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ORIGINAL PAPER

Local-scale thermal history influences metabolic response of marine invertebrates to warming

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Abstract

As climate change continues, anticipating species' responses to rising temperatures requires an understanding of the drivers of thermal sensitivity, which itself may vary over space and time. We measured metabolic rates of three representative marine invertebrate species (hermit crabs *Pagurus hirsutiusculus*, periwinkle snails *Littorina sitkana*, and mussels *Mytilus trossulus*) and evaluated the relationship between thermal sensitivity (Q_{10}) and thermal history. We tested the hypothesis that thermal history drives thermal sensitivity and quantified how this relationship differs over time (short-term to seasonal time scales) and between species. Organisms were collected from tide pools in Sitka, Alaska where we also recorded temperatures to characterize thermal history prior to metabolic rate assays. Using respirometry, we estimated mass-specific oxygen consumption (MO_2) at ambient and increased temperatures for one individual per species per tide pool across three seasons. We evaluated relationships between thermal sensitivity and pool temperatures for time periods ranging from 1 day to 1 month prior to collection. For all species, thermal sensitivity was related to thermal history for the shorter time periods (1 day to 1 week). However, the direction of the relationships and most important thermal parameters (i.e., maximum, mean, or range) differed between species and seasons. We found that on average, *P. hirsutiusculus* and *L. sitkana* were more thermally sensitive than *M. trossulus*. These findings show that variability in thermal history over small spatial scales influences individuals' metabolic response to warming and may be indicative of these species' ability to acclimate to future climate change.

Keywords Climate change · Intertidal ecology · Marine invertebrates · Metabolic rate · Thermal history · Thermal sensitivity

Introduction

In this time of accelerating climate change, there is a crucial need to understand the processes that underly species vulnerability to warming. Environmental temperatures can greatly influence the rates of biological processes ("thermal sensitivity"), and the local conditions that organisms experience vary widely, creating a mosaic of physiological responses (Pörtner et al. 2001; Hochachka and Somero 2002; Angilletta Jr 2009; Huey et al. 2012; Pandori and Sorte 2021). Furthermore, organismal responses to climate warming can depend on previous thermal exposure ("thermal history") due to differences in allocation of energy to processes, such as thermal tolerance, growth, and metabolism (Calosi et al. 2008; Deutsch et al. 2015; van Denderen et al. 2020). Altered metabolic rates, themselves, can lead to changes in demographic rates (e.g., growth, reproduction), population sizes, and community structure and interactions (Angilletta and Sears 2000; Bartheld et al. 2015; Nelson et al. 2017). Therefore, it is essential to understand the spatial and temporal scales at which thermal history influences the sensitivity of physiological processes to warming.

The degree to which metabolic rates change with temperature (thermal sensitivity) is known to vary among life stages, individuals, populations, and species (Angilletta 2001; Vorhees et al. 2013; Careau et al. 2014; Pettersen et al. 2018; Pandori and Sorte 2019), and it is increasingly understood that thermal sensitivity can depend on thermal history. The effects of temperature exposure on thermal sensitivity of metabolic rates have been particularly well studied

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across large spatial scales (Steffensen et al. 1994; Irlich et al. 2009). For example, for Woolly Sculpins (*Clinocottus analis*), southern populations on the California coast experience warmer conditions and have greater individual variation in metabolic rates compared to more northern populations exposed to colder temperatures (Rangel and Johnson 2019). Links between thermal history and thermal sensitivity could be caused by either local adaptation or by acclimation (phenotypic plasticity) (Bennett et al. 2019) and are not universal: there were no differences in sensitivity between northern and southern populations of gypsy moth larvae (*Lymantria dispar L.*) (May et al. 2018). Importantly, less is known about the importance of small spatial and temporal scale variation in thermal history for thermal sensitivity; however, there is some evidence that this can lead to significant variation in thermal sensitivity between individuals within a single population. For example, high-shore intertidal limpets (*Lottia* spp.) that experience warmer and more thermally stressful conditions were estimated to have 5–14% higher respiration rates when compared to their low-shore counterparts inhabiting cooler habitats (Miller et al. 2015). To anticipate impacts of warming across populations as well as the ability of individuals to acclimate to changing temperatures, we need to understand the degree to which thermal sensitivity is driven by thermal history.

Thermal conditions can exhibit vast differences across time (e.g., seasonally) and space, including over small spatial scales (i.e., scales that encompass a portion of an entire population) (Braswell et al. 1997; Abraham et al. 2013), leading to large potential variation in individual thermal history. Across large spatial scales (i.e., encompassing entire populations), populations can experience different thermal conditions based on their latitude or elevation and seasonal shifts in temperature. For example, in freshwater streams from USA to Ecuador, organisms in temperate streams are exposed to greater seasonal thermal variation than those in tropical streams (Shah et al. 2017). Thermal conditions can also vary greatly between microhabitats within a single location in addition to over time. In freshwater ponds inhabited by the moor frog (*Rana arvalis*), the annual temperature range of ponds varied by 11 °C due to differences in canopy cover (Richter-Boix et al. 2015). The thermal conditions an individual experiences can, therefore, differ over space and time, and how this variation influences thermal sensitivity could be an indicator of responses to future climate warming.

