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ORIGINAL PAPER

Variation in metabolic rate during low tide aerial exposure in the Asian shore crab *Hemigrapsus sanguineus*

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Abstract

Intertidal animals deal with physical gradients daily that create stressful conditions across the shore. These physical gradients influence the physiological performance of organisms, requiring responses that may differ with height on the shore. We examined the respiratory response to aerial exposure in the invasive Asian shore crab *Hemigrapsus sanguineus* during periods of low tide emersion using two field experiments. The first experiment simultaneously measured respiration of individuals collected from different heights on the shore, which had therefore been emersed for different lengths of time. The second experiment measured respiration of individuals collected at different times from the same tidal height. Respiration rates of crabs in both experiments increased immediately after emersion, nearly doubling by and peaking at ~ 1.5 h of aerial exposure, before decreasing again over the next 1.5 h. These results suggest that the energetic cost of low tide exposure is greatest shortly after emersion during the first half of the typical low tide period, but then decreases thereafter. These respiration patterns facilitate the broad intertidal distribution of this species on rocky shores throughout its range.

Keywords Bimodal breathers · Intertidal · Metabolism · Physiological adaptation · Respiration

Introduction

The marine intertidal zone is characterized by intense gradients in wave exposure, food availability, temperature, and desiccation (Newell 1970; Denny 1988). Rather than being uniform, these stresses vary with the morphology of the shore and the intensity of sun and wave exposure (Helmuth et al. 2001). As a result, this zone has long served as a natural laboratory to examine the response of organisms to stress (Tomanek and Helmuth 2002). Animals that inhabit this zone display a range of morphological, behavioral, and physiological adaptations for dealing with stressful conditions (Newell 1976). These responses commonly incur an energetic cost, and so metabolic rate (often measured as respiration) is one of the key physiological metrics that varies in response to intertidal stressors (Dahlhoff et al. 2001).

Respiration rates of intertidal organisms are influenced by numerous factors, including the proportion of time spent in air vs. water (Gray 1957), temperature variations (with season, latitude, or microenvironment), body size (e.g., Griffen and Sipos 2018), nutritional state (McCue 2006), developmental stage (Pörtner et al. 2010), etc. In addition, there is now abundant evidence for local adaptation of marine invertebrates, including variation in respiration (reviewed in Sanford and Kelly 2011), even for species with a high dispersal potential due to a long planktonic larval stage (Burford et al. 2014). As a result of adaptations for stressful conditions, routinely observed respiration rates of intertidal organisms during low tide are elevated above resting (standard) rates, but are often substantially lower than would be expected for active animals (Newell 1973).

Given that respiration and metabolism may be adapted to local conditions, the differences between immersed and emersed respiration rates may depend on local conditions and the degree to which animals have adapted to local stress (Sokolova and Pörtner 2001; Nancollas and McGaw 2021). For instance, intertidal organisms show species-specific differences in respiratory adaptations, including the degree of aerobic vs. anaerobic respiration during low tide, based

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on their individual niches (Nicchitta and Ellington 1983). However, despite differences between local habitats and resulting need for local adaptations, there are some broad patterns across the intertidal. The intertidal barnacle *Balanus glandula* shows metabolic patterns reflecting differential tolerances for anaerobic metabolism and differential feeding patterns depending on the height on the shore where these sessile individuals occur (Horn et al. 2021). Similarly, mussels *Mytilus* spp. that occurred intertidally are better able to tolerate emersion with less disruption to respiration than are individuals taken from subtidal habitats, and these differences interacted with body size (Tagliarolo et al. 2012). These patterns appear to apply generally to intertidal organisms, as those that consistently occur higher on the shore have evolved increased capacity for aerial respiration (Truchot 1990).

When exposed to stressful environmental conditions, it is common for organisms to downregulate metabolic activities (Hand and Hardewig 1996). Given the periodic nature of the tides, these stressful conditions in intertidal environments (fluctuations in temperature, desiccation, food availability, etc.) are highly predictable. As a result, organisms often synchronize biological processes to coincide with tidal patterns (Palmer 1973; Chabot and Watson 2014), even synchronizing to shifts in tidal patterns that alter the relative height of the bimonthly spring tides (i.e., the syzygy tide inequality cycle, Skov et al. 2005; Carver et al. 2021). This synchronization includes changes in the timing of metabolic depression in response to elevated temperatures during low tide periods in high intertidal regions (Hui et al. 2020).

