.37	16.74	11	2.77	0.04*
32.4 -34.2C	28.49	19.21	11	1.48	0.53
32.4 - 39.1C	23.43	18.12	11	1.29	0.66
34.2 - 39.1C	-5.07	24.17	11	-0.21	1.00

T. funebralis Tukey pairwise comparison results

Temperature comparison	Estimate	Std. Error	df	z value	Pr(>|z|)
14 - 26C	-0.83	12.49	11	-0.07	1
14 - 32C	7.73	13.72	11	0.56	0.98
14 - 40C	17.92	15.90	11	1.13	0.78
14- 44C	-13.19	11.36	11	-1.16	0.76
26 - 32C	8.57	11.04	11	0.78	0.93
26 - 40C	18.75	13.65	11	1.37	0.63
26 - 44C	-12.36	7.93	11	-1.56	0.51
32 - 40C	10.19	14.78	11	0.69	0.96
32 - 44C	-20.93	9.74	11	-2.15	0.19
40 - 44C	-31.11	12.63	11	-2.46	0.09

Supplement 4

Table S4: Chi-squared tests of independence comparing the distribution of live animals when compared to the amount of each habitat available in sampled transects.

Species	**$\chi 2$**	**df**	***P-value***
Li. occidentalis	28.52	3	<<0.01
P. crassipes	366.55	3	<<0.01
T. funebralis	58.42	3	<<0.01
N. ostrina	28.22	3	<<0.01
L. digitalis	58.12	3	<<0.01
L. scabra	63.23	3	<<0.01
M. californianus	11.59	3	0.01
B. glandula	75.28	3	<<0.01

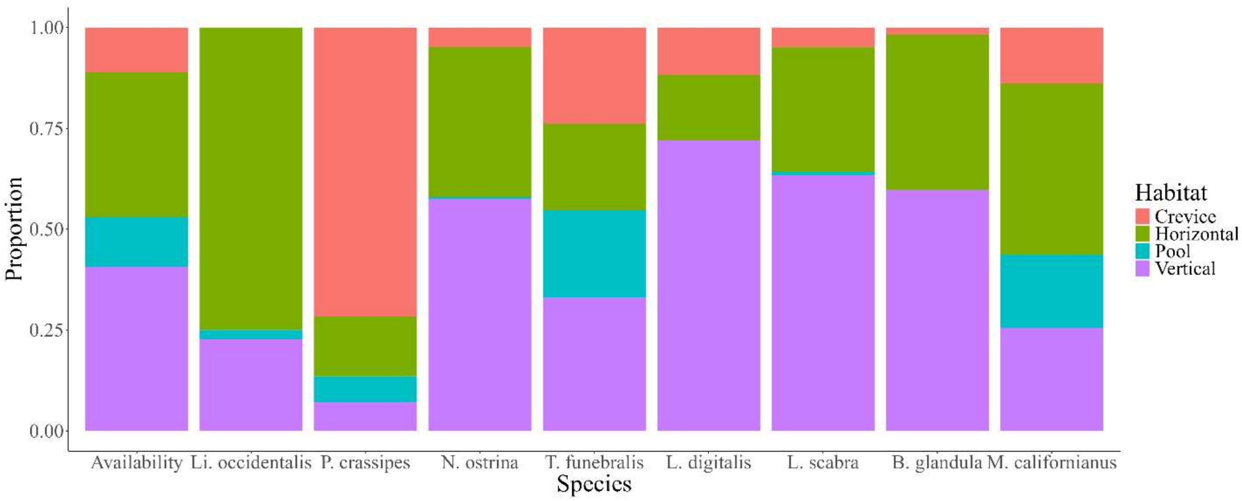

Figure S4: The proportion of habitats available at the field sites (“Availability”) in comparison to where our study species were found. At the sites, we quantified the number of available habitats (crevices, horizontal surfaces, vertical surface, and pools) using a 0.25m^2 quadrat on both sides of transects. Species’ habitat selection was recorded along the transects during the body temperature surveys.

Chapter 2

Quantifying the capacity for mobility to buffer or exacerbate the effects of climate change in the lined shore crab (*Pachygrapsus crassipes)*

Abstract

As climate change continues to progress, it is important to understand if species can acclimatize to elevated temperatures throughout their range and across seasons. Highly mobile organisms can exhibit the Bogert Effect, wherein organisms move among microhabitats that keep their body temperatures within a "safe" range most of the time, thus reducing the amount of selection for a physiological response to temperature. However, organisms must both be able to acclimatize and behaviorally stay below thermal limits to survive stressful temperature events, which is particularly important in the face of climate change. While the Bogert Effect has been well documented in terrestrial reptiles, it has yet to be shown in marine systems. In this study, we used *Pachygrapsus crassipes* – a highly mobile crab species – to measure if a marine species that must cope with large fluctuations in temperature on a temporal and geographic scale exhibits the Bogert Effect and/or physiological acclimatization. We compared body temperatures, environmental temperatures, thermal limits, and thermal safety margins between a thermally stressful part of the species' range (San Diego, CA) and a thermally benign part of the range (Bodega Bay, CA). To assess the degree of acclimatization we also compared thermal performance curves and thermal limits at the beginning and end of the summer in Bodega Bay, CA. We found that *P. crassipes* is not exhibiting the Bogert Effect but instead has higher body temperatures and higher thermal limits in San Diego than in Bodega Bay, and that there is acclimatization between seasons in Bodega Bay. Ultimately, the crabs have small thermal safety margins in both regions, leaving them at risk of rising temperatures due to climate change.

Introduction

As temperatures continue to increase as climate change progresses, ectotherms are at risk since environmental temperatures directly affect their body temperatures (Pinsky et al. 2019). Ectotherms will need to respond to increased temperatures both through behavior and physiological acclimatization (Muñoz 2022; Stellatelli et al. 2017). Behavioral thermoregulation through microhabitat selection can buffer organisms against elevated temperatures (Huey and Tewksbury 2009). Some organisms have demonstrated a reliance on behavior rather than physiology to cope with elevated temperatures and in some cases, have rarely experienced selection for an increased physiological response to stressful temperatures. This has been termed the Bogert Effect. To exhibit the Bogert Effect, animals must be selecting a narrower range of body temperatures than those available in their environment (Muñoz 2022; Huey et al. 2003). This range of temperatures will be within their "safe" range of temperatures that helps them maximize their performance; however, this has resulted in the lack of selection for organisms to have a physiological response to elevated temperatures (Huey et al. 2003; Bogert 1949). This phenomenon has been well documented in terrestrial systems, particularly in species of lizards (Muñoz 2022; Sunday et al. 2014; Buckley et al. 2013; Huey et al. 2003). While being able to maintain a precise body temperature has been beneficial historically, as climate change increases both extreme temperature events and average temperatures, this could potentially exacerbate the effects of climate change for these organisms if thermal refuges are not available since they lack the physiological mechanisms to compensate (Enriquez-Urzelai & Gvoždík 2024; Vinagre et al. 2018; Buckley et al. 2013).

Species will still need to be able to select safe thermal habitat in the face of climate change, but organisms could also benefit from plasticity in their thermal tolerances (Enriquez-

Urzelai & Gvoždík 2024; Gunderson and Stillman 2015). It will be increasingly important to study how organisms are able to acclimatize to elevated temperatures, since extreme temperature events in microhabitats may soon exceed species thermal limits (Huey and Kingsolver 2019; Stillman 2019; Stillman 2002). However, it has been demonstrated that there is more potential for physiological plasticity when there is less opportunity for behavioral thermoregulation (Muñoz 2022; Muñoz and Losos 2018; Gunderson and Stillman 2015), meaning that if organisms cannot behaviorally thermoregulate well, they will need to rely on physiological mechanisms in order to survive. Mobility is one key feature that can predict how well a species can behaviorally thermoregulate (Crickenberger et al. 2020). It has been demonstrated on the rocky shore in that organisms with higher mobilities have lower thermal limits and narrower thermal safety margins than the slower moving (i.e. snails and limpets) and sessile species (mussels and barnacles) in the same habitat (McIntire and Miller 2025). Consequently, it is important to test whether the Bogert Effect manifests in species and how that affects their physiological plasticity (Muñoz 2022; Buckley et al. 2015).

There are many tools to quantify how organisms are affected by temperature. One such tool is the thermal performance curve (TPC; Angilletta et al. 2002; Huey and Stevenson 1979). TPC's demonstrate the initial increase in ectotherm performance as temperatures begin to increase, but it will come to an eventual peak – a temperature or narrow range termed the thermal optimum - after which higher temperatures result in performance decreases, and the organism eventually dies. The temperature at which a population of organisms dies is often expressed using the temperature that is lethal for 50% of a sample of the species (LT_{50}). LT_{50}s and TPCs, in conjunction with operative (or environmental) temperatures from an organism's environment, can be used to measure how organisms are affected by temperatures in their environment

(Sunday et al. 2014). To exhibit the Bogert Effect, organisms must be selecting temperatures that are within their optimum range at all times (Fig. 1). To understand how organisms will be affected by climate change, it is important to combine all these aspects to measure both the Bogert Effect and the acclimatization potential of populations.

The rocky intertidal zone provides an ideal place to study how highly mobile organisms cope with dynamic temperature changes since during low tides animals are exposed to air temperatures that can fluctuate up to 20°C in just a few hours (Helmuth et al. 2011) and species' body temperatures can even rise above their thermal limits (Harley 2008). Environmental temperature variation in the intertidal, and consequently body temperature variation, exists at multiple different scales. At the microhabitat spatial scale (centimeters to meters), individuals must cope with different temperatures that can lead to mortality for some individuals, but not for others nearby (Miller and Dowd 2019). For example, within mussel beds thermal stress is greater near the surface and minor deep within the bed (Jurgens and Gaylord 2018). This variation in microhabitat temperature can be vast, and even within a few meters that variation can be as great as that expected at the regional scale over hundreds of km of latitude on a given day (Denny et al. 2011). Therefore, the rocky shore is a natural laboratory for studying the variation in thermal stress and thermal extremes within populations.

Thermal heterogeneity can also exist on larger scales that affect populations and species distributions. For instance, species can have a large latitudinal range so they are exposed to stressful temperatures depending on location, since populations that live on the edges of a species' range can experience more thermal stress than those at the center of their range (Sorte and Hoffman 2004). Thermal stress throughout species' ranges can also vary temporally, as the timing of the lowest – and most stressful – tides changes both over seasons and on a geographic scale (Helmuth et al. 2011; Harley 2008; Finke et al. 2007). For example, on a local scale, in northern California, summertime tides are during the early morning, while springtime tides occur at midday, making them the most stressful tides of the year (Harley 2008). Tidal timing also changes on a geographic scale. Along the west coast of North America, summertime low tides in southern regions (e.g. southern California) occur at night, but in more northern regions like the state of Washington they occur during midday (Helmuth et al. 2011; Mislan et al. 2009). This counterintuitively means that northern regions can experience more thermal risk in the summertime than those in more southern – and stereotypically warm – regions (Mislan et al. 2009). This creates a thermal mosaic along the west coast of the United States that can help us understand how populations in specific regions deal with variations in thermal stress throughout the year.

