Experiencing the salt marsh environment through the foot of *Littoraria irrorata*: Behavioral responses to thermal and desiccation stresses

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A R T I C L E   I N F O

A B S T R A C T

Behavioral responses to environmental conditions can determine both the microclimate surrounding an organism, as well as how an organism experiences that microclimate. The salt marsh snail *Littoraria irrorata* (Say) employs two types of behaviors that potentially affect its likelihood of experiencing thermal and/or desiccation stress: 1) retracting its foot into its shell and 2) vertically migrating on the marsh grass *Spartina alterniflora*. One aim of our study was to determine how the use of retracting behaviors by *L. irrorata* modifies its ability to tolerate thermal and desiccation stresses, and the interactions between these stresses. A related goal was to elucidate whether the snails move vertically on the stalks of *S. alterniflora* to avoid thermal and/or desiccation stresses. In the laboratory, snails were kept in 10 biomimic (~potential body) temperature (25–45 °C in 5 °C increments) and vapor density (VD) deficit (~3 g/m³ and ~17 g/m³) treatments to determine how they use retracting behaviors to avoid thermal and desiccation stresses. Performance measurements of water loss, body temperature, and mortality were made in relation to behavioral responses, with independent measures from 1.5 to 9 h. In the South Carolina salt marsh, snails' movements and retracting behaviors were monitored and compared to their body temperatures and microclimate conditions. Measurements were made in the high and low marsh (characterized by the height of *S. alterniflora*) as a function of height in the canopy. We found that the snails used retracting behaviors to shift their ability to tolerate thermal and desiccation stresses by changing their capacity for evaporative cooling through mantle exposure. *L. irrorata* consistently responded to emersion, or potential desiccation stress, by retracting into its shell, and continued to avoid water loss even under high thermal stress. Both field and laboratory experiments indicated that the snails' behavioral avoidance of thermal stress was severely limited by simultaneous avoidance of desiccation stress. Furthermore, snail movement was largely restricted to periods of tidal inundation in the low marsh and did not reflect behavioral avoidance of abiotic stresses. The use of retracting behaviors by *L. irrorata* to manipulate its tolerance to temperature and humidity levels exemplifies the importance of behavior as a functional trait that determines its climate space. Viewing behavior at a mechanistic level provides a more accurate picture of how organisms experience their environment and how these impacts translate to interactions at the community level.

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1. Introduction

Mechanistic approaches to measuring an organism's fundamental niche generally focus on physiological tolerance to environmental parameters, but including the effects of an organism's behavior can be challenging (McGill et al., 2006). For example, many studies of desert ectotherms have modeled behavioral responses of reptiles in response to changing environmental conditions, allowing animals to move between microhabitats in a heterogeneous landscape as a means of maintaining a preferred body temperature (eg. Huey et al., 1989; Huey, 1991). However, few studies have considered the role of behaviors other than movement, especially in marine invertebrates.

The fundamental niche (Hutchinson, 1957) has traditionally been defined as an organism's physiological tolerance to environmental parameters (Porter et al., 1973) and has been used to correlate environmental variables and performance measurements (Kearney et al., 2010). However, this method does not account for the fact that ambient environmental measurements are often poor predictors of an organism's physiological condition and that they do not necessarily reflect physiological and behavioral responses (Kearney et al., 2010). For example, body temperatures often differ from air temperature as a result of changes in parameters such as solar radiation and wind speed (Broitman et al., 2009; Davies, 1970; Edney, 1953; Etter, 1988; Gates, 1980; Lewis, 1963; Southward, 1958; Vermeij, 1971). Therefore, defining the axis of a fundamental niche space with a few environmental parameters, and no direct connection to the organism's physiological condition, may yield little or no correlation to survival, growth, or reproduction (Kearney, 2006).

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A mechanistically determined fundamental niche can be as defined as a "climate space", in which an organism's physiological condition is set by its functional traits and the surrounding microclimate (Porter et al., 1973; Porter and Gates, 1969). The relationship between environmental conditions and organismal performance can be more accurately determined with the climate space definition by measuring an organism's physiological condition due to the interactions of the environmental parameters of its microclimate with the traits of the organism (Kearney et al., 2010). For example, because the shape, color and size of an organism all affect the movement of heat into and out of its body, the body temperature of an ectotherm is strongly affected by these characteristics and cannot be determined by knowing the conditions of the microhabitat alone. The mechanistic determination of body temperature, or any other physiological condition, needs to account for physiological and behavioral responses, as body temperature is affected by these responses. An organism's total climate space includes any possible response (Porter and Gates, 1969), though climate space can also be determined separately for individual responses, such as specific behaviors. This study uses the mechanistic definition of fundamental niche and distinguishes between climate spaces based on behavioral responses, because different behaviors can shape very different climate spaces when considered independently.