Crabs are important members of many intertidal communities, but are highly mobile, traversing wide regions of the intertidal zone (Silva et al. 2010). Yet, species of crab differ in their habitat use relative to the intertidal zone, including land crabs that foray into the intertidal only to deposit eggs (e.g., Christmas island red crabs *Gecarcoidea natalis*, Adamczewska and Morris 2001), upper intertidal species that avoid the water (e.g., the many species of fiddler crab, Barnwell 1968), and species that adopt a tidal migratory strategy that brings them in and out of intertidal habitats to forage with the tidal fluctuations (e.g., the European green crab *Carcinus maenas*, Hunter and Naylor 1993). These tidal migratory species at times become stranded in intertidal regions as the tides recede and must spend the low tide emersed. This can result in rapid reductions in oxygen uptake during low tide exposure due to the absence of adaptations for dealing with desiccation of the gills during long periods of emersion (Watson-Zink 2021) and may lead to mortality if crabs are locked into the energetic costs of digesting food during emersion that was consumed during the high tide period (McGaw et al. 2009). Other species inhabit the intertidal zone exclusively or predominantly and remain there throughout the tidal cycle. These intertidal species can readily breathe in both air and water, termed "bimodal breathers" (Henry 1994), and have a range of metabolic adaptations that are similar to sessile intertidal inhabitants.

When compared across species, respiration rates in crabs generally increase with body size and temperature, are inversely correlated with height on the shore to which they are adapted, and vary with dietary strategy (Griffen and Sipos 2018). Intertidal species differ in whether metabolic rates are higher when emersed or immersed, likely due to species-specific differences in the extent to which they can maintain moist gills during aerial exposure (Defur 1988). In addition, there are also differences within species due to acclimation to specific conditions. When primarily air-breathing land crabs *Cardisoma guanhumi* were submerged in water, oxygen uptake decreased by ~ 50%, and upon re-emersion (after 1–2 weeks of immersion), oxygen uptake initially increased during the first hour or so, but eventually dropped back down to immersion rates over the next 24 h (Gannon et al. 2001). As another example, individual *C. maenas* acclimated to cyclical emersion/immersion associated with the intertidal zone had higher levels of oxygen delivery to tissues compared to subtidal crabs (Nancollas and McGaw 2021).

Despite the abundance of information available on differences in respiration between species and acclimation to tidal cycles, there is relatively little information available on how metabolic rate differs throughout the low tide period for crab species that are bimodal breathers and that inhabit the intertidal region full-time. A few previous studies have measured ventilation rates during low tide periods. For instance, the blue crab *Callinectes sapidus* does not alter its ventilation rate during low tide exposure and is able to maintain oxygen extraction efficiency throughout an 8-h low tide period (Batterton and Cameron 1978). The European green crab *C. maenas* in hypoxic waters undergoes bradycardia, and will purposefully emerge under these conditions to take advantage of the relative ease of aerial respiration in order to meet its aerobic needs (Taylor et al. 1973). This species responds to aerial exposure behaviorally by taking cover under rocks and seaweed where it can avoid desiccation, and therefore is able to respire during emersion at rates that are ~ 50% of rates during immersion (Simonik and Henry 2014).

Here we investigated the metabolic rate of the invasive Asian shore crab *Hemigrapsus sanguineus*, common across intertidal elevations (Ledesma and O'Connor 2001), during low tide exposure to understand how respiration changes shortly after crabs become emersed. Previous work found that *H. sanguineus* emersed for short periods (1.5 h) experienced bradycardia, with a heart rate just 1/3 that of immersed individuals (Depledge 1984). Finally, Fletcher et al. (2022) showed that low-tide aerial respiration rates of *H. sanguineus* were elevated relative to previously measured immersed rates (Jungblut et al. 2018) and were influenced by body size, sex, limb loss, and regeneration.

We measured aerial respiration rates of *H. sanguineus* using two field experiments to test the null hypothesis that respiration remains constant throughout the low tide period once crabs are emersed. In the first experiment, we synchronously measured respiration of crabs from different tidal heights that had therefore been emersed for differing lengths of time. In the second experiment, we measured respiration of crabs from the same tidal height, but that had been emersed for different amounts of time (i.e., measured non-synchronously) to determine whether differences observed in the first experiment likely reflected desiccation or differential acclimation across intertidal heights.