Shore crabs are an example of a highly mobile organism that can mitigate its thermal stress through microhabitat selection. For instance, the purple shore crab (*Hemigrapsus nudus*) will shuttle back and forth between cool tide pools and warm rocks to mitigate thermal stress during low tide (McGaw 2003). The Bogert Effect has not yet been documented in populations of shore crabs, though they have the potential to exhibit it as a species that relies heavily on behavioral thermoregulation in the form of microhabitat selection (McIntire and Miller 2025). The lined shore crab (*Pachygrapsus crassipes*) is an amphibious crab that ranges from Oregon, USA to Baja, MX (Roberts 1957). It lives in the intertidal zone, in which many other crab species are living close to their thermal limits (Stillman 2002). They also have a wide geographic range, so they experience different thermal regimes based on location. *P. crassipes* provides a potential model species for understanding the effects of multiple stressors on a highly mobile intertidal invertebrate, as well as acclimatization on across spatial and temporal scales.

Our objective was to quantify if *P. crassipes* is exhibiting the Bogert Effect and if crabs are also acclimatizing to ambient temperatures. We did this by comparing the thermal physiology of *P. crassipes* and how crabs select thermal microhabitat between two distinct biogeographic regions: northern California (Bodega Bay, CA, USA) and southern California (San Diego, CA, USA). Additionally, to see if *P. crassipes* from the same population were acclimatizing, we measured the TPCs and LT_{50}s at the end of springtime - the most stressful time of year in Bodega Bay, CA (Harley 2008) - and early fall.

To achieve our objectives, we measured 1) live animal body temperatures (T_b); 2) operative (or environmental) temperatures (T_e) from biomimetic models; 3) physiological thermal limits in the laboratory (LT_{50}s); and 4) thermal safety margins (TSM) calculated from thermal limits and T_es. A TSM, expressed as the difference between a species' thermal tolerances and the extreme operative temperatures of their environment, provides a metric to estimate the vulnerability of organisms to both high and low temperatures within their environment (Sunday et al. 2014). T_es are typically measured with biomimetic models, devices that mimic the heating and cooling properties of the live organisms (Denny et al. 2011, Helmuth et al. 2011). Biomimetic models, in conjunction with laboratory-measured physiological responses to temperature, can help quantify species' TSM and therefore potential vulnerability to warming within habitats under climate change (Sunday et al. 2014). We predicted that crabs would exhibit the Bogert effect, which would reduce their ability to acclimatize, so crabs would have similar T_bs and LT_{50}s regardless of ambient temperatures in two distinct regions and crabs would have similar LT_{50}s between seasons.

Methods

Field sites

We conducted northern California field surveys at four sites in Bodega Bay: two on the Bodega Marine Reserve (Fig. 2; BMR, 38.31ºN, 123.07ºW) and two in Bodega Harbor (Fig. 2; BH, 38.32ºN, 123.06ºW). The intertidal zone at BMR is composed of granite benches that face predominantly west. Within the Harbor, it consists of granite riprap and a soft, muddy bottom that is sheltered from waves by Bodega Head. All locations experience semidiurnal mixed tides with the lowest low occurring in the early to mid-mornings in the summertime.

In southern California, we set up six sites in San Diego: four at Cabrillo National Monument (Fig. 2; CAB, USA, 32.67ºN, 117.24ºW) and two on Harbor Island (Fig. 2; HI, 32.43ºN, 117.12ºW). CAB consists of sand-stone substrates, while HI is within San Diego Bay and consists of granite riprap on a muddy bottom that is sheltered from waves by Point Loma. We had more sites in San Diego to increase the number of crabs we could measure, since during daytime low tides crabs are more scarce (McIntire, personal observation). San Diego during the fall, winter, and spring months experiences semidiurnal mixed tides with the lowest low occurring during midday. Summertime low tides occur primarily at night, so we did not sample during that time.

Microhabitat selection surveys

In both regions, we set up 40-meter transects at each site, in the upper/mid intertidal zone at shore heights between +1.52 and 2.13 meters above Mean Lower Low Water (MLLW).

We quantified the availability of microhabitat types (exposed surfaces, pools, and crevices) within 1 meter of the transect using a 0.25 m^2 quadrat to quantify the percent coverage along each transect (n = 160 quadrats/site).

Body temperature surveys

Surveys in Bodega Bay were carried out in the late spring to late summer (June – August) from 2021-2024 and in San Diego from late summer to late spring (September – June) during daytime low tides lower than +1 m above MLLW that occurred during daylight hours (Northern California: 2021 n = 7, 2022 n = 18, and 2023 n = 10; San Diego: 2023 = 6; 2024 = 6; 2025 = 6). Since the lowest tides occur at night during the summer in SD, we chose to only monitor in San Diego when tides were during the day (fall, winter, and spring) and due to logistical constraints, we only monitored in Bodega Bay during the summer when tides occur early morning. We quantified the T_bs and microhabitat selection of *P. crassipes* within a meter of the transect within three hours of the low tide.

Since *P. crassipes* would retreat deep into crevices if disturbed, we used a thermal imaging camera (FLIR Model TG267, Goleta, CA, USA; emissivity = 0.97) with a 2x lens attached so we could measure crab T_b from a distance, after making preliminary comparisons of internal body temperature versus external temperatures (McIntire and Miller 2025).

In addition to in person surveys, we also recorded the crabs using timelapse video recorded on an action camera (apeman, Longgang, Shenzhen, China). The timelapse was analyzed in ImageJ (Schneider et al. 2012) by using the box tool to track individual crabs within the frame and they were categorized as exposed, sheltered, or in a pool.

Biomimetic models (T_es)

We designed and built *P. crassipes* biomimetic models to measure environmental temperatures (T_es). These were a carapace filled with resin with a water filled microfiber sponge placed on top of a resin cast of a crab to allow for evaporative cooling. *P. crassipes* size impacted how quickly thermal transfer occurred, so smaller crabs were made from black resin and larger ones were made from clear resin (McIntire and Miller 2025). Biomimetic models were validated by comparing them to live crab temperatures and they were on average within ~1°C of the live animals (McIntire and Miller 2025).

Respiration rate measurements

In the laboratory, we quantified *P. crassipes* respiration rates in air with closed chamber respirometry. Crabs were captured from the field, tagged using Bee Tags (BetterBee®, Greenwich, NY, USA), and placed in a flow-through aquarium held at 12-14.5°C (monitored with Onset HOBO Tidbit Water Temperature Logger, USA) for at least 1 hour before being tested to give them time to recover from handling stress. All organisms were tested within 72 hours of capture to avoid acclimation.

The respiration chambers were aluminum containers (volume = 52.3mL) with a paper towel (4 cm^2) soaked with 2mL of seawater to keep humidity near 100%. For smaller individuals, we used resin blocks to reduce the volume of air in the chamber so crabs would be able to measurably reduce oxygen in the chambers (volume = 8 – 35mL). We submerged the respiration chambers in water baths (ThermoFisher Scientific, Waltham, USA) that started at 14.5°C that were then heated at a rate of 8°C $hour^{-1}$ to the treatment temperature. The chambers had ports that were left open during the ramping period to allow air exchange and closed once the treatment temperature was reached, followed by a one-hour sampling period where oxygen sensor spots (Pt3, PreSens, Regensburg, Germany) placed inside the chamber were sampled using fiber optic cables attached to a data logger (oxy-4, PreSens). Twelve unique individuals were exposed to each temperature treatment (~14.5, 20, 26, 32, 34, 36, 37, 38°C). In Bodega Bay in the fall and in San Diego, we did not expose crabs to 38°C in the since all crabs died in the 37°C treatment. Treatments were done in random order to avoid any potential acclimatization that could have occurred over the course of the experiment. Temperatures inside the chambers were monitored with an iButton temperature logger (Thermochron, Sydney Australia). Each trial had an empty chamber that was used as a blank control and subtracted from each replicate. Sensors were calibrated with a two-point calibration using nitrogen gas and 100% oxygen saturation.

Thermal performance curves

Respiration data was analyzed in the rTPC package in R (Padfield et al. 2025). Thermal performance curves were fitted to the data for each location/season (Sharpe-Schoolfield; Smith et al. 2019).

LT_{50} and TSMs

We monitored mortality during respirometry trials to determine the temperature at which 50% mortality (LT_{50}) was achieved. If 100% mortality was not achieved, we then would increase the temperature treatment until complete mortality occurred (BB fall 37.4°C; BB summer 38.3°C; SD 37.3°C). LT_{50}s were calculated using the MASS package (Venables and Ripley 2002).

We calculated TSMs by subtracting the upper 99th percentile of T_es and species' thermal limits (LT_{50}). Negative numbers indicate that a microhabitat is not thermally safe for organisms, and crabs may need to avoid stressful T_bs, while positive TSM values indicate that temperatures typically do not exceed species' thermal limits (Sunday et al. 2014).

Data analysis

We calculated the frequency at which T_bs were within a range of stressful temperatures and at/above the thermal limits in the field. Stressful temperatures were defined based on the trial temperature when species' respiration rates peaked. We also quantified how often the biomimic T_es were within their stressful range and at/above species' thermal limits.

To compare T_bs between regions and microhabitats, we fit ANOVA models; however, the data violated the assumption of homogeneity of variances even after transformation, so we weighed each average proportional to its variance using the nlme package to (Pinheiro et al. 2025) in R (version 4.1.2, R Core Team 2021) before running the ANOVA. Microhabitat selection was compared using a χ^2 analysis of goodness of fit.

Results

Thermal performance

P. crassipes respiration rates in Bodega Bay did vary between seasons. At the end of spring, their respiration peaked at 33.6°C, while at the end of summer they peaked at 35.8°C (Fig. 3). In San Diego their respiration peaked at 34.7°C in the late spring (Fig. 3).

Additionally, crab LT_{50}s were different both seasonally and geographically. In Bodega Bay, at the end of spring before the summer surveys, they were 35.1°C, while at the end of summer they were 33.5°C. In San Diego, the LT_{50} was 36.1°C (Fig. 3).

Body and operative temperatures and microhabitat selection

On average, *P. crassipes* were cooler ($T_b = 16.2 \pm 0.12$°C) in northern California, but warmer ($T_b = 22.2 \pm 0.40$°C) in southern California (Fig. 4 and Fig. 5; $F_{1,619} = 207.23$; $P < 0.0001$). On average, microhabitat T_bs were also cooler in Bodega Bay than in San Diego (Fig. 4). Further, crabs were selecting microhabitat non-randomly in both regions (BB: $\chi^2 = 425.4$, df = 3, *P-value* << 0.001; SD: $\chi^2 = 93.9$, df = 3, *P-value* << 0.001).

In Bodega Bay, *P. crassipes* never experienced T_bs above their thermal limits or within their stressful range of temperatures, but biomimic T_es were above their thermal limits 0.5% and within their stressful range less than 0.01% of the time (Fig. 5A). *P. crassipes* in Bodega Bay respiration and lethal limits trials died over a wide range of temperatures, so their respiration peaked at a higher temperature than their LT_{50} (see Fig. 3). Conversely, in San Diego, *P. crassipes*' T_bs were above their thermal limits and within their stressful temperatures 2% of the time. Their T_es were above their thermal limits and within their stressful temperatures 1.5% and 1.6% respectively (Fig. 5B).