This relationship between thermal history and thermal sensitivity of metabolic rates could also be influenced by traits of the species themselves, especially those such as mobility that affect ability to avoid stressful conditions (Menge et al. 2002; Halsey et al. 2015; Bennett et al. 2019). Sessile (non-moving) species can have limited ability to redistribute themselves after settlement and thus, to avoid thermal extremes, are limited to behaviors such as gaping and re-positioning in place which can modify body temperature to some degree (Miller and Dowd 2017). When avoidance of thermal extremes is not possible, individuals must rely on plasticity in thermal performance metrics such as via increased heat shock protein production (Petes et al. 2008), and other mechanisms for increasing the thermal maximum to allow their survival. For example, individuals of the Olympia oyster (*Ostrea lurida*) exhibited higher thermal performance (greater critical thermal maximum) under increasing temperatures when compared to two mobile oyster drill predators that can move to avoid thermal extremes (Cheng et al. 2017). However, there are also cases where sessile species—including habitat-forming species such as corals and mussels—are unable to maintain metabolic processes, such as respiration rates, after critical temperatures are reached and exhibit decreased respiration as well as increased mortality (Hoegh-Guldberg and Bruno 2010; Gazeau et al. 2014). In contrast, mobile species are better able to redistribute themselves to locations with more favorable thermal conditions, and, consequently, to alter their thermal conditions and avoid extreme temperatures (Hayford et al. 2018). Generally, individual body size and locomotion, as well as availability of local microhabitats, is likely to determine an individual's ability to alter their thermal environment (reviewed in Kearney et al. 2009; Crickenberger et al. 2020). Understanding whether the relationship between small-scale thermal variation and thermal sensitivity of metabolic rates differs between species will be useful in identifying traits that modify responses to warming.

Intertidal habitats are an ideal study system for evaluating the relationship between thermal history and thermal sensitivity of metabolic rates, because small-scale thermal variation occurs across tide-height elevation gradients due to daily tidal emersion (Menge and Sutherland 1987; Helmuth et al. 2006). Each tide pool in rocky intertidal habitats possesses a unique thermal environment that can be monitored over daily and seasonal time scales. Furthermore, many species living in rocky intertidal habitats are exposed to thermal conditions that are close to their thermal tolerance limits, meaning that individuals may be particularly vulnerable to changing temperatures (Somero 2002, 2010; Marshall et al. 2015). Intertidal communities are composed of species with differing abilities to behaviorally avoid thermal extremes, from sessile species (e.g., mussels, barnacles, and sea anemones) to mobile species (e.g., hermit crabs, periwinkle snails, and limpets) (Seed and Suchanek 1992; Crickenberger et al. 2020).

In this study, we evaluated the importance of both temporal and spatial scale in the relationship between thermal history and thermal sensitivity of metabolic rates for three different intertidal invertebrate species that vary in their mobility: the sessile Pacific blue mussel (*Mytilus trossulus*) and two mobile species, the Sitka periwinkle snail (*Littorina sitkana)* and hairy hermit crab (*Pagurus hirsutiusculus*). This study addressed three questions: (1) Does thermal history influence thermal sensitivity of metabolic rates at small spatial scales? (2) Does the relationship between thermal history and thermal sensitivity depend on time scale? (3) Does thermal sensitivity of metabolic rates vary between three species that differ in their mobility? Our approach integrates fine-scale temperature data across space and time with measurement of species-specific metabolic rates to quantify the relationship between thermal history and thermal sensitivity. Based on preliminary observations, we knew that thermal conditions varied between pools and seasonally. We also knew that sessile species (mussels) would spend the entirety of the study period within the pools, while mobile species would have the ability to move out of and between pools. For mobile species, we expected site fidelity on the order of days to weeks, based on work by Bates (2005) who recovered > 84% of snails after 12 days and Bertness (1981) who recovered ~ 75% of hermit crabs after 5 days. We hypothesized that thermal sensitivity is related to thermal history. Specifically, we predicted that this relationship would (1) be stronger for the sessile than mobile species, (2) be stronger at shorter than longer timescales, (3) lead to greater thermal sensitivity during colder months, and (4) lead to higher thermal sensitivity for sessile species (*M. trossulus*) as compared to mobile species (*P. hirsutiusculus and L. sitkana*). Our overarching goal was to evaluate how thermal sensitivity of metabolic rates responds to thermal history, in the context of predicting the ability of organisms to acclimate to climate warming.

Materials and methods

Study region and collections

Our study site was located on a rocky shoreline in Sitka, Alaska, USA, on the historic territory of the Tlingit people. The adjacent Gulf of Alaska experiences large seasonal temperature variation, with warmer temperatures during the summer months (June–August) and intense cooling during the fall (September–November) and winter (December–February) (Xiong and Royer 1984; Royer 2005). A total of 31 tide pools at John Brown's Beach, located on Japonski Island (57.06°N, 135.37°W) were used in this study. All pools were located between the mid- and high-intertidal zone at an average tide height (all values are mean ± 1 SE) of 2.46 ± 0.06 m, and volume of 12.60 ± 1.75 L (Fig S1, Table S1). In these tide pools, *Mytilus trossulus* is the most common sessile invertebrate (similar to abundance to barnacles), and *Littorina* and *Pagurus* spp. are two of the three most numerous mobile invertebrates (along with limpets) (Sorte and Bracken 2015).

We collected individuals of *M. trossulus*, *P. hirsutiusculus*, and *L. sitkana* at 3 seasonal time points (1) March 2019, (2) July 2019, and (3) September 2019, during which individuals of each species were collected across 2–4 days. Only individuals that were submerged were manually removed from the rock substrate, and adult mussels (size range 20.4–28.6 mm) were collected haphazardly from clumps. We collected no more than 1 individual per species per pool in each season; however, not all species were present in each of the 31 pools in each season (Table S1). Thus, for each species, the number of individuals collected was, respectively, as follows: *M. trossulus* (03/2019: $n = 16$; 07/2019: $n = 13$; 09/2019: $n = 13$)*, P. hirsutiusculus* ($n = 12$, 11, and 13), and *L. sitkana* ($n = 13$, 10, and 9). On each day of the experiment, we visited eight different tide pools, collecting one individual of a single species (i.e., all metabolism assays were conducted with a single species at one time). Specimens were placed in individual containers with seawater from their respective pools and immediately transferred to the Sitka Sound Science Center where metabolic assays took place within 3 h of collection.