Methods

Experiment 1: Synchronous measurements across the intertidal

We conducted our first experiment at Land's End on Bailey Island, Maine (43°43′3.70″N, 70°0′8.52″W) during low tide on July 18, 2022. This is a low energy site characterized by a steep slope with boulders and extensive macroalgae in the intertidal. For this experiment, we collected crabs simultaneously from different heights on the shore that had therefore been emersed for differing lengths of time, and measured their metabolic rates simultaneously. We therefore considered tidal height (or emersion time) as the treatment in this experiment. We collected 38 crabs by hand from five different vertical heights on the shore (approximately −0.4, 0.1, 0.6, 1.1, 1.6 m relative to mean lower low water, MLLW). This sampling included 6–9 replicate crabs per tidal height, including a total of 12 females and 26 males, all between 16.8 and 28.5 mm carapace width. Our primary interest in both of our experiments was to examine the influence of tidal height, or the duration of aerial exposure during the low tide period, on respiration. Consequently, our sampling was constrained both spatially (to specific tidal heights) and temporally (to ensure all crabs had been exposed for the specific desired amount of time). The differences in replication across tidal height, the use of both male and female crabs, and the use of different sizes of crab, all reflect crab availability at the time and locations needed, and the imperative of collecting all crabs within a short window of time so that all crabs were treated in an identical manner and had been exposed to air for the appropriate length of time. We account for these demographic differences in the statistical analysis as described below. We sampled at low tide so that crabs at these different tidal heights had been exposed for 0, 0.75, 1.5, 2.25, and 3 h, respectively.

Methods for measuring metabolic rates followed those described for this species by Fletcher et al. (2022), using oxygen consumption with a constant volume technique (e.g. Lighton 2018). Upon collection, we immediately placed crabs into individual chambers for measuring metabolic rates. Each chamber consisted of a 150-ml plastic syringe with the tip sealed with silicone and a hole drilled in the end of the barrel for sample extraction (Fig. 1). The volume of the syringe was adjusted based on crab size, so that larger crabs were placed in a larger volume (Fletcher et al. 2022). Crabs were not analyzed at a common location, but rather, each crab in its experimental chamber was placed in the shade under macroalgae at the tidal height at which it was collected. Crabs were then left for 5 min to acclimate. The metabolic rate of disturbed crabs can remain elevated for several hours (Wilson et al. 2021). However, all experimental crabs in both experiments were treated in an identical manner, ensuring that comparisons of metabolic rates between crabs within an experiment reflected differences in experimental treatments and not handling/disturbance artifacts.

During the 5 min acclimation period, we used a BTMeter to measure barometric pressure, temperature, and humidity next to each set of replicate crabs located at the different tidal heights. Following this acclimation period, we initiated the experiment by sealing each metabolic chamber using a septum (Bridge Analyzers Incorporated, model #001620) designed for headspace gas analysis placed over the sampling port. Crabs were left undisturbed for 70 min. During this time, we measured the temperature next to each set of replicates every 10 min. We did not quantify crab activity levels during the experiment because, while activity is known to influence metabolic rates in crabs (Toscano and Monaco 2015), *H. sanguineus* in previous studies using this same method (Fletcher et al. 2022), as well as in our preliminary trials, remained motionless in experimental chambers throughout the duration of the trials. At the conclusion of the trial, we measured the oxygen concentration in each chamber by inserting a needle through the septum covering the sampling port that was connected to an oxygen probe from

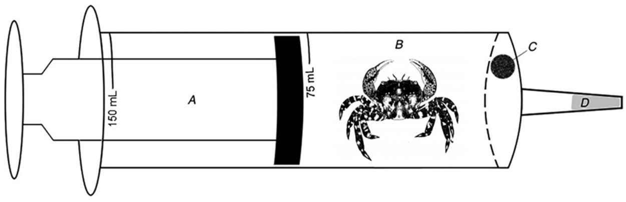

Fig. 1 Diagram of experimental apparatus (150 ml syringe) used for measuring metabolic rates. **A** Plunger, **B** barrel with crab inside, **C** port that was covered by septa during trial to create a sealed chamber and through which the gas sample was extracted at the end of a trial, **D** tip of chamber sealed with silicone

Forensics Detectors™ (Modl #FD-600, 0.01% resolution) and drawing a sample of gas using the built-in pump at 0.5 l min^{-1}. Following this trial, crabs were placed into individual numbered plastic bags and frozen before being shipped to Brigham Young University on dry ice.