When left undisturbed and filmed with timelapse, the crabs in Bodega Bay were in exposed microhabitats 37% of the time, sheltered microhabitats 54% of the time, and in pools 9% of the time (n = 220; 525.5 hours of footage). Similarly, in San Diego crabs were exposed 32% of the time, sheltered 63% of the time, and in pools 5% of the time (n = 24; 135 hours of footage).

Crabs were selecting a narrower range of temperatures in both regions for T_bs than their T_es. In Bodega Bay their range of T_bs 15.4°C (Fig. 3, Fig. 4, and Fig. 5) which is 10.1°C narrower than the range of T_es available (25.5°C; Fig. 5A). Similarly, in San Diego their range of T_bs was 22.9°C (Fig. 3, Fig. 4, and Fig. 5), which was 6.6°C narrower than their T_es which were 29.3°C (Fig. 5B). Crabs had a higher range of T_bs and T_es in San Diego than in Bodega Bay (Fig. 3, Fig. 4, and Fig. 5).

Thermal safety margins

In Bodega Bay, the 99th percentile temperatures were above 32.9°C and in San Diego they were 39.3°C. Thermal safety margins were small, but positive in Bodega Bay (0.6°C), but negative in San Diego (-3.2°C). In exposed habitats in Bodega Bay their thermal safety margins were 0.7°C, but in San Diego they were -3.5°C. Sheltered habitats in both regions were positive. In Bodega Bay they were 10.9°C and in San Diego they were much smaller, but still positive at 1.9°C.

Discussion

P. crassipes is not exhibiting the Bogert Effect, since crabs must be selecting a similar range of body temperatures regardless of ambient temperatures (Fig. 1; Muñoz 2022; Buckley et al. 2015; Huey et al. 2003; Bogert 1949). Crabs were on average 6°C warmer in San Diego than they were in Bodega Bay, meaning that the crabs were not selecting the same T_bs in both regions (Fig. 3, Fig. 4, and Fig. 5). Crabs were selecting a range of T_bs in San Diego nearly the same their range of T_es in Bodega Bay, which further indicates that crabs are not exhibiting the Bogert Effect. While these temperatures were recorded during different seasons, we focused on only tides that occurred during the day. Further research directly comparing seasons could further elucidate the effects of climate change on *P. crassipes*. However, since our data suggests that crabs are not exhibiting the Bogert Effect, these crabs are potentially going to be buffered from climate change to an extent.

The Bogert Effect is known to hamper acclimatization, since the organism may experience less selection to acclimatize if they can buffer themselves from elevated temperatures by behaviorally modifying their body temperature (Muñoz 2022; Buckley et al. 2015). However, *P. crassipes* is acclimatizing across seasons within a population and between populations in two distinct geographic locations (Fig. 3). In summer in Bodega Bay, when tides occurred during the cooler part of the day, crabs had lower thermal limits (LT_{50}) than in the spring when tides occurred during midday (Fig. 3; Harley 2008). Crabs also had higher thermal limits and T_bs in San Diego, than either season in Bodega Bay (Fig. 5).

While we expected *P. crassipes* to be selecting T_bs similarly in both regions, there are some possibilities as to why this was not the case. First is that *P. crassipes* was selecting microhabitat (sheltered vs exposed) similarly in both regions when undisturbed, so it could be that crabs cannot select the same T_bs, since in San Diego even the sheltered crevices are much warmer on average and their thermal safety margins were much smaller than the ones in Bodega Bay. Sheltered habitats had positive thermal safety margins in both regions, but that does not mean that crabs were without risk. In San Diego, their thermal safety margins are very small which might mean that in San Diego crabs are at a higher risk as climate change progresses and warms those habitats further. Overall, *P. crassipes* needs to select habitat more carefully in San Diego than in Bodega Bay and climate change may further exacerbate thermal stress for the San Diego populations. Further studies measuring their thermal selection year-round in Bodega Bay are needed to fully understand how this species will be impacted in a more thermally benign part of their range.

Further, microhabitat selection may not only be due to thermal quality of microhabitats, since crabs may also be avoiding predators, seeking mates, or foraging for food. *P. crassipes* could move to a lower intertidal zone where there is less thermal stress, but it is possible that crabs must stay higher on the shore to avoid predators. Many species distributions in the intertidal are dictated by exposing themselves to thermal stress that their predators cannot cope with. For example, the mussel *Mytilus californianus* lives higher on the shore, where its seastar predator *Pisaster ochraceus* cannot access all the mussel beds due to thermal stress, thus providing a refuge from predation stress for the mussels (Monaco et al. 2015). Crabs may also be trying to access food or mates. For instance, species of fiddler crabs (*Uca pugilator)* will traverse dry hot terrain to access mates (Allen and Levinton 2014). It is possible that *P. crassipes* is selecting microhabitat to prioritize other needs in both regions and must be able to cope with higher temperatures to avoid predation or access food and mates. Therefore, it is important to understand what tradeoffs these crabs must make during thermally stressful seasons.

Further, life history might also explain why *P. crassipes* is not exhibiting the Bogert Effect. *P. crassipes* is a broadcast spawner (Morgan et al. 2011) and, therefore, must prepare its offspring for environments that might differ from those of the parents (Logan et al. 2012). Most species that have been studied for the Bogert Effect are terrestrial reptiles that have direct development (Buckley et al. 2015; Sunday et al. 2014; Huey et al. 2003). Therefore, further research into how reproductive mode affects the evolution of thermal physiology between populations is needed. Additionally, *P. crassipes* populations above and below Point Conception (a known biogeographic break) have different genetic structures despite being historically thought of as a homogenous population, but the variation is confounded by the south to north migration of adult individuals (Cassone and Boulding 2006). Therefore, crabs have a weak, but still present, difference in genetic population structure (Cassone and Boulding 2006). Overall, further research is needed to understand more about how reproductive strategies and genetic structure of populations affect the Bogert Effect in populations.

While *P. crassipes* does not exhibit the Bogert Effect, highly mobile species often do not face the same selection for thermal tolerance as their less mobile or sessile counterparts within a system (McIntire and Miller 2025, Crickenberger et al. 2020). Therefore, their ability to shuttle between microhabitat temperatures quickly could potentially buffer them from selection from more extreme temperatures (Huey and Tewksbury 2009; Kearney et al. 2009). While these crabs do have the capacity for acclimatization, it is worth noting that crabs still have small thermal safety margins, meaning that crabs could be at increased risk from climate change without further acclimatization potential (Sunday et al. 2014). Measuring the maximum limits of acclimatization still needs to be done to fully understand how these organisms will be impacted by climate change. Overall, while these crabs are not exhibiting the Bogert Effect, crabs may be selecting “safe” microhabitats well enough to buffer them from the need to have higher acclimatization and higher thermal limits like some of the species that inhabit the same ecosystem (i.e. mussels and barnacles; McIntire and Miller 2025).

Further research that looks at how *P. crassipes* microhabitat selection changes throughout seasons would help to further elucidate how well these organisms are selecting microhabitat throughout the year. It is worth noting that during the winter season in San Diego, *P. crassipes* becomes scarce in the intertidal zone until late spring (McIntire personal observation). Crabs also become less abundant in the springtime in Bodega Bay when tides are similarly occurring in midday (McIntire personal observation). This may be due to the increased risk of thermal stress during the daytime low tides that occur at that time of year. *P. crassipes* have been used as an indicator of microhabitat condition and this is possibly why the crabs become scarce (Morgan et al. 2006). Studies looking into what energetic tradeoffs *P. crassipes* may be making during times of the year when tides occur during more stressful times of the year (i.e. spawning, predation, or food availability) are needed to fully understand their microhabitat selection.

Overall, while our initial predictions were not correct and *P. crassipes* is not exhibiting the Bogert Effect, we did find that these crabs are able to acclimatize to a certain degree. This could potentially aid them under future climatic regimes (Huey and Tewksbury 2009). However, since their TSMs are so small in exposed habitats in Bodega Bay and negative in San Diego, it seems unlikely that crabs will be able to acclimatize enough to be able to survive climate change in the warmer parts of their range (Sunday et al. 2014). It seems likely crabs will have to either shift their range northward or migrate lower on the shore in order to survive elevated temperatures caused by climate change.

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Chapter 2 Figures and Tables

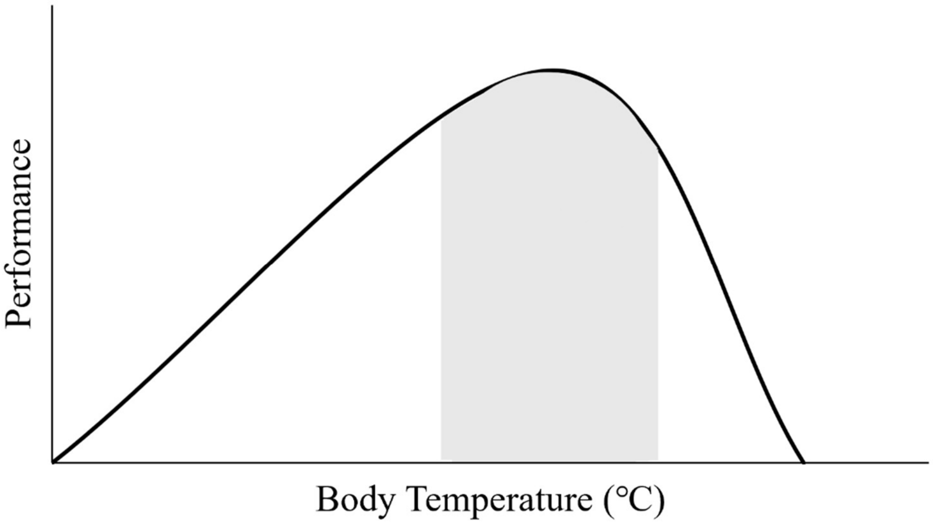

Figure 1: Theoretical thermal performance curve. The shaded grey region represents the range of body temperatures that the animal could be selecting in the field. To exhibit the Bogert Effect, animals must be selecting a range that is within their “safe” zone. Adapted from Buckley et al. 2015 and Huey et al. 2003.