We chose to use snails to analyze the relationship between behavior and fundamental niche space (or, more properly, climate space, as in Porter and Gates, 1969), since snails have been found to employ several behaviors in response to abiotic conditions in both rocky intertidal (McMahon, 1990; McMahon and Britton, 1991; Vermeij, 1971) and salt marsh (Gòmez-Cornejo, 1993) habitats. Intertidal snails exhibit a range of behaviors that alter their morphology through retraction of the foot into the shell. The change in morphology shifts how they experience their environment, specifically how sensitive they are to heat fluxes and desiccation. Therefore, retraction of the foot can be thought of as a functional trait that affects their fundamental niche, while their movement determines the parameters of their realized niche, i.e. the microclimate to which they are exposed.

Retracting behaviors of snails have been classified based on the amount of mantle tissue they expose (McMahon, 1990; McMahon and Britton, 1991; Vermeij, 1971). The "attached" behavior signifies that the snail's foot is stuck to the substratum but still has its tentacles withdrawn in the shell. When the snail withdraws its foot into the shell and seals its operculum, it is considered "retracted". If there is an opening in the operculum, the behavior is identified as "gaping". Snails may also exhibit a "glued" behavior in which they retract and glue themselves with a mucus holdfast that allows them to lift their body off the substratum in rocky intertidal habitats (Vermeij, 1971), or hang on a plant stalk from the edge of their shell in the salt marsh.

Snails are able to regulate their body temperatures through evaporative cooling to a greater degree as either:

- they expose more tissue area (A_{evap}, m^2)
- the vapor density difference ($VD_{surface}$–VD_{air}, g/m^3) between the surface of their tissue and the air increases
- wind speed increases the rate of mass transfer (h_m, m/s):

$$E = \lambda\, h_m A_{evap} \left(VD_{surface} - VD_{air} \right)$$

where E is the rate of evaporative cooling (J/s) and λ is the latent heat of vaporization of water (J/kg; Campbell and Norman, 1998). Snails therefore reduce their potential for evaporative cooling and desiccation when retracted, but they experience higher body temperatures than snails that are attached under the same aerial conditions. By retracting, snails are shifting one axis of their functional niche to lower air temperatures, as their ability to withstand high temperatures by evaporative cooling is reduced. On the other hand, retracted snails can withstand lower humidity levels and longer emersion times at

low tide, and thereby have wider functional niches for humidity and emersion.

The importance of incorporating behavioral responses into mechanistic models of energy flows between an organism and its environment has been shown for terrestrial ectotherms, but most previous studies have focused on the role of movement behavior (Kearney et al., 2009; Porter et al., 1973; Porter and Gates, 1969). In particular, Porter and colleagues have focused on modeling the physiological condition of lizards in relation to their behavioral thermoregulation (Kearney et al., 2009; Porter et al., 1973) and have discussed how thermoregulation may constrain energy acquisition (Kearney et al., 2009). Snails are known to behaviorally thermoregulate and to avoid desiccation through retracting behaviors (McMahon, 1990; McMahon and Britton, 1991; Vermeij, 1971), though there have been no direct studies of how snails cope with simultaneous thermal and desiccation stresses via retracting behaviors. Studies comparing body temperatures of glued snails versus attached snails have been made in rocky intertidal habitats, where the substratum temperature is hotter than the snails. These findings indicate that when snails glue and lift their body off the substratum, they are cooler than attached snails (McMahon, 1990; Vermeij, 1971), because they reduce the amount of heat that is flowing from the substratum to the attached snails via conduction (Helmuth, 1998), and increase heat lost via convection. Snail behaviors have also been found to correspond with different levels of water loss and body temperatures (McMahon, 1990), though how these behaviors change with different levels of heat stress and desiccation has not yet been elucidated.