Experiment 2: Asynchronous measurements from constant tidal heights

We conducted a second experiment on Sept. 1, 2023 to determine whether metabolic rate patterns observed in Experiment 1 resulted from differences in emergence time of experimental crabs, or from other factors (acclimation to specific tidal heights, artifacts from holding experimental crabs at different tidal heights during trial, etc.). We conducted this experiment on the south side of Rye Harbor, New Hampshire (43°0′6.95″N, 70°44′39.08″W), in a boulder field characterized by an intermediate slope and medium-sized boulders with very little macroalgae. We collected 54 crabs from one of two specific tidal heights (1.5 or 2 m above MLLW, which for ease of reference we will refer to as mid- and upper-intertidal, respectively), reflecting a 30 min difference in emergence times between these two tidal heights. We collected crabs from each of these tidal heights at 3 time points, separated by 45 min. Thus, at the mid-intertidal height, crabs had been emersed for 0.5, 1.25, and 2.0 h at the time of collection, while at the upper-intertidal height, they had been emersed for 1.0, 1.75, and 2.5 h. This sample included adult crabs ranging from 14.4 to 28.3 mm carapace width, and included 24 females and 30 males. The metabolic rates of sampled crabs were then measured immediately after collection (i.e., in three temporal blocks) in an identical manner to that described above for Experiment 1, with the exception that all crabs were measured at a single location in the supratidal zone in the shade of some bushes. Finally, we also measured oxygen content of a limited number (n = 3 per experiment) of syringes without crabs to examine background respiration. No changes were observed in any of these relative to atmospheric oxygen concentrations (20.94%). These were therefore not included in further analysis.

Crab processing

Frozen crabs were first thawed to room temperature. We then assessed the number of limbs missing and the number of limbs regenerating (based on the presence of limb buds). We then measured the volume of each crab by measuring water displacement when the crab was submerged in a graduated cylinder. We then dried each crab to constant weight at 60 °C, and then weighed each to 0.0001 g using a Mettler Toledo DualRange scale (Model number XS205).

Metabolic rate calculations

We calculated metabolic rate for each crab individually using Eq. 4.4 from Lighton (2018):

$$VolO_2 = \frac{\left[V\left(\mathrm{F_iO_2} - \mathrm{F_eO_2}\right) - \mathrm{F_eO_2}\left(\mathrm{VolH_2O}\right)\right]}{\left[1 - \mathrm{F_eO_2}(1 - \mathrm{RQ})\right]}$$

where VolO_2 is the volume of oxygen consumed by the crab.

To find V, the volume of the syringe chamber, we subtracted the crab's volume from the volume of the chamber, which differed slightly based on crab size. $\mathrm{F_iO_2}$ and $\mathrm{F_eO_2}$, the initial fractional concentration of oxygen (i.e., 0.2094, the atmospheric concentration) and the fractional concentration at the end of the trial, were both measured at the time of the trials using the oxygen probe as described above. We included a small amount of water (~ 0.5 ml) in each chamber during each trial so that water vapor was saturated (Lighton 2018). We then determined the water vapor pressure using the relative humidity measured at the start of each trial and the mean temperature during each trial and employing the water vapor pressure calculator found at respirometry.org. We then used this estimate of water vapor pressure to calculate the VolH_20 as outlined in Lighton (2018). Finally, we set the respiratory quotient (RQ) to 0.85. This parameter can vary between 0.7 and 1.0, depending on the substrate being metabolized. We chose a value of 0.85 because *H. sanguineus* is omnivorous (Reese et al. 2023; Saborowski et al. 2023) and because this middle-of-the-road value minimizes possible error from over- or underestimation of the RQ, with a maximum error of 3% (Burnett 1997).

We then standardized VolO_2 to standard temperature and pressure using Eq. 2.1 from Lighton (2018) and using the average temperatures (*T*) and barometric pressures (*BP*) that we measured during each trial. Finally, we divided standardized VolO_2 by the dry mass of each crab and by the duration (hours) of the trial for each crab to yield the volume of oxygen consumed per gram of crab per hour.