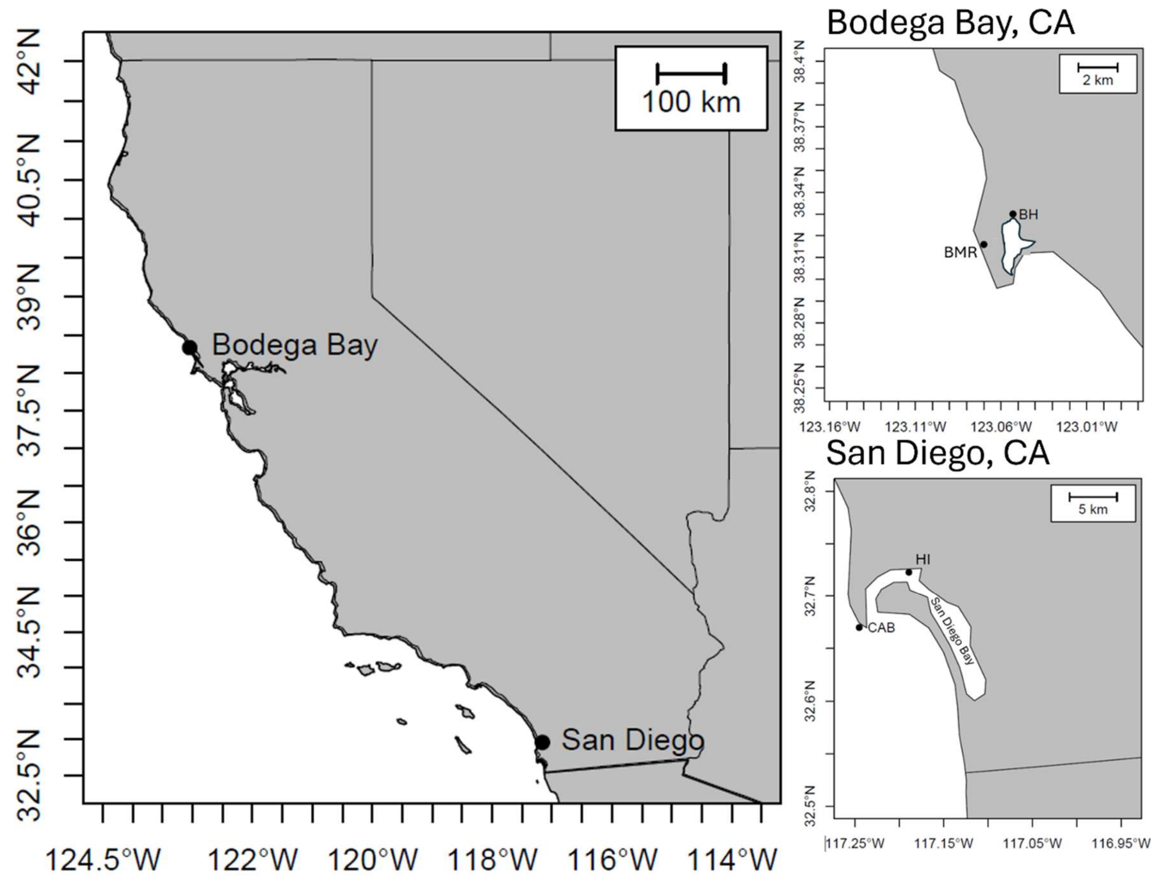

Figure 2: Map of field sites in Bodega Bay and San Diego, CA. Bodega Bay surveys were done at Bodega Marine Reserve (BMR, 38.31ºN, 123.07ºW) and in Bodega Harbor (BH, 38.32ºN, 123.06ºW). San Diego surveys were done at Cabrillo National Monument (CAB, 32.67ºN, 117.24ºW) and Harbor Island (HI, 32.43ºN, 117.12ºW).

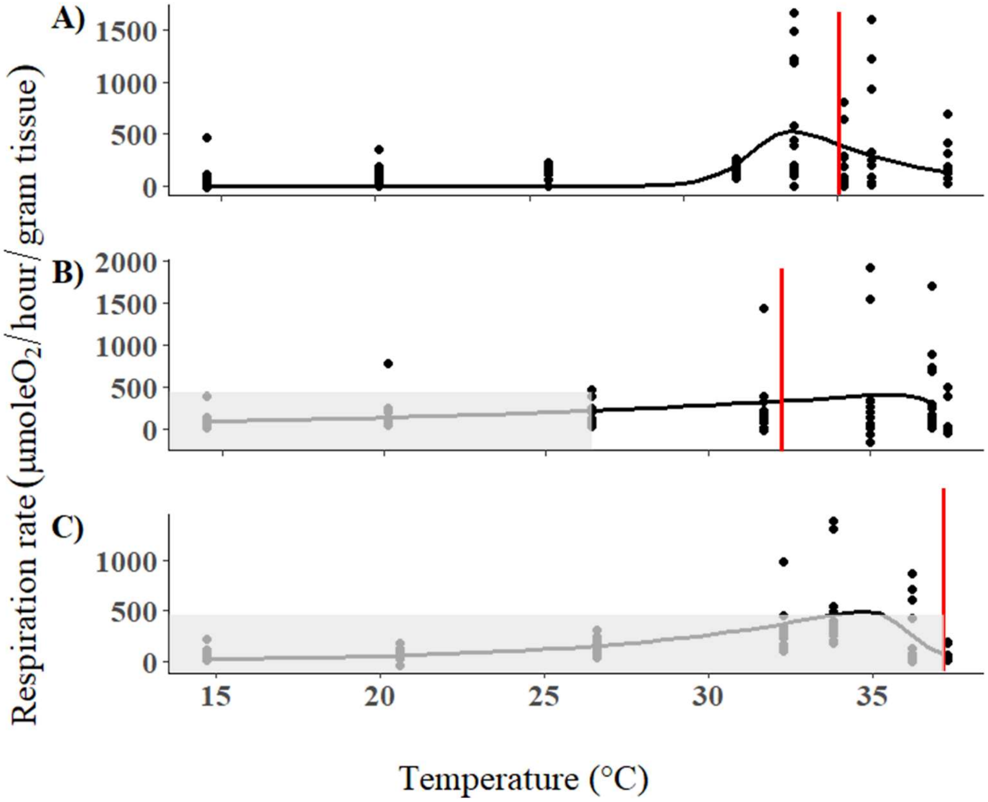

Figure 3: *P. crassipes* thermal performance curves of mass-adjusted respiration rates for A) spring in Bodega Bay, B) fall in Bodega Bay, and C) San Diego. T_{opt} is as follows: A) 33.57°C, B) 35.75°C, and C) 34.7°C. Red lines indicate LT_{50}s A) 35.1°C, B) 33.5°C, and C) 36.1°C. The shaded regions indicate the range of T_bs in the field (BB: 26.5-11.1°C; SD: 37.4-14.5°C). T_bs were not collected in spring in BB (A), so no data is available for shading.

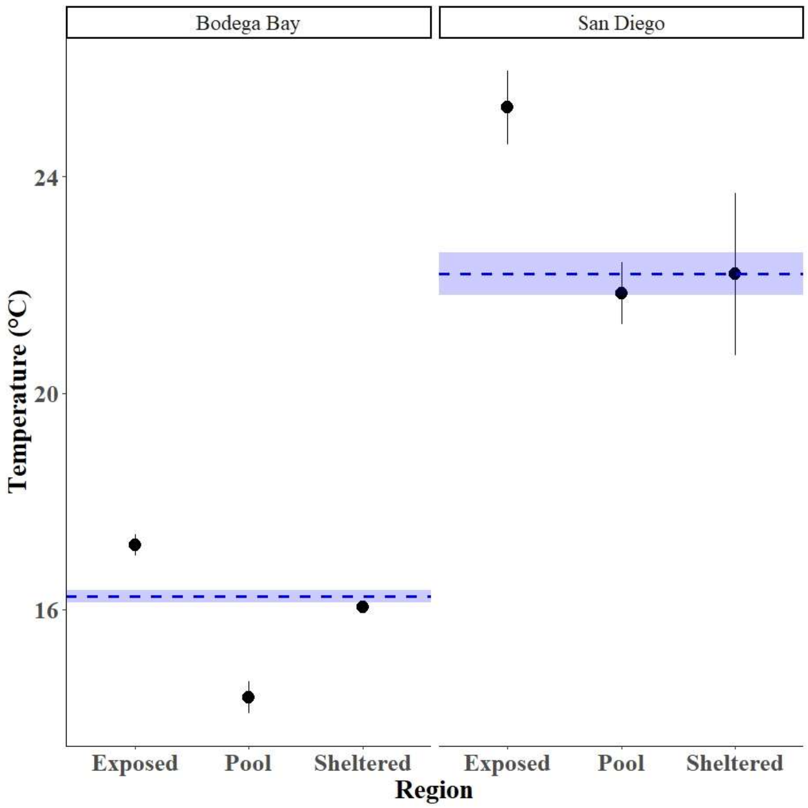

Figure 4: The average body temperatures of *P. crassipes* in exposed, pool, and sheltered microhabitats at northern and southern California field sites. Bars represent standard errors. Sheltered crevices: BB: 16.1 ± 0.1°C; SD 22.2 ± 1.5°C; Pools: BB: 14.4 ± 0.3°C; SD: 21.8 ± 0.6°C; Exposed BB: 17.2 ± 0.2°C; SD: 25 ± 0.7°C.

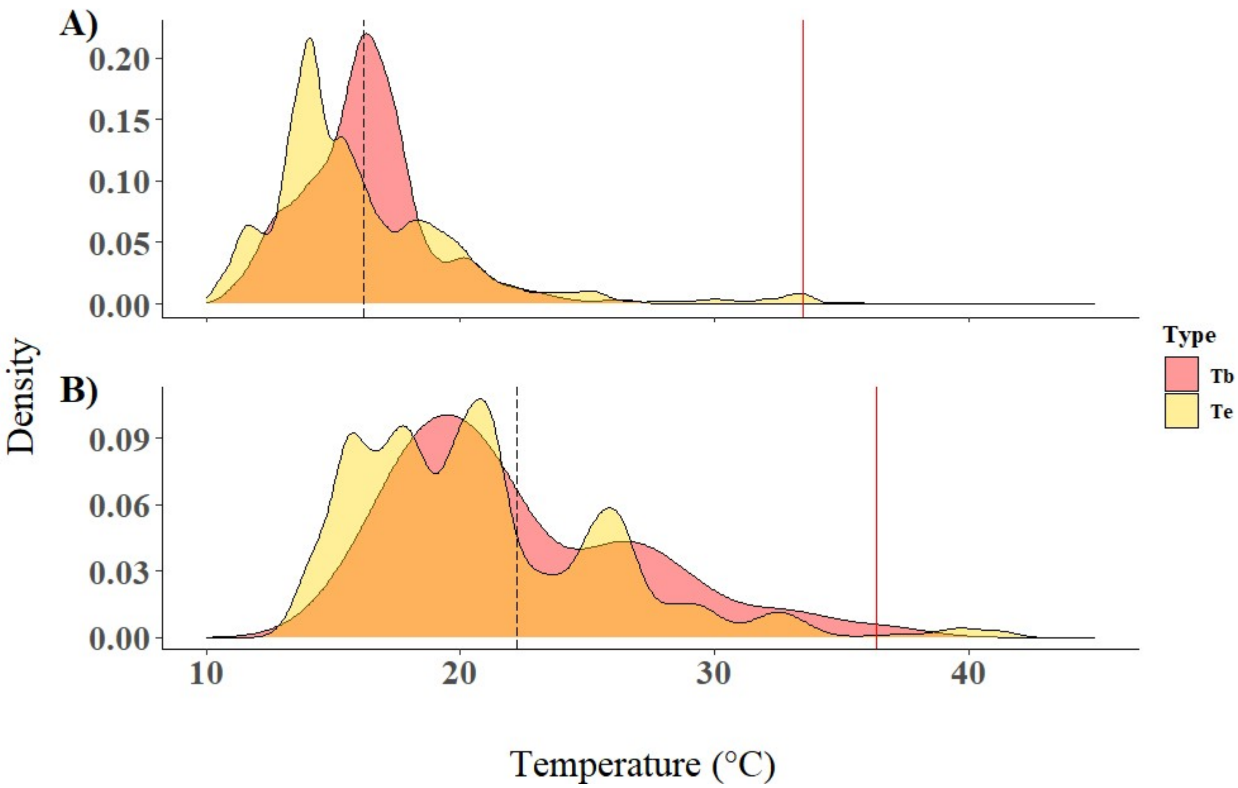

Figure 5: The densities of measurements for live crab T_bs and biomimic T_es in A) Bodega Bay throughout the summer and B) San Diego throughout the fall, winter, and spring. The dashed black line indicates the average T_b and the solid red line represents the LT_{50}.