1.1. Characteristics of L. irrorata in the salt marsh

Littoraria irrorata (Say) is a major herbivore in salt marshes and is typically found on stalks of the dominant habitat-forming plant *S. alterniflora* (Stiven and Hunter, 1976; Stiven and Kuenzler, 1979). The snails are known to migrate up the *S. alterniflora* stalks with tidal inundation to avoid predators such as blue crabs (Vaughn and Fisher, 1992; West and Williams, 1986), and have also been found to migrate vertically to avoid high sediment temperatures at low tide (McBride et al., 1989). Such movement, whether due to biotic or abiotic interactions, alters the snail's microclimatic conditions, as environmental parameters such as solar radiation, temperature, humidity, and wind velocity change with height from the ground. The vertical migration of snails therefore causes them to experience different realized niches within a gradient of thermal and desiccation stresses (Gòmez-Cornejo, 1993).

L. irrorata is found in both high and low marsh areas, with juveniles and sub-adults located in the low marsh, and adults in the high marsh (Hamilton, 1978). Adults are thought to migrate from the low to the high marsh to avoid predation once they have surpassed their maximum growth rate (Baxter, 1983). After they have migrated to the high marsh, they travel very small distances and primarily move parallel to the shoreline (Hamilton, 1978). Differences in microclimates between the high and low marsh are likely to be very large, because a tall form of *S. alterniflora* (~80 cm high at study site) characterizes the low marsh, and a short form *S. alterniflora* (~30 cm high at study site) dominates the high marsh habitat (Kiehn and Morris, 2009; personal observation). In addition to height differences in the canopy, there is also less tidal inundation in the high marsh, and *S. alterniflora* leaf temperatures are higher as a result (Shea, 1977). Therefore, the position of snails on the *S. alterniflora* stalk, and their location in the marsh, may lead to very different environmental conditions.

The aim of our study was to determine how *L. irrorata* alters its fundamental niche through retracting behavior, and its microhabitat through movement, in order to tolerate thermal and desiccation stresses in mid-Atlantic salt marshes. We hypothesized that snails would be able to moderate their amount of evaporative cooling through retracting behaviors to tolerate higher temperatures and

lower humidity but would be unable to avoid both simultaneously. We also predicted that *L. irrorata* would move on the stalk to the height that was the least abiotically stressful. The results of our study provide a mechanistic framework for understanding the relationship between abiotic drivers and biotic interactions of *L. irrorata* within the salt marsh ecosystem. Furthermore, our study emphasizes the importance of behavior in determining an organism's physiological condition and the effectiveness of behavioral modification for coping with stressful environmental conditions.

2. Methods

2.1. Thermal and desiccation stresses, lab experiments

We introduced *L. irrorata* to combinations of temperature and relative humidity (RH) in the laboratory in order to determine its physiological and behavioral response to different levels of thermal and desiccation stresses. Snails were collected from the North-Inlet Winyah Bay National Estuarine Research Reserve in South Carolina (33.335°N, 79.195°W) on May 23rd, May 30th, and June 6th, 2010 from a high marsh site at 1.4 m above Mean Lower Low Water (MLLW). Snails with an aperture width range of 10.9–16.4 mm (measured from the aperture lip of the shell to the edge of the body whorl on the opposite side with digital calipers, Fig. 1) were taken a day prior to the experiment, numbered, and placed into tanks with aerated seawater in an environmental chamber held at 20 °C. We drilled twenty snails just below the first shell whorl (Fig. 1) with a 1.6 mm diameter dremel bit, then inserted and super-glued a 32-gage type T thermocouple wire in place. It was clear if the drill had touched the snail tissue, as a brown liquid would come out of the hole in the shell, though this only happened during initial drilling practice. The thermocouple wire was inserted until resistance was felt so that it was touching the tissue of the snails. These snails were kept in the same tank conditions with enough free wire to allow them to move. Snails with drilled shells were observed to behave similarly to snails without drilled shells, with some crawling around and some remaining retracted. The following morning, we separated snails into numbered containers, then dried and weighed them in a randomized order based on their shell number. To dry them, the foot was lightly poked until they retracted, and the excess water was blotted off with tissue (McGwynne, 1984). The retraction of the foot before weighing minimized variation in mantle cavity fluid (Henry et al., 1993). On a separate occasion, we measured mantle cavity fluid in 40 snails found on stalks in the high marsh ~25 min after the tide had uncovered the site to determine how much fluid they held at the beginning of a low tide cycle. The snails were weighed within 30 min of collection and were predominantly retracted from the time they were on the stalk to when they were weighed. We first weighed the snails, then lightly poked their foot and blotted off any extracted mantle cavity fluid and reweighed them. We then rehydrated the snails in seawater for 20 min and reweighed them to determine how much water their mantle cavities can hold.