Thermal history quantification

Thermal history of the organisms was calculated based on temperatures recorded at the pool level using HOBO TidbiT temperature loggers (Onset, Massachusetts, USA; ± 0.2 accuracy) that recorded temperature consecutively every 5 min from December 2018 to September 2019. Pool temperatures were summarized for the 1-month, 1-week, and 1-day periods preceding each seasonal collection for every individual. For each tide pool, we calculated the following thermal parameters: variance, minimum, mean daily minimum, 10th percentile, range, mean daily range, average, maximum, mean daily maximum, 90th percentile, mean daily 90th percentile, 95th percentile, and mean daily 95th percentile temperatures (Table S2, Fig. S4). To account for collinearity among thermal parameters, we used a Principal Component Analysis (PCA) using the *FactoMineR* R package (Lê et al. 2008) to reduce the dimensionality of the thermal history data set.

Metabolic rate trials

To measure metabolic rates of field-collected individuals, we recorded temperature-compensated oxygen consumption using the Pre-Sens PSt3 dissolved oxygen sensor spots, Pt100 temperature sensor, and system (PreSens Precision Sensing, Germany) and standard techniques (e.g., Paganini et al. 2014; da Silva et al. 2019; Killen et al. 2021). Sensor spots were directly glued to the lids of the acrylic chambers that were used in trials. Prior to the start of every oxygen consumption trial, sensor spots were calibrated using a two-point calibration method, first in an oxygen-free solution and second in an air-saturated water solution. Individuals were randomly placed in chambers (11.6 mL for *M. trossulus* and *P. hirsutiusculus* and 6.3 mL for *L. sitkana)* with a false bottom and stir bar to ensure water flow within each chamber. Chambers were submerged within a 16 L water bath sitting on top of stir plates. The water bath (using water from which the chambers were flushed between trails) was aerated throughout trials using an air pump (Tetra, Virginia, USA), and water was continuously circulated using an aquatic pump (Uniclife, Colorado, USA). Metabolic rate was measured at three temperatures (10 °C, 18 °C, and 26 °C), tested in order starting at 10 °C. Individuals were acclimated to the chambers and the water bath for 40–60 min, while temperature was lowered by 1 °C every 20 min using a mini Arctica 1/15 HP aquatic chiller (JBJ Chillers, Missouri, USA) from ambient seawater temperature until the first experimental temperature of 10 °C was reached (40–60 min). Oxygen concentration (mg L^{-1}) was recorded every 3 s until oxygen levels reached 80% saturation, and then, each chamber was flushed with fresh oxygenated seawater. One metabolic rate was calculated for every individual at each experimental temperature. Temperature in the water bath was then elevated 2 °C per h using a ceramic 200-Watt aquarium heater (Aqueon, Wisconsin, USA) until the next target temperature was reached, and the next round of oxygen consumption trials began. This rate of warming mimics the natural change in temperature over time within the tide pools at our field site (Fig. 1).

Once metabolic trials were run at all experimental temperatures, individuals were inspected for movement (i.e., closure of open *M. trossulus* shells, foot response or movement in *L. sitkana*, and movement in *P. hirsutiusculus)* to ensure if they were alive, and after removal from the chambers individuals were blotted dry to obtain mass (wet weight, g) and volume (mL), and then sacrificed in an ice bath. The mass and standard deviation of each species at the time of respirometry trials for each seasonal collection can be found in Table S4. Volume of individuals was calculated by filling a graduated cylinder and measuring the displaced water following the Archimedes principle. All individuals' wet tissues were removed from the shells, and wet tissue and shells were dried for 72 h at 60 °C and reweighed to obtain dry mass (Table S3). Prior to drying, *L. sitkana* were inspected for parasite infection (Ayala-Díaz et al. 2017); however, no parasitized individuals were found throughout this study.

A linear regression of oxygen concentration over time was used to determine the rate at which each individual consumed oxygen in each temperature treatment. The oxygen consumption rate (VO_2) was calculated from the slope of the regression line (all slopes used in the analysis had an $R^2 > 0.90$) and then converted into an hourly rate (mgO_2 L^{-1} h^{-1}). During each trial, one-to-two blanks (chambers containing only seawater) were also run to account for microbial oxygen consumption, and the average blank VO_2 for each run was subtracted from each individual's VO_2.