Chapter 3

Evaluating the ability of a novel coastal armoring structure for providing thermal refuges for intertidal ectotherms

Abstract

Urbanization combined with climate change is reducing the amount of available habitat for species. In urbanized seaports, like San Diego Bay in California, USA, habitats have been transformed from tidal wetlands to hard coastlines lined with quarried riprap. These riprap installments were not originally built to sustain sea life and may not provide the most suitable habitat for organisms. In recent years, many managers have been working to increase the amount of suitable habitat for organisms while also balancing the economic and structural needs of urbanized ports and bays – this has been termed the "greening of grey infrastructure." In 2021, the Port of San Diego installed two installations of COASTALOCK, which are standardized rows of cast concrete tide pools. These novel coastal armoring structures differ from the existing riprap in terms of coloration, exposed and sheltered microhabitats, and have the addition of a pool. Our goal was to examine if these new structures provided added thermal refuges for organisms of differing mobilities when compared to the existing riprap. We achieved this by measuring how organisms of differing mobilities (*Ligia occidentalis* and *Pachygrapsus crassipes* [fast] and *Lottia limatula* [slow]) are selecting microhabitat and body temperatures in both the traditional riprap and this new coastal armoring technology. We quantified body temperatures of live organisms and operative temperatures using species-specific biomimetic models. We found that organisms were warmer in the riprap, particularly on sun-exposed surfaces, and thus had smaller thermal safety margins compared to the new concrete blocks. This suggests that these novel coastal armoring units are providing potential thermal refuge more effectively than the

existing riprap, which may be valuable as climate change continues to increase temperatures and organisms need access to more thermal refuges in order to survive.

Introduction

As climate change continues to increase extreme temperature events and average temperatures, it is important to understand how organisms select the temperatures in their environment. The availability of thermally favorable microhabitat is one of the driving factors for species distributions on a global scale (Sunday et al. 2011) since environmental temperature is one of the most important factors that affects the physiology of organisms (Angilletta et al. 2006). However, through urbanization of habitats, many organisms are losing access to thermally favorable microhabitats (Cryan et al. 2021). In recent years, the "greening of grey infrastructure" – creating structures that aid in both human and ecological uses – has become a topic of interest particularly in heavily trafficked ports and harbors (Hosseinzadeh et al. 2022; Dyson and Yocom 2015). Traditional seawalls and riprap may not provide sufficient substrate and microhabitat heterogeneity that allows animals to access thermally benign microhabitat (Chapman and Blockley 2009). Consequently, when designing new coastal armoring technologies, it is important to consider how the substrate and microhabitat complexity allow animals to behaviorally mitigate thermal stress (Cryan et al. 2021; Aguilera et al. 2019).

High environmental temperatures can have significant impacts on organismal energetic requirements through temperature-mediated impacts on metabolic rates, so access to thermally-favorable microhabitats may be a requirement for organisms to survive in a particular site (Sinclair et al. 2016, Bjelde and Todgham 2013). Particularly for ectotherms, coping with changes in temperature is energetically expensive (Laspoumaderes et al. 2022), since it can impact physiological function, which can have cascading effects on ecological functions, including access to food or mates (Kearney et al. 2009; Allen & Leviton 2014) Elevated environmental temperatures do not impact all organisms equally, since morphology and mobility can both affect how animals experience and cope with harmful temperatures (Crickenberger et al. 2020; McIntire and Miller 2025). For example, highly mobile organisms like crabs and isopods can have lower thermal limits and lower body temperatures on average than slower organisms like snails and limpets in the same habitat (McIntire and Miller 2025). Additionally, morphology can also play a role in a species' thermal experience; for example, limpet body temperatures are most affected by substrate temperatures since they have a large foot that connects to the rock (Denny et al. 2006). Overall, it is important to understand how animals of different mobilities and morphologies are coping with thermal stress to predict how organisms will react to climate change.

The rocky intertidal zone is one of the most thermally dynamic environments on earth since during low tides animals go from being immersed in stable temperature ocean water to being exposed to air temperatures that can fluctuate up to 20°C in just a few hours and even rise above species' thermal limits (Harley 2008). Habitat temperature is one of the main drivers of body temperature in the intertidal, and habitat temperatures can vary widely at small spatial scales. Rock crevices, tide pools, and biogenic structures such as algal canopy or mussel beds can provide shelters that are several degrees cooler than nearby sun-exposed surfaces (Denny et al. 2011, maybe some other relevant references here). Urbanized environments often consist of human-made structures that lack the complexity of a natural rocky shore, but it is still important to understand how intertidal organisms in highly urbanized environments mitigate thermal stress and how the type of substrate used in coastal armoring technologies may buffer or exacerbate the effects of elevated temperatures caused by climate change (Cryan et al. 2021).

Natural habitat in San Diego Bay has been reduced dramatically in the last century and what used to be tidal wetland is now primarily hard substrate like quarried riprap (Hennessey 1993). This riprap consists of smooth, dark colored rocks that are haphazardly arranged along the shoreline. In 2021, the Port of San Diego replaced two sections of traditional riprap with two installations COASTALOCK (CL; Econcrete, Brooklyn, NY) on Harbor Island in San Diego Bay, CA (Fig. 1A). These units are large, uniform concrete blocks (Fig. 1B) made with a relatively rugose surface at the centimeter scale that may help promote settlement and establishment of algae and invertebrates (Sella et al. 2021). These blocks differ from the existing riprap (Fig. 1C) in that they can be oriented to have a large pool of water (134 L) in the center and have purposely designed shelters for animals. While these blocks do provide microhabitat structure and pools of water for organisms, it is yet to be determined if these blocks will be able to buffer organisms from elevated temperatures like those caused by climate change.

Our objective was to expand on the Port's efforts of quantifying the function of the CL by comparing the thermal quality of the riprap and new CL installation and how temperature conditions in these two habitat types affect the microhabitat selection of animals of differing mobilities: shore crabs (*Pachygrapsus crassipes*) and western sea slater (*Ligia occidentalis*) [fast-moving]; and the file limpet (*Lottia limatula*) [slow-moving]. We evaluated this by comparing the body temperatures (T_bs) and operative temperatures (T_es) of species in the riprap and CL.

We predicted that the microhabitat heterogeneity in the CL will provide thermal refugia for the intertidal invertebrates of all mobilities in contrast with the traditional riprap. We hypothesized that faster-moving animals like *P. crassipes* and *Li. occidentalis* will be able to access similar temperatures in both substrate types, while the slower-moving *Lo. limatula* will benefit more from the added structure of the CL.

Methods

Sites

Harbor Island was created from dredgings in the 1960's inside San Diego Bay. Historically, it was a tidal wetland, but now it is predominantly quarried riprap. It experiences mixed semidiurnal tides, and the lowest tides occur at night during the summer and early fall, but during midday the rest of the year. It is sheltered from waves by Point Loma, but does experience some boat wake disturbance from recreational, military, and commercial boating.

Site set up

We set up four sites on Harbor Island. Within each site, we placed two permanent 20m transect lines, one in the high zone (approximately +1.5 m above mean lower low water [MLLW]) and one in the mid-zone (approximately +0.9m above MLLW) – these levels were determined based on the tidal height of the CL installations. The two original CL installations are 60 meters apart, so we placed the reference riprap sites 60 meters away from the CL installations for consistency (Fig. 1A). CL blocks are produced using a standard design, so that the blocks are all the same size and shape, and they are placed in a consistent orientation on the shore in the two deployment sites. On the CL, we categorized the types of microhabitats available into one of three categories: crevice, sun-exposed face, and pool. We used ImageJ to measure the percentage of the area taken up by each microhabitat type (Schneider et al. 2012). The rock riprap is not uniform, and so we quantified the types of microhabitats within one meter of the transect using percent cover surveys with a 0.5 m^2 quadrat as exposed rock faces and crevices. Due to the shape and arrangement of the riprap, no tide pools are available for animals to use.

Body temperature surveys

To quantify variation in microhabitat thermal quality between the CL blocks and traditional riprap we measured microhabitat selection and body temperatures of animals in two mobility classes: shore crabs (*Pachygrapsus crassipes*) and western sea slater (*Ligia occidentalis*) [fast]; and the file limpet (*Lottia limatula*) [slow]. We used an infrared camera (Fluke Ti480PRO, Everett, Washington, USA) to measure crab temperatures from a distance (McIntire and Miller 2025). Isopod body temperatures were measured using fine-gauge thermocouple wire pressed against the body since there is no way to measure internal temperatures non-lethally (McIntire and Miller 2025). For slower-moving limpets, a thermocouple wire was placed along the mantle cavity to directly measure body temperature.

Operative (environmental) temperatures

In order to measure the range of available microhabitat temperatures in the environment, we utilized species-specific biomimetic models – devices with internal temperature sensors that heat up and cool down at the same rate as the live animals - placed in each of the microhabitats available to the study species. These models provide *in situ* measurements of available body temperatures that animals could achieve in the different microhabitats during low tide, even if the animals are not currently occupying those microhabitats. *P. crassipes* biomimics were made from resin-filled carapaces glued to a resin cast of a crab (McIntire and Miller 2025). *L. occidentalis* biomimics were a black-colored resin cast of the live animals (McIntire and Miller 2025). Limpet mimics used a resin-filled shell with a thin mucus layer between the substrate and the mimic (McIntire and Miller 2025; Denny et al. 2006).

In addition to biomimetic models, we also placed temperature loggers throughout the intertidal in each microhabitat type (n = 5/site/microhabitat type; Onset HOBO Tidbit Water

Temperature Logger, Bourne, MA, USA; EnvLogger T7.3, Electric Blue, Porto, Portugal). Loggers were haphazardly placed using epoxy splash zone compound (A-788, Pettit Paint, Greensboro, NC, USA) for attachment in pools, crevices, and on sun-exposed surfaces from May 2024 until June 2025 (when daytime tides are the lowest and most stressful (Mislan et al. 2009)) and offloaded every few months.