Statistical analyses

We analyzed the two experiments separately using general linear models. For each experiment, we first fit a full model, and then used the step function in the base package of R v. 4.1.2 (R Core Team 2021) to reduce the model based on AIC to the best-fitting model (Warton 2022). For Experiment 1, we used standardized mass-specific metabolic rate (ml O_2 g^{-1} h^{-1}) as the response variable, and as predictor variables in the full model we included emersion time, emersion time squared (based on graphical analysis that suggested a nonlinear change in respiration with emersion time), crab dry mass, sex, the number of limbs missing, and the number of limbs regenerating. For Experiment 2, we again used standardized mass-specific metabolic rate as the response variable, and as predictor variables in the full model we used tidal height, emersion time, the interaction between tidal height and time emerged, crab dry mass, sex, the number of limbs missing, and the number of limbs regenerating.

Results

As expected, metabolic rate in both experiments scaled with crab size. We controlled for this in our analyses by using mass-specific metabolic rates, and as a result, body mass was not included as a factor in the best fitting model for either experiment (see below). However, we show the increase in metabolic rate (ml O_2 h^{-1}) with crab dry mass for each of the two experiments in Fig. 2.

Experiment 1: Synchronous measurements across the intertidal

Our first experiment examined changes in metabolic rate when individuals at different tidal heights (i.e., that had been emersed for different amounts of time) were all measured simultaneously at the tidal height from which they were collected. Crabs in this experiment ranged from 1.02 to 4.05 g dry mass. We found that mass-specific metabolic rate, standardized to standard temperature and pressure, was 0.055 ± 0.024 ml O_2 g^{-1} h^{-1} greater in males than in females ($t = 2.20$, $P = 0.035$, Fig. 3). Crabs in this experiment were missing 0.71 ± 1.33 limbs on average, with 0.47 ± 1.11 of these regenerating on average. We found that metabolic rate increased by 0.112 ± 0.024 ml O_2 g^{-1} h^{-1} for each additional limb that was missing ($t = 4.57$, $P = 0.003$), and decreased by 0.120 ± 0.030 ml O_2 g^{-1} h^{-1} for each additional limb that was regenerating ($t = -4.04$, $P = 0.0003$). In addition, we found that metabolic rate increased with emergence time from 0 to 1.5 h (linear term in model, $t = 3.98$, $P = 0.0004$, Fig. 4) and then decreased with additional emergence time from 1.5 to 3 h (squared term in model, $t = -4.02$, $P = 0.0003$, Fig. 4). In addition, while both male and female crabs were used in this experiment, metabolic rates of both sexes responded to aerial exposure in a similar manner (see individual data

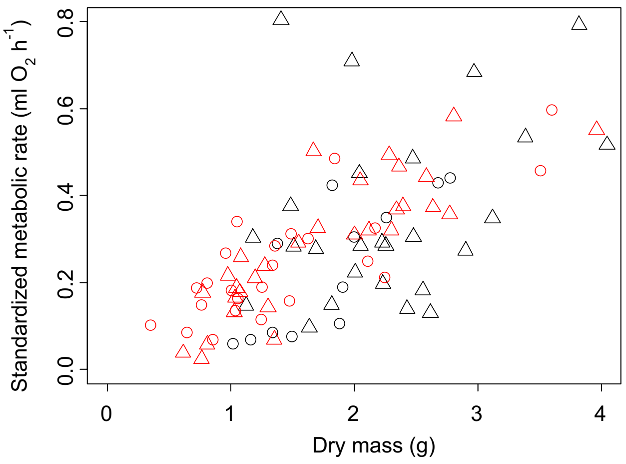

Fig. 2 Standardized metabolic rate of *Hemigrapsus sanguineus* as a function of dry body mass from both experiments, where circles are females and triangles are males, and where black symbols show crabs from Experiment 1 and red symbols show crabs from Experiment 2