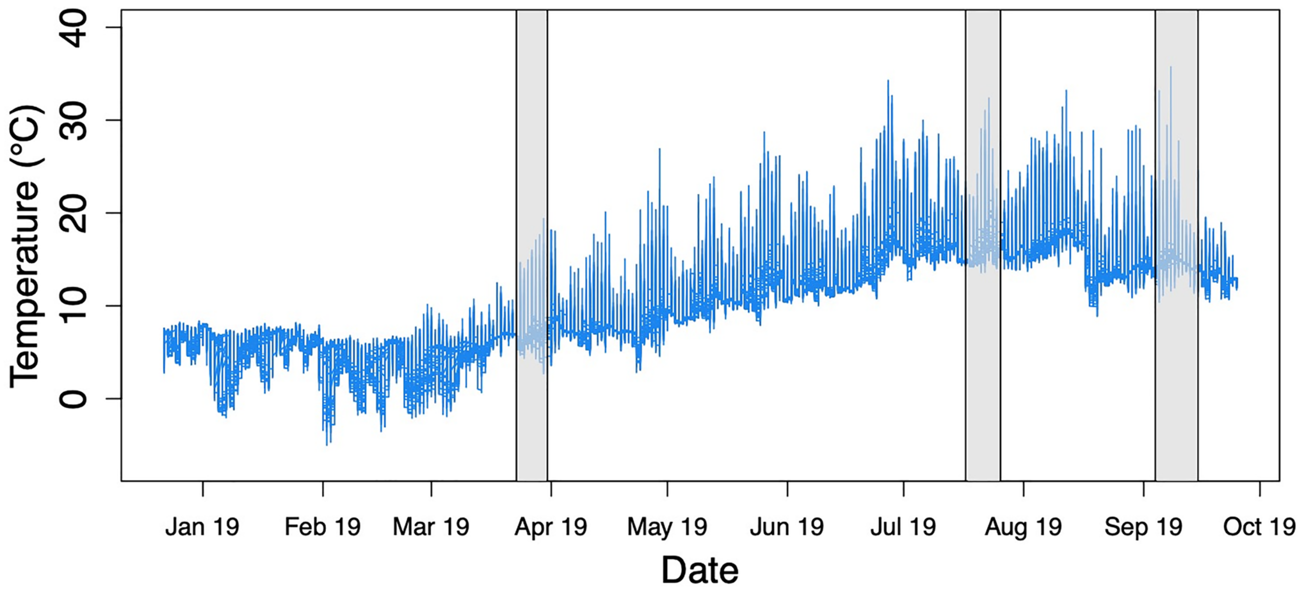

Fig. 1 Temperatures recorded in tide pools ($N = 31$) located at John Brown's Beach in Sitka, Alaska from December 2018 to September 2019. Data were recorded every 5 min by Tidbit dataloggers. Shaded gray regions indicate collection season at which metabolic assays were conducted for *P. hirsutiusculus*, *L. sitkana*, and *M. trossulus*

Mass specific oxygen consumption rate (MO_2) was calculated for each individual using the following equation:

$$MO_2 = \frac{R \times \left(V_{total} - V_{ind}\right) - (Bl \times V_{total})}{m},$$

where R is the average rate of oxygen consumption for each individual (mgO$_2$ L^{-1} h^{-1}), Bl is the rate of oxygen consumption measured for the seawater blank for the corresponding run (mgO$_2$ L^{-1} h^{-1}), V_{total} is the volume of water in the chamber and associated tubing in liters, V_{ind} is the volume of water (L) displaced by each individual, and m is each individual's dry mass (g) resulting in a final calculated MO_2 rate as mgO$_2$ g^{-1} h^{-1}. To see a detailed checklist of respirometry methods as detailed by Killen et al. (2021), see Table S4.

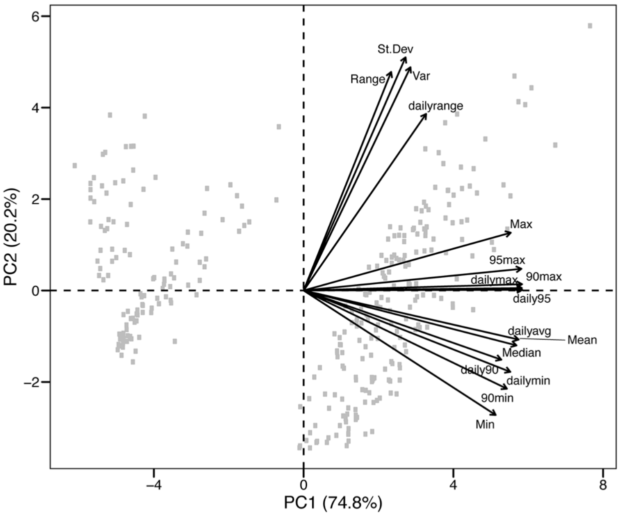

Fig. 2 Principal components analysis used to reduce the temperature metrics and account for collinearity**.** Values shown represent temperatures measured in $N = 31$ tide pools during 3 seasons (shown in Fig. 1) over the 3 time intervals tested (1 day, 1 week, and 1 month prior to metabolic assays). The PC1 axis was driven by the maximum and 95% of tide pool temperatures and explained 74.8% of the variation in the data. The PC2 axis was driven by the range of tide pool temperatures and explained 20.2% of the variation in the data

Statistical analysis

We calculated the among-individual variation in MO_2 between species as in Rangel and Johnson (2019). We used the thermal coefficient Q_{10} as a metric for determining thermal sensitivity of oxygen consumption rates (MO_2) using the following equation:

$$Q_{10} = (\frac{MO_{2_{T2}}}{MO_{2T1}})^{\frac{10}{T_2 - T_1}}.$$

This equation uses two different temperatures T_1 and T_2; however, because we measured MO_2 at three different temperatures, we used the *respirometry* package version 1.3.0 in *R* (Birk 2020) to calculate, for each individual, Q_{10} across our experimental temperatures using a linear function. This allowed us to determine the change in rate of mass-specific oxygen consumption over a 10 °C increase in temperature.

As described above, we used a PCA to summarize our thermal metrics, and we found that PC1 accounted for 74.8% of variation and was driven by mean daily maximum and mean daily 95th percentile temperatures. PC2 accounted for 20.2% of the variation and was driven by temperature range and variation (Fig. 2). In our analyses, we used PC1 and PC2 as our main metrics of thermal history, and we also ran analyses using the individual metrics most closely associated with each of the PC axes: the mean daily maximum and daily 95th percentile temperatures for PC1 and range of tide pool temperatures for PC2.

We analyzed the relationship between thermal sensitivity and three factors—the time interval used to calculate thermal history (1 month, 1 week, and 1 day), species (*M. trossulus*, *L. sitkana*, and *P. hirsutiusculus*), and collection season (March, July, and September 2019). To do this, we used linear mixed-effects models (*lmer* package in *R*; Bates et al. 2014). To account for non-independence across repeated samplings within the same tide pools, we included pool in our models as a random effect. The full models (one per time interval) included all factors and their interactions (Q_{10}, PC1, PC2, Season, and Species along with [1|Pool]). The significance of the fixed effects was determined using Type 3 F-tests with Satterthwaite's degrees-of-freedom. A stepwise elimination approach was used to determine the least complex model with the best fit, based on Akaike information criterion (AIC). After the simplest model was identified, fit was assessed by visually inspecting the residuals using the qqplot function in the *R car* and *stats* packages, and normality was quantified using the Shapiro test in the *R* stats package. The significance of fixed factors given in the text is for the reduced model and all other models are summarized in Table 1 and Table S5. Post hoc tests were used to determine which groups were statistically different using the *R emmeans* package. All statistical analyses were carried out in the R environment (version 3. 6. 3) (Team and others 2013).