Laboratory based respirometry

To quantify how environmental temperatures are affecting the animals physiologically, we measured the respiration rates of *P. crassipes* and *L. occidentalis* when exposed to elevated air temperatures in the laboratory. This was done using closed chamber respirometry to estimate oxygen consumption as a proxy for overall energetic demand during warm temperature exposure (Bjelde & Todgham 2013). Animals were collected from San Diego Bay, tagged with BeeTags (BetterBee®, Greenwich, NY, USA), and placed in stable temperature seawater (~14.5°C, monitored with an Onset HOBO Tidbit Water Temperature Logger, USA) for at least one hour to recover from handling stress. All animals were used within 72 hours of collection to avoid acclimation. They were then placed in aluminum chambers with two open ports to allow air exchange and a 4cm^2 paper towel soaked in 2mL of seawater to maintain near 100% humidity inside.

The chambers were submerged in a temperature-controlled water bath (Thermo Scientific Model AC200-A25B) that was held at 14.5°C for 15 minutes before the temperature was increased at a rate of 8°C/hour until desired temperature treatment was reached (14.5, 20.6, 26.6, 32.3, 33.8, 36.2, and 37.3°C). We monitored the temperatures inside the chambers with temperature loggers (iButtons, Thermochron, Sydney, Australia) to get the exact temperatures. *L. occidentalis* has higher thermal limits than *P. crassipes* (McIntire and Miller 2025) so we also exposed them to 39.1 and 41.1°C. Oxygen uptake was measured using sensor spots inside the chamber (PreSens Oxygen Sensor Spots PSt3, Regensburg, Germany) and fiber optic sensors (PreSens Oxy-4). Once the desired treatment was reached, the chambers were sealed, and organisms were held in the chamber at the target temperature for one hour. Individuals were exposed to a single treatment (n = 12/temperature/species). For *L. limatula,* thermal performance data from the literature was used to create the TPC (Miller et al. 2015).

Respiration rates were analyzed using the rTPC package in R (Padfield et al. 2025). A thermal performance curve was fitted to the respiration data for each species (Sharpe-Schoolfield; Smith et al. 2019). We then were able to calculate the temperatures at which respiration peaked for these organisms (T_{opt}).

Thermal limits and thermal safety margins

During respirometry trials, we also assessed the mortality of organisms to determine median lethal thermal death time (LT_{50}). At the end of each respiration trial organisms were removed from chambers and probed for responsiveness. If they did not react, they were presumed dead. LT_{50}s were calculated using the MASS package (Venables and Ripley 2002).

Miller et al. (2015) reported the critical maximum temperature (CT_{max}) for *Lo. limatula* as the temperature where locomotor function was lost (36.9°C). Our methods in determining death (lack of response) were comparable, so this value can be used as a substitute for LT_{50} for our purposes, although we note that the duration of the high temperature exposure was 1 h longer in the Miller et al study, which would likely yield a slightly lower CT_{max} value than our trials (McIntire and Miller 2025).

We calculated TSMs for both substrates by subtracting the maximum 99th percentile of T_es and species' thermal limits (LT_{50} or CT_{max}). Negative numbers indicate that a microhabitat is not thermally safe for organisms, and they may need to avoid stressful T_bs, while positive values indicate that temperatures typically do not exceed species' thermal limits (Sunday et al. 2014). Additionally, we calculated how often species T_bs and T_es were at or above their T_{opt} and their thermal limits for both substrates and the microhabitats within them.

Data analysis

T_bs between the substrates and microhabitats were compared on an individual species level using ANOVA. The data did not meet the assumptions of homogeneity of variances even after transformation, so we weighed each average proportional to its variance using the nlme package to (Pinheiro et al. 2025) in R (version 4.1.2, R Core Team 2021) before running the ANOVA. The data was then analyzed using a post-hoc Tukey test for significant ANOVAs. For *Li. occidentalis*, there were too few individuals found in sheltered microhabitats to run an analysis ($n < 4$), so they were only compared between substrates. Microhabitat selection was compared using a χ^2 analysis of goodness of fit.

Results

Respiration and LT_{50}s

Respiration rates for both measured species were dependent on body temperatures. *Li. occidentalis* respiration peaked at 36.83°C and declined after that temperature. Their LT_{50} was 38.9°C (Fig. 2A). *P. crassipes* had lower thermal thresholds as their respiration peaked at 34.7°C and their LT_{50} was 36.1°C (Fig. 2B). *Lo. limatula* respiration peaked at 35.5°C and their thermal limits were 36.5°C (CT_{max}; Fig. 2C; adapted from Miller et al. 2015).

Microhabitat selection

Li. occidentalis were found more often in exposed microhabitats most often in both riprap and CL substrate types, though only the habitat choice in CL was different from random (Fig. 3A; CL: $\chi^2 = 7.7$; df = 2; *P – value* = 0.02; riprap: $\chi^2 = 0$; df =1; *P – value* = 1.0). Isopods were never found in pools in the CL (Fig. 3A). Conversely, *P. crassipes* was significantly selecting sheltered habitats more often in the CL (Fig. 3B; $\chi^2 = 9.8$; df = 2; *P – value* = 0.01). Additionally, *P. crassipes* were found more often in pools than in exposed habitats where they were available in the CL (Fig. 3). In the riprap, they were not selecting habitat significantly different from random (Fig. 3B; $\chi^2 = 0.6$; df = 1; *P – value* = 0.45). Finally, *Lo. limatula* was found most often in sheltered microhabitats and pools in the CL, though this was not statistically significant (Fig. 3; $\chi^2 = 6.2$; df = 2; *P – value* = 0.05). In the riprap, they were found significantly more often in sheltered microhabitats than exposed ($\chi^2 = 35.3$; df = 1; *P – value* << 0.001).

T_bs and T_es

There was a statistically significant difference between the T_bs in CL and the riprap for all species. *Li. occidentalis* was on average 27±0.8°C in the CL, but in the riprap, they were 29.7±0.5°C (Fig. 4; ANOVA; $F_{1,34} = 21.6$; *P-value <<0.01*). No analysis was done to compare sheltered and exposed microhabitats due to low numbers of *Li. occidentalis* in sheltered microhabitats, so we could not compare the microhabitats. We were able to compare the exposed surfaces in the riprap and CL, and *Li. occidentalis* were warmer in exposed riprap when compared to CL exposed microhabitats (Fig. 4; Tukey HSD; *P-value <<0.01*).

P. crassipes was on average 22.3±0.6°C in the CL but were averaging 27.0±0.8°C in the riprap (ANOVA; $F_{1,85} = 22.29$; *P-value << 0.01*). *P. crassipes* T_bs in the pools were the coolest at 19.6±0.4°C (Fig 3). The significant differences between microhabitats were between pools and exposed riprap (Fig. 4; Tukey HSD; *P-value* << *0.01*) and exposed riprap and sheltered CL (Fig. 4; Tukey HSD; *P-value* << *0.01*) with the exposed riprap being warmer in both cases.

Lo. limatula was similarly cooler in the CL (19.9±0.3°C) than in the riprap (Fig. 4; 23.1±0.7°C; ANOVA; $F_{1,212} = 18.4$; *P-value* <<*0.01*). T_bs also differed by microhabitat and substrate type. T_bs in exposed microhabitats were significantly warmer in the riprap than in the CL (Fig. 4; Tukey HSD; *P-value* << *0.01*). Similarly, Tbs in sheltered microhabitats were also significantly warmer in the riprap than in the CL (Fig. 4; Tukey HSD; *P-value* = 0.04). *Lo. limatula* were also cooler in pools than in exposed CL (Fig. 4; Tukey HSD; *P-value* << *0.01*) and in sheltered riprap than exposed CL (Fig. 4; Tukey HSD; *P-value* << *0.01*).

Li. occidentalis had the highest incidence of being within their thermally stressful ranges. In exposed microhabitats T_bs were within their thermally stressful ranges and lethal limits 20% of the time. In sheltered microhabitats, *Li. occidentalis* were within their stressful ranges 33% of the time, but never above their lethal limits. It is worth noting that there were very few of these organisms in sheltered microhabitats, which is affecting how often they were exposed to their thermal limits. *P. crassipes* T_bs in the riprap were never above their thermal limits but were within their stressful range 4% of the time. Conversely, crab T_es were above their thermal limits 4% of the time and within their stressful range 7% of the time. In the CL, *P. crassipes* were never within their stressful range or lethal limits for either their T_bs or T_es. *Lo. limatula* T_bs were never above their thermal limits or within their stressful ranges in the CL or the riprap, but limpet T_es were within their stressful ranges 3% of the time in both exposed and sheltered microhabitats in the riprap.

For the substrate temperatures collected by temperature data loggers, exposed surfaces in the riprap were warmer than in the CL. The upper 99th percentile was 42.8°C (riprap) and 39.9°C

(CL) and maximum temperatures were 52.9°C and 49°C respectively (Fig 5). Conversely, sheltered microhabitats in the CL were warmer than in the riprap, where 99th percentile temperatures in the riprap were 30.1°C and maximum temperatures were 40.1°C, while in the CL they were 35.5°C and 44°C respectively (Fig 5). Pools were the coolest microhabitat with a maximum temperature of 34.4°C and a 99th percentile at 26.9°C (Fig 5).

Thermal safety margins

Thermal safety margins were higher for all species and all substrates within the sheltered microhabitats (Fig. 6; Table 1). *Li. occidentalis* had positive TSMs all microhabitats and substrates. In the riprap, *P. crassipes* TSMs were negative for both exposed and sheltered microhabitats, but in the CL, they were positive (Fig. 6; Table 1). *Lo. limatula* had negative TSMs in exposed microhabitats in riprap, but they were positive in sheltered microhabitats in the riprap and both microhabitats in the CL (Fig. 6; Table 1).

Discussion

Overall, the manufactured concrete COASTALOCK armoring units provided more thermally benign microhabitats for all our study species. The riprap experienced more extreme temperatures, particularly in the exposed microhabitats that reduced organisms' thermal safety margins (Fig. 6). This is likely due to the dark coloration of the riprap when compared to the CL, which is a lighter gray color. In the Caribbean, Leal et al. (2020) demonstrated the importance of substrate color by manipulating the coloration of the substate of settling barnacles. Barnacles grew faster on darker tiles but were at higher risk to thermal stress than their counter parts on lighter colored tiles (Leal et al. 2020). Microhabitat availability at our study sites is also important for species, since in both substrates, sheltered microhabitats were more thermally benign than sun-exposed microhabitats, thus reducing the thermal stress for organisms in those microhabitats (Fig. 5). It has been well documented in both natural (Jurgens and Gaylord 2018; Denny et al. 2011) and human-made microhabitats (Cryan et al. 2021) that availability of varied microhabitat types has a strong impact on providing thermal refugia for organisms. Therefore, both coloration and microhabitat availability are important factors that should be considered when managers are implementing new coastal armoring technologies.