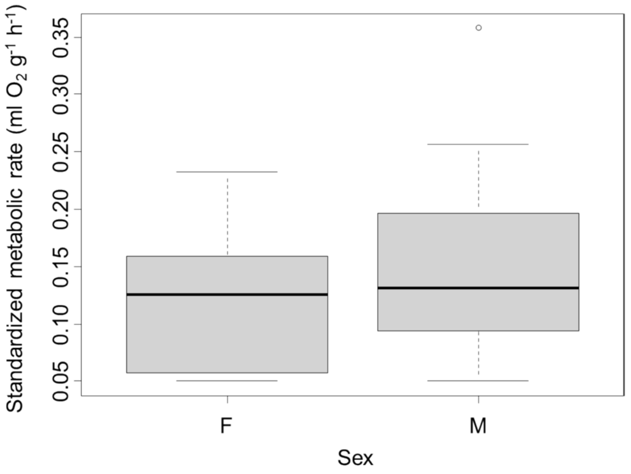

Fig. 3 Standardized mass-specific metabolic rate of female (F) and male (M) *Hemigrapsus sanguineus* from Experiment 1. Heavy horizontal line shows median values, boxes encompass the 1st–3rd quartiles of the data, whiskers show 1.5× the interquartile range, and circles show data points that fall outside this range (outliers)

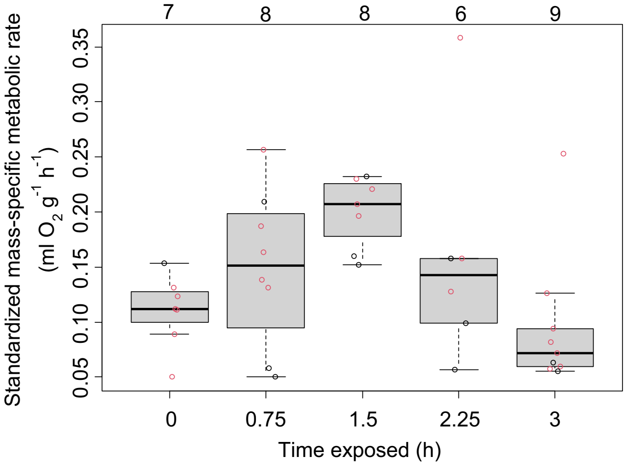

Fig. 4 Standardized mass-specific metabolic rate of *Hemigrapsus sanguineus* as a function of time emersed in Experiment 1. Boxplots are as described in the legend to Fig. 2, with the exception that circles show individual data points, where red are from male and black are from female crabs. Numbers along the top of the graph indicate sample sizes at each tidal height

points in Fig. 4). No other terms were included in the best-fitting model.

Experiment 2: Asynchronous measurements from constant tidal heights

Our second experiment examined changes in metabolic rate when individuals from two different tidal heights (mid- and upper-intertidal) were collected at different times since emergence and measured. Figure. 5A shows the expected changes in metabolic rate during Experiment 2 with emersion time, based on patterns observed during Experiment 1. Blue lines show the expected pattern during Experiment 2 if metabolic rate changes during Experiment 1 resulted from emersion time due to factors such as desiccation or physiological changes that occur with emersion time. Red lines show the expected pattern during Experiment 2 if metabolic rate changes observed in Experiment 1 resulted from acclimation to specific tidal heights or experimental artifacts from conducting measurements at different tidal heights.