Results

Pool temperatures varied appreciably across seasons for all thermal metrics and time intervals (1 day to 1 month): water temperature was lowest in March, highest in July, and intermediate in September (Figs. 1, S4). Mean (SD) tide pool temperatures for March, July, and September, for the

Table 1 Results from type 3 analysis of variance table calculated with Satterthwaite's method for the linear mixed-effects models of the relationship between thermal sensitivity and thermal conditions (reduced using a PCA analysis; Fig. 2) across the 1-week time interval

1-Week time interval				
Fixed effects	Num DF	Den DF	*F* Value	*p* Value
Initial linear mixed effect model (df = 17, AIC = 140.1)				
PC1	1	90.0	0.176	0.675
PC2	1	90.2	0.071	0.791
Season	2	85.5	0.827	0.441
Species	2	82.3	3.169	**0.047**
Season: PC1	2	90.2	2.470	0.090
Season: PC2	2	89.9	2.949	0.058
Species: PC1	2	87.0	1.547	0.219
Species: PC2	2	79.8	0.482	0.620
Random effects	St. Dev			
Pool	0.048			
Final linear mixed effect model (df = 15, AIC = 130.2)				
PC1	1	92.0	0.153	0.697
PC2	1	91.8	0.040	0.843
Season	2	87.1	0.802	0.452
Species	2	86.2	4.226	**0.018**
Season: PC1	2	92.7	2.843	0.063
Season: PC2	2	92.5	3.549	**0.033**
Species: PC1	2	89.1	1.391	0.254
Random effects	St. Dev			
Pool	0.043			

1-month time interval was: 5.5 (0.6), 16.6 (0.8), and 15.5 (0.5) °C (for other time intervals and metrics, see Table S2).

Metabolic rates of our study species, as indicated by mass-specific oxygen consumption (MO_2), generally increased across the experimental temperatures (10 °C, 18 °C, and 26 °C) and tended to vary among species (Table S3). For *P. hirsutiusculus* and *L. sitkana*, MO_2 increased across the experimental temperatures in all seasons, whereas for *M. trossulus*, MO_2 tended to increase from 10 °C to 18 °C with a decrease from 18 °C to 26 °C in all seasons. Species differed in the amount of individual variation in MO_2 across all temperatures and seasons. The more mobile species had consistently higher levels of among-individual variation than the sessile species. The highest among-individual component of variation for *P. hirsutiusculus* was 66.4% (in July), 61.2% for *L. sitkana* (in March), and 23.1% for *M. trossulus* (in March) (Fig S5).

The relationship between thermal history and thermal sensitivity varied across time scales. Thermal sensitivity (Q_{10}) was related to thermal history for the short-term time intervals (1 week and 1 day: $p < 0.047$) but not for the long-term time interval of 1 month ($p = 0.912$). The direction of this relationship varied seasonally (Table 1, Table S5). Thermal sensitivity (Q_{10} values) was highest during September and lowest during March (Fig. S3). PC1, an indicator of daily maximum and 95% pool temperatures, interacted with season (Fig. S2) to influence thermal sensitivity, when calculated for 1-day preceding metabolism assays ($F_{2,97} = 3.16$, $p = 0.047$; Table S5, Fig. 3) and marginally for 1-week prior to collection ($F_{2,93} = 2.84$, $p = 0.063$). Additionally, the range of tide

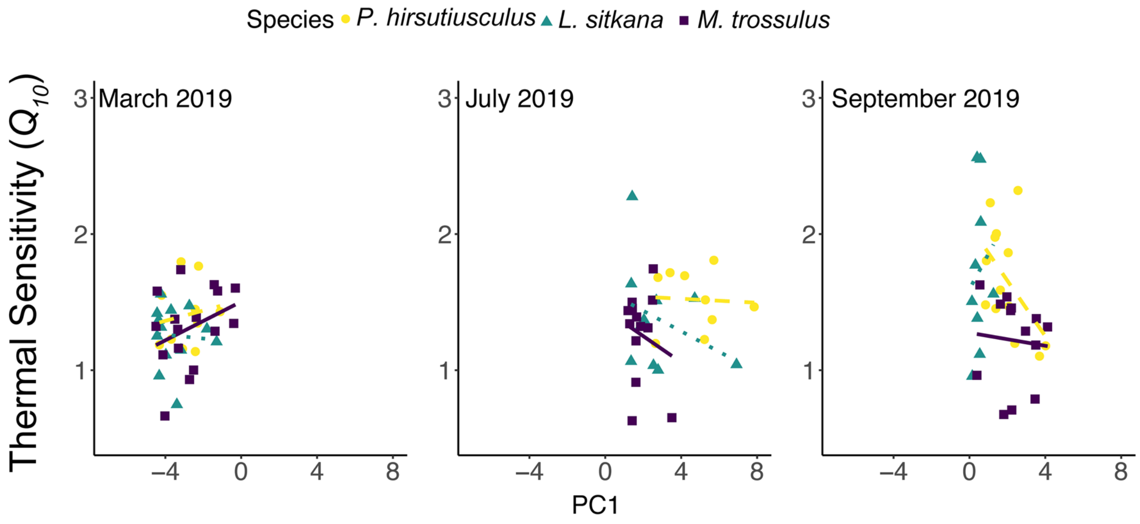

Fig. 3 Relationship between thermal sensitivity (Q_{10}) and the PC1 axis which corresponds with the maximum and 95% tide pool temperatures experienced the 1 day prior to collection. Each point represents a single individual of *Pagurus hirsutiusculus* (yellow circles), *Littorina sitkana* (green triangles), and *Mytilus trossulus* (purple squares). Colored lines are individual species trendlines across seasons by species: *P. hirsutiusculus* (yellow dashed), *L. sitkana* (green dotted), and *M. trossulus* (purple solid)