Mobility and morphology also played a role in the thermal safety margins of our study organisms. For starters, *Li. occidentalis* is fast moving, and previous research has shown that more mobile species have lower thermal limits since they rely primarily on behavioral thermoregulation than physiological responses (McIntire and Miller 2025). However, *Li. occidentalis* had positive thermal safety margins in both microhabitats and substrates, meaning their relatively high thermal limit is buffering them from some thermal stress in both substrate types. It is worth noting that *Li. occidentalis* were within both their thermally stressful and lethal ranges fairly frequently in the riprap, but due to their fast movement, they are likely able to escape these stressful temperatures before they become lethal. *Li. occidentalis* may be experiencing these more elevated temperatures since their smaller body size means that they heat more quickly due to their lower thermal inertia (Rohr et al. 2018). *Li. occidentalis* were also predominantly found in exposed microhabitats, which is likely exposing them to higher instances of thermal stress than if they were utilizing sheltered microhabitats. It is possible that *Li. occidentalis* are not selecting microhabitat for thermal quality but instead seeking food or avoiding predation. Further research aiming to explain why *Li. occidentalis* more frequently selects thermally stressful microhabitats is needed to fully understand how these organisms are more often found in “unsafe” locations.

Our other fast species, *P. crassipes,* was selecting microhabitat more carefully than *Li. occidentalis* and was rarely found within its most stressful temperatures. The negative thermal safety margins of *P. crassipes* in both microhabitats in the riprap indicated that they are at higher risk of dying if they do not select microhabitats carefully. Since *P. crassipes* rarely selected microhabitats that were within their stressful temperature range, this suggests that they are relying on their ability to shuttle to non-stressful microhabitats to avoid thermal stress (McIntire and Miller 2025; Huey et al. 2003; McGaw 2003).

The slowest moving of our study species, *Lo. limatula,* was the most selective about microhabitat in the riprap. This may be due to the limpet's morphology, as their large foot that is in contact with the substrate, which is the primary form of heat transfer for most limpets (Harley et al. 2009). Since the exposed surfaces in the riprap are dark, and often warmer as a result, it is likely that the riprap is causing more heat transfer to these animals (Fig. 5; Leal et al. 2020). At locations where rock coloration is lighter, there may be a better match between the light-colored limpet and the background rock color. In northern regions, rock coloration is lighter and more closely resembles limpet coloration. While this possibly helps them avoid predation, the lighter rock color could reduce the heat transfer to the limpets from the rock (Denny and Harley 2006). Therefore, the darker coloration of the riprap may result in increased heat transfer to *Lo. limatula* compared to the lighter-colored CL. Despite the estimated negative thermal safety margins of *Lo. limatula* in the riprap based on the biomimetic models – meaning that they would be at risk in the most extreme high temperature scenarios – the live limpets were selecting thermally safe locations in all microhabitats and substrates. However, this observed distribution could be a byproduct of selection, where *Lo. limatula* that occupied surfaces that are too hot eventually died from exposure to elevated temperatures and were not present during our surveys in those microhabitats. Further, since *Lo. limatula* cannot shuttle between microhabitats quickly, their available microhabitat in the riprap was restricted to primarily sheltered microhabitats where their thermal safety margins are positive. This is most evident in their microhabitat selection where they predominately occupied sheltered microhabitats in the riprap (Fig. 3). In the CL their thermal safety margins are positive in both sheltered and exposed microhabitats, meaning that they can be less particular in their microhabitat selection since these surfaces do not reach the same high temperatures as the riprap as frequently (Fig. 5). Overall, the CL is allowing organisms to have larger thermal safety margins, which means the CL is currently providing a buffer from climate change.

One anomaly worth discussing is that the CL crevices did experience more stressful warm substrate temperatures based on surface-attached temperature logger data, which is counter to what we found with our biomimetic model data. These loggers were placed in the same crevices, but the biomimetic models were only left out for a few hours during low tide and intentionally placed within shaded areas in the CL crevices. It could be that the crevices that we chose in the CL are not always sheltered as the sun moves through the sky, since the CL is more uniform and the CL is oriented on a south-facing shore where the sun may shine into the crevice habitats as it transits east to west. Previous research has demonstrated the importance of microhabitat complexity for habitat use of ectotherms when constructing seawalls (Ushiama et al. 2019); consequently, it is important to create microhabitat complexity within new coastal armoring technologies. Overall, sheltered habitats still were cooler than the exposed surfaces in both substrate types (Fig. 5) and are still acting as a shelter from elevated temperatures.

The newly-created pools in the CL are also potentially providing a refuge for the animals as well; these pools provide a more stable microhabitat temperature than the crevices and exposed surfaces. However, many species in the intertidal have lower thermal limits in water than air (Bjelde et al. 2015; Bjelde and Todgham 2013). Variation in dissolved oxygen in tidepools when they are isolated from the ocean could be a potential stressor for organisms (Legrand et al. 2018). These pools do support an algal community that is likely to increase the dissolved oxygen in the pools through photosynthesis (Legrand et al. 2018) during the daytime, though at night when photosynthesis is not occurring the community respiration is potentially reducing the dissolved oxygen in these pools, which could have consequences for the communities in the tidepools (Legrand et al. 2018). Further, there could be other abiotic stressors in these pools, like changes in salinity. More research is needed to understand the dynamics of temperature, salinity, and dissolved oxygen in these pools over a wide range of conditions to understand if these pools can provide a thermal refuge while not eliciting other abiotic stressors.

In conclusion, the CL are providing thermally benign microhabitat for intertidal organisms in San Diego Bay. CL is not the only effort to this effect, as coastal communities in Australia and Florida, USA, have also installed these types of manufactured structures (Chapman and Blockley 2009; Suedel et al. 2022, respectively). These places have similarly found that consciously selecting substrate that provides microhabitat structure and a pool of water, increases the thermal refuges within this “grey infrastructure” (Chapman and Blockley 2009; Strain et al. 2018; Suedel et al. 2022). Overall, these structures are acting as a potential buffer for these organisms as they face increased temperatures from climate change, which is vital for organisms as climate change continues to progress.

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Chapter 3 Figures and Tables

Figure 1: A) Map of Harbor Island, San Diego, CA (32.724435, -117.206360); B) COASTALOCK installation; C) traditional riprap.

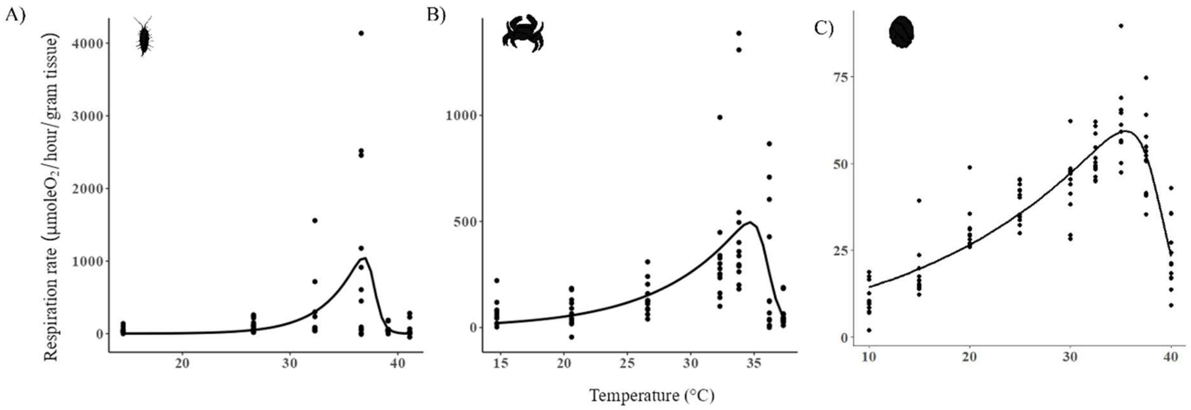

Figure 2: Mass adjusted thermal performance curves of aerial respiration for A) *Ligia occidentalis* (T_{opt} = 36.8°C and LT_{50} = 38.9°C); B) *Pachygrapsus crassipes* (T_{opt} = 34.7°C and LT_{50} = 36.1°C) measured in the laboratory; and C) *Lottia limatula* thermal performance and limits were taken from the literature (Miller et al. 2015; T_{opt} = 35.5°C and CT_{max} = 36.5°C).

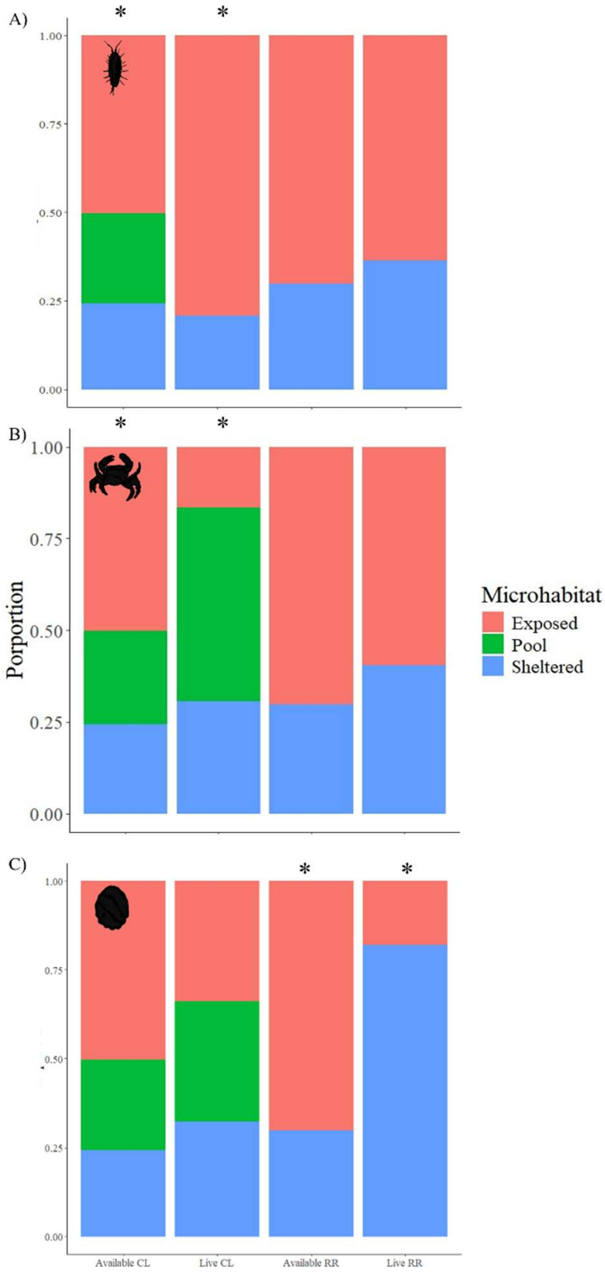

Figure 3: Microhabitat selection of A) *Li. occidentalis;* B) *P. crassipes*; and C) *Lo. limatula.* Asterisks indicate statistical differences from χ^2 analysis. “Available” is how much of each microhabitat is available at a given site and “live” is where the animals were found. CL is COASTALOCK and RR is riprap.