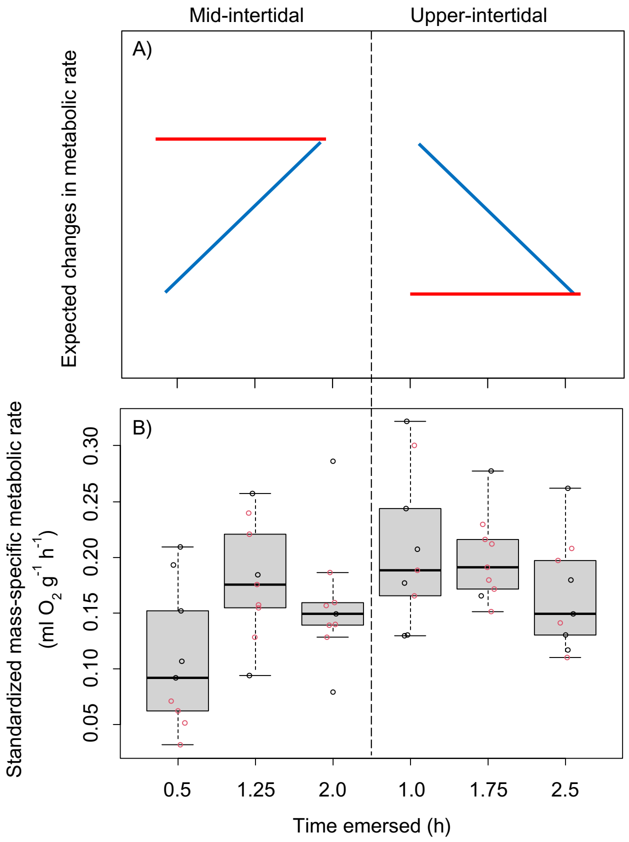

Fig. 5 **A** Expected changes in metabolic rate in mid-intertidal and upper-intertidal zones as a function of time emersed in Experiment 2. Blue lines show the expected pattern during Experiment 2 if metabolic rate changes during Experiment 1 resulted from emersion time due to factors such as desiccation or physiological changes that occur with emersion time. Red lines show the expected pattern during Experiment 2 if metabolic rate changes observed in Experiment 1 resulted from acclimation to specific tidal heights or experimental artifacts from conducting measurements at different tidal heights. **B** Standardized mass-specific metabolic rate of *Hemigrapsus sanguineus* in mid-intertidal and upper-intertidal zones as a function of time emersed in Experiment 2 at Rye Harbor, New Hampshire. Box plots are as described in the legend for Fig. 2, with the exception that circles show individual data points, where red are from male and black are from female crabs

We found that mass-specific metabolic rate, again standardized to standard temperature and pressure, was 0.134 ± 0.041 ml O_2 g^{-1} h^{-1} higher in the upper-intertidal than in the mid-intertidal ($t = 3.25$, $P = 0.002$, Fig. 5B) and varied with emergence time ($t = 1.87$, $P = 0.067$); however, we also found that the pattern of variation in metabolic rate with emergence time differed between the mid- and upper-intertidal locations (interaction term in the analysis, $t = -2.40$, $P = 0.020$, Fig. 5B). Specifically, metabolic rate increased with emersion time in the mid-intertidal where emersion times had been shorter, and decreased with emersion time in the upper-intertidal where emersion times had been longer. No other parameters were included in the best-fitting model.

Discussion

We have shown that the metabolic rate of the Asian shore crab *Hemigrapsus sanguineus* during low tide periods varies with the amount of time emersed. Specifically, we found that metabolic rate increased from the time of emersion until it peaked at approximately 1.5 h after aerial exposure, after which it then gradually declined to initial values over the next 1.5 h of continued emersion. These changes occurred after statistically accounting for other factors that have already been shown to influence metabolic rates in this species, including body size, sex, and the degree of injury (limb loss) or recovery (regeneration). The similar pattern with emergence time seen in Experiments 1 and 2 confirms that this pattern reflects changes in metabolism with emersion time rather than physiological acclimation to different tidal heights or experimental artifacts. Additionally, as has previously been shown for *H. sanguineus* (Jungblut et al. 2018; Fletcher et al. 2022), we found that metabolic rates increased with body mass and differed between males and females, but not in a consistent way. Below we discuss potential mechanisms leading to these respiratory changes and energetic implications for life in intertidal habitats.

H. sanguineus is well adapted to aerial exposure for long periods of time and is clearly capable of bimodal breathing. Individuals at the upper extreme of its intertidal distribution (2+ m above MLLW, Kraemer et al. 2007) may be exposed for 6 h or more during daily low tide periods. The respiratory pattern observed here is similar to that observed for the blue land crab *Cardisoma guanhumi*, found in topical

Atlantic regions, which is well adapted to bimodal breathing. Gannon et al. (2001) acclimated individual *C. guanhumi* to immersed conditions for 1–2 weeks, followed by respiratory measurements during emersion. They found a similar pattern to that observed here: immersed crabs showed low oxygen consumption rates that approximately doubled upon emersion, peaking at 0.5 h and then declining gradually over the next 24 h to levels seen during immersion. Interestingly, a congener to our study species found on the Pacific North American coast, *H. nudus*, voluntarily leaves the water, splitting its time between alternating immersed and emersed periods, but shows no change in oxygen consumption across these voluntary aquatic and terrestrial cycles (Greenaway et al. 1996). It is unclear whether the differences between *H. sanguineus* (this study) and *H. nudus* reflect different physiological adaptations to emersion in these congeners, or whether different oxygen consumption patterns occur during voluntary movements in and out of the water compared to conditions where water recedes due to tidal fluxes.