pool temperatures (PC2 axis) influenced thermal sensitivity, and the direction of this relationship also differed by season (1-week: $F_{2,93} = 3.55$, $p = 0.033$; Table 1; Fig. 4). Typically, sensitivity was higher for individuals that experienced higher and more variable temperatures in the cooler months, but this relationship shifted to negative in the warmer months (Figs. 3, 4, and S2). Our overall results were the same when using single thermal metrics in our models rather than the PC axes: we found that the direction of this relationship varied seasonally (Tables S7, S8, S9, and Fig. S6) and support for a short-term effect of thermal history on thermal sensitivity. Specifically, the interaction of thermal history and season was significantly related to thermal sensitivity for the 1-day time interval for 95th percentile temperature ($p = 0.018$), and temperature range ($p = 0.010$). There was a similar increase in thermal sensitivity during the cooler months from pools experiencing higher and more variable temperatures and a negative relationship with thermal sensitivity and pool temperature in warmer months. However, there was no relationship for the 1-week time interval (Tables S7, S8, and S9).

The relationship between thermal history and thermal sensitivity also varied among species, beyond the seasonal patterns described above, for all time intervals both when looking at the models incorporating all of the thermal metrics ($p \leq 0.027$; Table S6, Fig. 5), and those incorporating single thermal metrics (Table S10). Post hoc tests revealed greater thermal sensitivity (i.e., higher Q_{10} values) in *P. hirsutiusculus* when compared to *M. trossulus* (e.g., from PC analysis: $t = 2.887$, $p = 0.013$; Fig. 5) for all time scales.

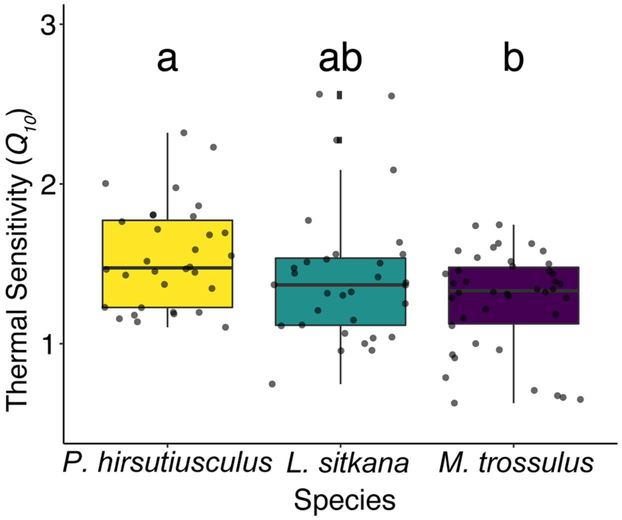

Fig. 5 Thermal sensitivity (Q_{10}) values of hermit crabs, snails, and mussels. Values were averaged across 3 seasons that all species were sampled. Tukey post hoc comparisons were used to test for Q_{10} differences between species, and letters indicate significant differences ($p < 0.05$). The boxes include data within the 25th to the 75th percentile, with the middle solid line representing the median, and the whiskers show both the highest and lowest values within 1.5-fold of the 25th and 75th percentile range. Dots represent data points outside of this range

Discussion

This study revealed that small-scale thermal history influences the thermal sensitivity of metabolic responses in three representative species of intertidal invertebrates. Specifically, we found that (1) thermal sensitivity was related to

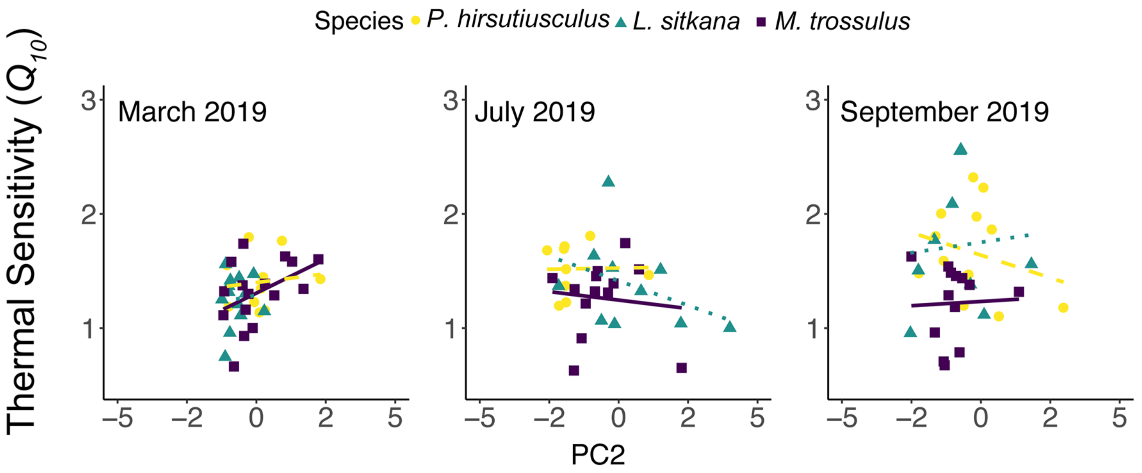

Fig. 4 Relationship between thermal sensitivity (Q_{10}) and the PC2 axis which corresponds with the range of tide pool temperatures experienced for the 1 week prior to collection. Each point represents a single individual of *Pagurus hirsutiusculus* (yellow circles), *Littorina sitkana* (green triangles), and *Mytilus trossulus* (purple squares). Lines are individual species trendlines across seasons for *P. hirsutiusculus* (yellow dashed), *L. sitkana* (green dotted), and *M. trossulus* (purple solid)

thermal history for the short-term time intervals (1-week and 1-day), and (2) this relationship differed seasonally and (3) between species with differing traits, including ability to behaviorally avoid thermal extremes.