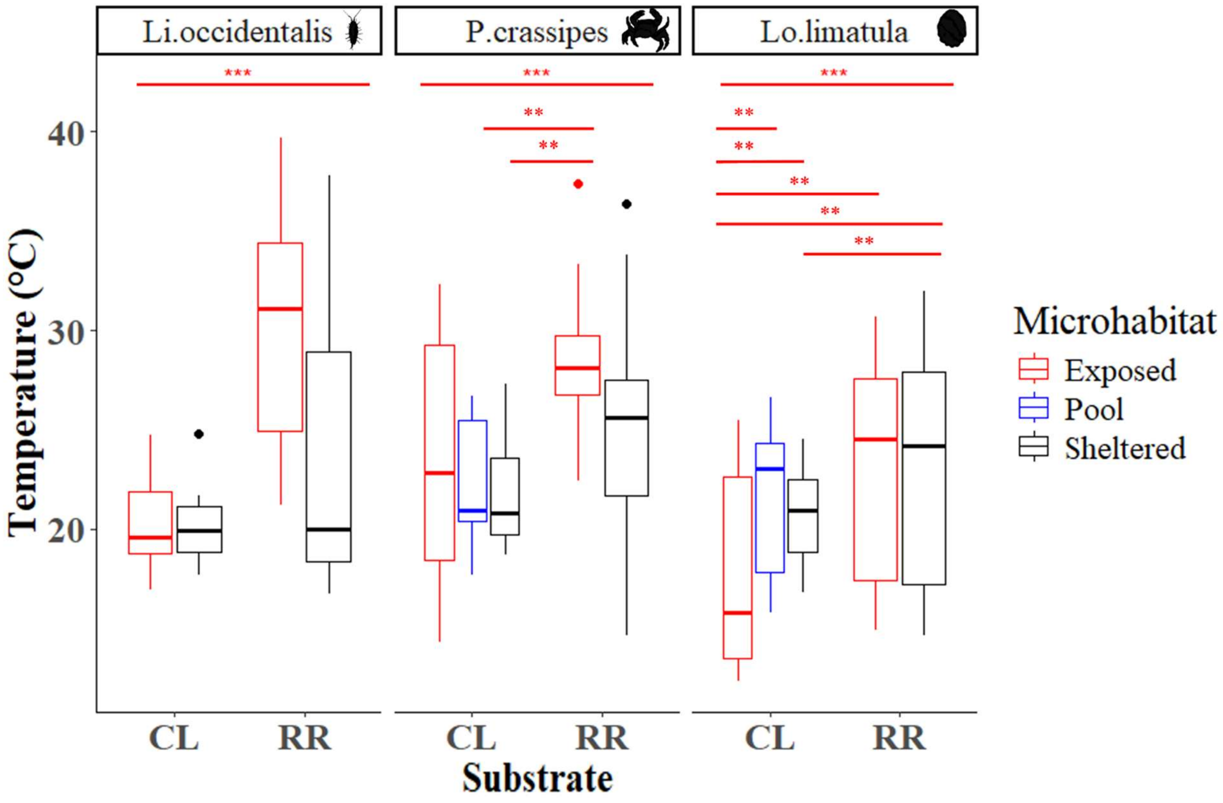

Figure 4: Boxplot comparing the body temperatures of *Li. occidentalis, P. crassipes,* and *Lo. limatula* in both CL and RR substrates and each microhabitat within the substrates. ** indicates a statistical difference between microhabitat and *** indicates a statistical difference between substrate types ($\alpha < 0.05$). Microhabitat comparisons could not be done for *Li. occidentalis* due to low sample size in the sheltered habitats in both substrate types (n < 4).

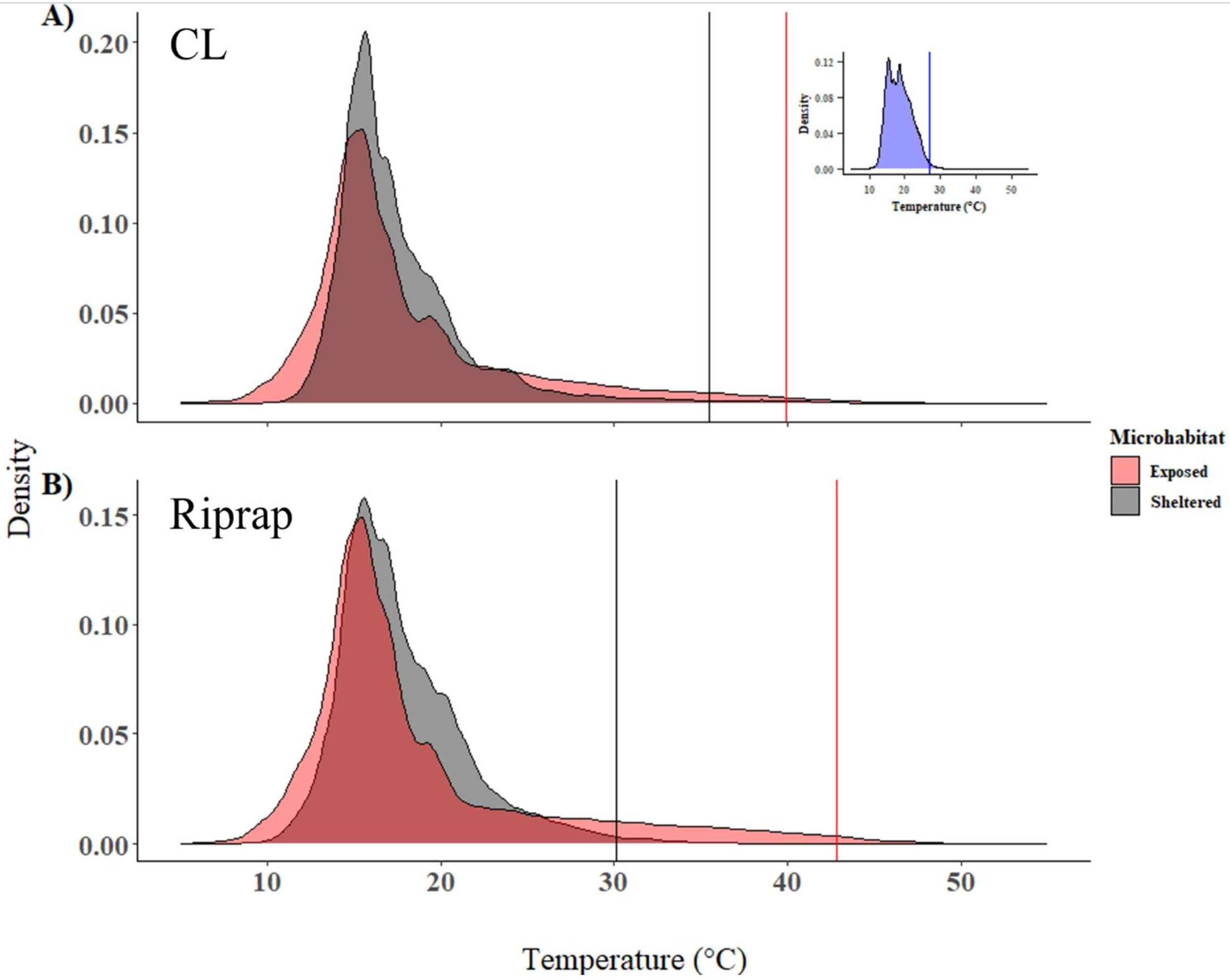

Figure 5: The density of substrate temperatures measured by installed temperature loggers in both substrate types A) CL and B) riprap in exposed (red) and sheltered (grey) microhabitats. Pool temperatures are inlayed in blue on the CL panel, the blue line is the 99th percentile of highest temperatures. Red lines indicate upper 99th percentile temperatures of exposed microhabitats and dark lines are the 99th percentile of the sheltered microhabitats.

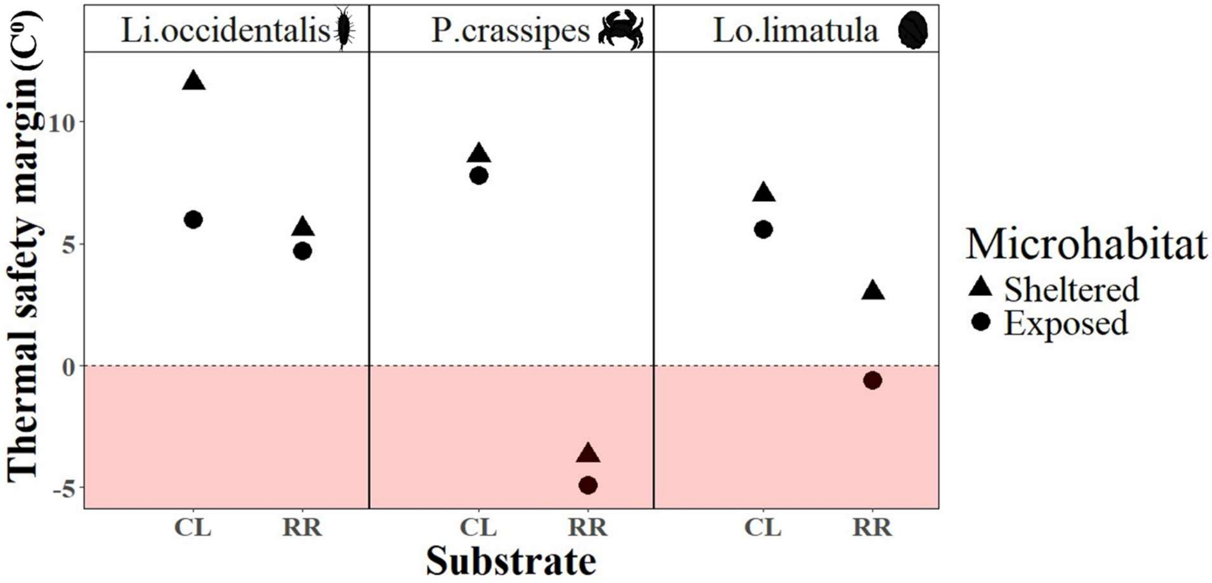

Figure 6: Thermal safety margins (Cº) of *Li. occidentalis, P. crassipes,* and *Lo. limatula* in both CL and RR substrates and each microhabitat within those habitats. Pools were excluded since the aerial thermal limits measured in this study will differ from thermal limits in water (Bjelde and Todgham 2013). Red indicates negative thermal safety margins, which means that animals are at risk of overheating in their environments, while white indicates positive values meaning that their habitat is overall benign (Sunday et al. 2014).

Table 1: The calculated thermal safety margins for each study species within each microhabitat and substrate type.

Species	**Substrate**	**Microhabitat**	**TSM (C⁰)**
Li. occidentalis	CL	Exposed	6
Li. occidentalis	CL	Sheltered	11.6
Li. occidentalis	Riprap	Exposed	4.7
Li. occidentalis	Riprap	Sheltered	5.6
P. crassipes	CL	Exposed	7.8
P. crassipes	CL	Sheltered	8.6
P. crassipes	Riprap	Exposed	-4.9
P. crassipes	Riprap	Sheltered	-3.7
Lo. limatula	CL	Exposed	5.6
Lo. limatula	CL	Sheltered	7
Lo. limatula	Riprap	Exposed	-0.6
Lo. limatula	Riprap	Sheltered	3