The increase in oxygen consumption over the first 1.5 h of emersion seen here coincides with decreases in heart rate that have been documented in *H. sanguineus* over the same emersion timeframe. Depledge (1984) showed that the heart rate of adult individuals decreased steadily upon emersion, dropping from a mean of 192 beats min^{-1} during immersion to 72 beats min^{-1} at 1.5 h of emersion. Increasing respiration at the same time that heart rate decreases would suggest an increase in cardiac stroke volume. An inverse relationship between heart rate and stroke volume has previously been documented in crabs under stressful conditions of hypoxia (Airriess and McMahon 1994) and elevated temperature (De Wachter and McMahon 1996). This same pattern may therefore occur in *H. sanguineus* during low tide periods.

The temporary increase in oxygen consumption during initial emersion observed here may be associated with one or more physiological drivers. For instance, it may be associated with an effort to control the internal acid-base balance. Carbon dioxide is highly soluble in water, but not in air (i.e., it has low capacitance), and therefore requires a high gradient to diffuse into air (DeJours 1981; Truchot 1990). As a result, pCO_2 is generally lower in water breathers than in air breathers (Truchot 1987). Respiratory changes with emersion may therefore possibly be associated with efforts to avoid a buildup of CO_2 during low tide periods. Second, increased oxygen consumption during initial emersion may conceivably reflect temporary changes due to temperature discrepancies between immersion in relatively cool water and emersion in relatively warm air (at least during summer periods when these experiments were conducted). Mean aerial temperature during our two experiments were 26.37 ± 0.63 °C (Experiment 1) and 21.9 ± 1.31 °C (Experiment 2), while normal coastal water temperatures in the Gulf of Maine during these same periods are commonly around 20 °C (we did not measure water temperature at the time of our experimental trials). In addition, while trends in metabolic rates were consistent across our two experiments conducted at different locations, there may have been site-specific factors, including potential local adaptation, in addition to temperature differences that contributed to variation in our results. While these or other factors may be at play, data collected in our study do not allow us to determine the precise physiological reason(s) for the observed changes in respiration with emergence time.

Respiration and the impacts of emersion have been studied much more heavily in other crab species than in *H. sanguineus*. The European green crab *C. maenas* has been heavily studied, and a wide range of patterns have been reported (from increased respiration upon emersion to decreased respiration, reviewed in Simonik and Henry 2014), demonstrating the context-dependency of respiration to deal with individual variation in physiological condition and environmental conditions. Our study suggests that some of this variation may be accounted for by differences in tidal height that influence the timing and duration of emersion.

The pattern of increasing and then decreasing respiration observed here indicates that respiratory patterns, and resulting energetic consequences, will differ for crabs depending on where they occur within the intertidal environment, and therefore how long they are emersed during low tide. Sessile intertidal animals show elevation-specific adaptations to differing periods of exposure (Horn et al. 2021), but crabs are highly mobile, and may therefore experience variable exposure periods from day to day, depending on the tidal height they occupy during any particular low tide. *H. sanguineus* is highly mobile, generally moving > 5 m during a 24 h period, and at times moving more than 15 m (Brousseau et al. 2002). However, it is unclear how much of this mobility is horizontally along the shore and how much includes movement across different tidal heights.

In conclusion, previous work has examined the respiratory patterns of the Asian shore crab *Hemigrapsus sanguineus* when immersed (Jungblut et al. 2018). We have measured respiration when emersed, demonstrating that this species is a bimodal breather. Further, we have shown that respiration rates increase shortly after emersion, peaking ~ 1.5 h after aerial exposure before decreasing again to levels observed immediately after emersion. Assuming that respiration rates remain at or near these final measured low levels throughout the remainder of the low tide period, our results suggest that energetic impacts of emersion may be highest for *H. sanguineus* during the first 2–3 h of emersion. Additional research is required to confirm this conclusion and to further understand the energetic consequences of these oxygen consumption patterns for this species across its broad intertidal niche.

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Data availability All data included in this study are included as supplementary files.

Declarations

Conflict of interest The authors have no relevant financial or non-financial interests to disclose.

Ethical approval This study was conducted using invertebrate animals that are not subject to protection in the country where this work was performed. No ethical approval was therefore required.

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