Contrary to our prediction, average Q_{10} values (without accounting for species differences) were lowest in March, with higher thermal sensitivity in July and September. Similar seasonal cycles of lowered metabolic rates and decreased thermal sensitivity during colder months have been reported for other ectothermic species (Angilletta 2001; Toledo et al. 2008). In addition, for many mollusks and crustaceans, metabolic depression and thermally insensitive metabolism can be beneficial adaptive responses to allow for survival under prolonged thermal stress and desiccation, which are common within intertidal habitats (Guppy and Withers 1999; Marshall et al. 2011). Although Q_{10} values were low on average during March (< 1.40), all species exhibited a trend of greater thermal sensitivity with increasing range of tide pool temperatures (PC2 axis). This relationship was reversed for *P. hirsutiusculus* during September, when pools with higher maximum and range of temperatures were associated with decreases in individual Q_{10} values (Figs. 3, 4, S2). Thus, the relationship between thermal sensitivity and thermal history differed between seasons, which could be a result of seasonal changes in oxygen consumption rates. In March, when thermal variability in the tide pools is low, *P. hirsutiusculus* exhibited a direct relationship between thermal sensitivity and pool temperatures; however, when thermal variability is highest (i.e., in September), this relationship is reversed.

When habitats encompass high variability in thermal regimes, whether on small or large spatial scales, this variability can lead to a diversity of metabolic responses to climate warming across the population, even within the range of local thermal conditions, due to physiological plasticity (Stillman 2003; Sorte et al. 2011; Seebacher et al. 2015; Gaitán-Espitia et al. 2017). We interpret the importance of season in thermal sensitivity as an indicator that plasticity is possible and is occurring in these species. For many intertidal species, physiological plasticity is a crucial strategy to survive thermal fluctuations that exceed existing thermal thresholds (Hofmann and Todgham 2010). Under continued climate change, more variable thermal conditions are expected to arise, and thus, populations and species with more plastic physiological responses should be favored (Angilletta Jr 2009; Seebacher et al. 2015). Similar seasonal patterns in metabolism have been observed in intertidal fish, such as gobies and sculpin (Healy and Schulte 2012; da Silva et al. 2019). When long-term (seasonal) thermal variation is large but predictable, this can lead to individuals having a larger breadth for thermal performance and decreased thermal sensitivity (Dillon et al. 2016; da Silva et al. 2019; Pack et al. 2021). Changes in oxygen consumption could also be affected by seasonal alterations in food availability and life-history processes (e.g., growth, reproduction) that are dependent on water temperatures (Clarke 1993). Our findings indicate that seasonal changes can influence the direction of the relationship between thermal history and thermal sensitivity.

In addition to larger seasonal time scales influencing thermal sensitivity, our results align with our prediction that short-term time intervals (1 day and, in some analyses, 1 week) were more influential than the 1-month time scale on thermal sensitivity (Table 1, Table S5). Similarly, previous studies with marine invertebrates within the lab showed stronger effects of short-term than long-term acclimation on physiological sensitivity to temperature increase (Osovitz and Hofmann 2005; Juárez et al. 2018). These observations of stronger relationships to more recent than longer-term climatic conditions could be because species in our study are regularly exposed to relatively high variation in thermal conditions over the tidal cycle. Thus, a strong and recent departure in conditions might be required to elicit a measurable change in sensitivity. This also suggests that these species may be able to acclimate rapidly to changing thermal conditions (Todgham et al. 2006; Giomi et al. 2016; da Silva et al. 2019; Rangel and Johnson 2019). Species life-history traits may also contribute to the observed differences between time intervals. Growing seasons and reproductive events may lead to higher metabolic demands resulting in altered thermal sensitivity on shorter time scales (Glazier 2015; Auer et al. 2018). Both *L. sitkana* and *M. trossulus* have peak reproductive output during the spring (March–May) and beginning of fall (September), with a decrease in output during the summer (June–August) (Buckland-Nicks et al. 1973; Benito et al. 2019), whereas *P. hirsutiusculus* females can carry multiple broods throughout the spring and summer months (Hiebert et al. 2015). All of these factors could contribute to the finding that thermal variation over short-term time intervals (< 1 month) appears to be a predictor of thermal sensitivity of metabolic rates in these intertidal species. As climate warming continues to increase variability in temperatures (Pershing et al. 2019), there is potential for short-term time intervals to more often reach levels eliciting acute stress responses and requiring acclimatory responses to avoid mortality.

After accounting for seasonal and short-term thermal variability, we found that thermal sensitivity varied by species (Table 1; Table S6). Contrary to our prediction, *P. hirsutiusculus* exhibited higher thermal sensitivity than *M. trossulus*, with thermal sensitivity of *L. sitkana* falling between that of *P. hirsutiusculus* and *M. trossulus* in March and July, but not September (Figs. 3, 4; Table S6). This result could be explained by differences in mobility: *P. hirsutiusculus* are highly active and mobile compared to *M. trossulus*, which could lead to overall higher resting metabolic rates for *P. hirsutiusculus* (Halsey et al. 2015). An alternative explanation for this difference in thermal sensitivity could be related to how mobility affects the species' abilities to alter thermal exposure (Crickenberger et al. 2020). For example, intertidal shore crabs have been shown to exhibit shuttling behavior between air and water to better regulate their body temperatures (McGaw 2003). In this study, we were limited to using temperature data from the tide pools individuals were collected from during the time intervals considered (i.e., 1 month to 1 day), due to the difficulty of tracking individual *L. sitkana* and *P. hirsutiusculus* (who regularly change shells). We did conduct a small tagging study (92 snails tagged) and observed that tagged *L. sitkana* tended to have high tide pool fidelity (61% of snails were recovered from the tide pool of release after 7 days; R. Rangel unpubl. data). Littorine snails, such as *L. sitkana*, have also been observed regulating body temperature by withdrawing their foot from the substratum and into their shell to lower their body temperature by 3–5 °C (Miller and Denny 2011). In our study, both *P. hirsutiusculus* and *L. sitkana* had greater amounts of among-individual variation when compared to *M. trossulus* as seen by the variability between individual curves in Fig. S5. These results may be an indication that our measurements of thermal histories (i.e., tide pool temperatures) are better able to describe the environmental conditions for sessile species rather than mobile species. This aligns with our prediction that the relationship between thermal history and thermal sensitivity would be stronger for sessile species compared to the two mobile species. At the same time, these results underscore that more mobile species are likely to encounter different thermal conditions as a result of attempts to mediate thermal stress and maintain thermal preference (Crickenberger et al. 2020), and by extension, will undergo different thermal challenges as climate warms. However, given that thermal sensitivity was strongly related to thermal history over the shorter time intervals examined, this might also suggest that the fidelity of the mobile individuals to the tide pool of collection was greater the closer in time to the date of collection and metabolic assays.

We found that thermal sensitivities for one sessile species, *M. trossulus*, and two mobile species, *L. sitkana* and *P. hirsutiusculus*, ranged between Q_{10} values of 0.63 to 2.56. Under non-stressful conditions, many physiological reactions are characterized by Q_{10} values ranging from 1.0 to 3.0, with lower Q_{10} values (~ 1.0) indicating temperature independence (Zippay and Helmuth 2012). Our findings suggest that the measured metabolic rates in this study are relatively temperature-independent and show increases in temperature-dependence and thermal sensitivity among species and during specific seasons. Highest Q_{10} values were measured for *L. sitkana* (1.72) and *P. hirsutiusculus* (1.67) during September (Table S3). As climate models predict overall increases in average temperatures of 1.5 °C within the next 30 years (Allen et al. 2019), with the occurrence of more variable seasonal and recurring climate patterns (i.e., El Niño events, marine heat waves such as the 2014–16 "Blob"; Bond et al. 2015; Yang et al. 2019), species' metabolic rates may be increasingly impacted by warming due to altered thermal history.

Mytilus trossulus had the lowest thermal sensitivity (particularly during July and September) and showed decreases in oxygen consumption at the highest experimental temperature during all time points (Table S3). This decrease in oxygen consumption may be a sign of metabolic depression which has been observed in mollusks experiencing thermal stress (Guppy and Withers 1999; Anestis et al. 2007; Connor and Gracey 2012; Lesser 2016). During the summer months, tide pool temperatures were more variable (Fig. S4). Adaptative physiological attributes such as metabolic depression and fluctuating thermal environments may increase thermal tolerance of ectothermic species (Marshall et al. 2011; Kern et al. 2015; Drake et al. 2017). For *M. trossulus,* individuals from tide pools experiencing greater fluctuation in temperatures may become acclimated in a way that provides physiological benefits allowing them to cope with climate warming over time, similar to other *Mytilus* species inhabiting intertidal zones and experiencing fluctuating temperatures (Moyen et al. 2020). It is also important to note that trade-offs can lead to increased performance in higher temperatures at the cost of reduced acclimation capacity (Stillman 2003). However, we did not detect this effect across the range of conditions in our study. Under sustained climate warming, temperatures may eventually pass critical thresholds for mussel metabolism leading to mass mortalities (Gazeau et al. 2014). We also observed that when metabolic rates were measured at higher temperatures (34 °C, higher than the maximum of 26 °C used in this study), all mussels died (R. Rangel unpubl. data). Thus, a temperature threshold between 26 °C and 34 °C may represent an upper thermal limit for physiological activities of *M. trossulus*. In comparison, immersed temperature tolerances have been reported to be ~ 34 °C for *L. sitkana* (Iwabuchi and Gosselin 2020) and 33 °C for *P. hirsutiusculus* (Taylor 1982). Mussels may have a lowered thermal sensitivity up to a critical threshold, and after prolonged climate warming, they may become more susceptible to mortality than hermit crabs and snails.

We found that for three representative marine invertebrate species, thermal history over small spatial scales influenced the thermal sensitivity of metabolic rates and that this relationship varied over time (i.e., seasonal and shorter timescales) and by species, possibly due to traits such as activity levels or ability to behaviorally avoid thermal stress. Our results from this study indicate that these common intertidal invertebrates in this dynamic ecosystem have relatively low thermal sensitivities (i.e., Q_{10} values) and high acclimation capacity, suggesting that they have some scope to cope with temperature increases. As ocean warming continues, greater variability in thermal history may lead to larger differences in thermal sensitivity among individuals within a single population. High variability in thermal responses among individuals within a population may allow for a natural buffer to temperature increases and potentially a larger scope for adaptation in response to climate change.

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Author contributions RR designed the study, performed the experiments, analyzed the data and created all figures, and drafted the manuscript. CS advised on experimental design, collected the temperature data, assisted in data interpretation, and revised the manuscript. All authors edited and revised the manuscript and gave final approval for publication.

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Data availability The datasets and R scripts that support this study are available during peer review on the Dryad Local-scale thermal history influences metabolic response of marine invertebrates Repository, https://datadryad.org/stash/share/jwPvQUfa9zqlikQv7nXU4nuFehaRsg9fk9HSIvN7pNg and on zenodo/github: https://doi.org/10.5281/zenodo.6464075, https://github.com/racine-rangel/RangelandSorte_ThermalHistory.

Declarations

Conflict of interest The authors have no conflict of interests.

Ethical approval All applicable national and institutional guidelines for sampling, care, and experimental use of organisms for the study have been followed. This work was approved and conducted under Alaska Department of Fish and Game Aquatic Resource Permits for Scientific/Collection purposes (ID numbers CF-18–071 and CF-20–050).

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