After all of the snails from a container had been weighed for the experiment, they were placed into a temperature and RH treatment (10 in total). We also randomized which container was used for

Fig. 1. Aperture width measurement (arrow) and thermocouple insertion location (filled circle) for *Littoraria irrorata*.

each treatment to reduce container effects. Temperatures were set at 25–45 °C in 5° increments (25, 30, 35, 40, 45 °C) using ceramic heat emitters ranging from 60 to 250 W. The temperature values were based on the temperatures of a biomimic snail placed inside of each container, an estimation of the potential body temperature of the snail, independent of any behavior or evaporative cooling. We made biomimic snails by filling empty snail shells of a similar width with silicone, and inserting a thermocouple wire through a drilled hole in the shell (Yamane and Gilman, 2009). The biomimic provides an operative temperature (Bakken, 1992) that is independent of behavioral avoidance. Therefore, the difference between the temperatures of a biomimic versus a live snail indicates the amount of evaporative cooling exhibited by the snail. To measure live snail temperatures, two snails with thermocouple wires were also placed in each container and were connected to a Campbell Multiplexer, attached to a Campbell CR1000 data logger (Campbell Scientific Inc., Logan, UT).

For each temperature level, there was a dry and a humid treatment. High humidity treatments were kept as close to 100% RH as possible, and low humidity treatments were set at an air vapor density (VD) that was ~15 g/m^3 lower than the high humidity treatment of the same temperature. We controlled humidity levels with water vaporizers or silica gel, depending on the desired air VD. Air VD values were used instead of RH values so that the evaporative potential was the same at every temperature. Humidity treatments were tracked with an HIH 4010 humidity sensor (Honeywell International Inc., Morristown, NJ) attached to the top of each container. The experiment was run for 9 h, because that was the most frequent (~35% of instances) length of emersion at the high marsh site (1.4 m above MLLW) during the day as recorded in the field between June and September, 2009 (Station 8662245, www.tidesandcurrents.noaa.gov). We took measurements more frequently at the beginning of the experiment, because we predicted more rapid water loss rates in the first 3 h. Specifically, five snails were taken out of each container after 1.5, 3, 6, and 9 h, for a total of 20 snails. The order in which the snails were measured remained the same as the order of the first weighing. At the time of a measurement, we recorded the snails' behaviors and their weight. Behaviors were divided up into the following categories: attached, gaping, retracted, and glued. After the snails were weighed, they were returned to room temperature (~25 °C) seawater and checked for mortality 24 h later. If the snails did not respond to being poked in the foot, we assumed that they were dead. The experiment was replicated three times.

A multifactor analysis of variance (ANOVA) was used to compare weight loss due to temperature and humidity treatments over time. Weight loss was compared as the proportion of weight loss to original weight in order to control for variation in snail size. We assumed weight loss to be entirely due to loss of water during the experiment. Live snail body temperatures were compared between high and low RH conditions for each temperature treatment using non-parametric Kruskal–Wallis tests and a Bonferroni correction. We also compared biomimic and live snail body temperatures between high and low RH conditions with temperature treatments combined using Kruskal–Wallis tests and a Bonferroni correction.

2.2. Desiccation due to behavior and wind speed, lab experiment

We determined the water loss of *L. irrorata* due to behavior and wind speed to elucidate how effectively its retracting behavior reduces desiccation. Snails that had been placed in the three least stressful temperature and desiccation treatments (25 °C high RH, 25 °C low RH, and 30 °C high RH) in the previous experiment were used in the wind speed experiment within a week. We re-used snails from non-stressful conditions since they were still in good physical condition, and because for this experiment, we were not looking at how they behaviorally responded to conditions, but rather were interested in measuring the
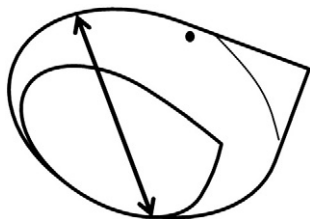
effect of induced behaviors on their weight loss. Between experiments, these snails were kept in aerated seawater in an environmental chamber held at 20 °C. Snails from these treatments were randomly assigned to a wind speed of 0.5, 1.0, or 1.5 m/s. Prior to placing them in the wind tunnel, we submerged the snails in seawater (20 °C) for ~30 min to make sure their tissues were equally hydrated since some snails crawled out of the water onto the sides of the tanks. The snails were then kept in a dry container for 10 min. During this time, they were forced to stay in the retracted position by being lightly poked on the foot repeatedly. When we poked the foot to extract mantle cavity fluid, the snails remained active, but repetitive poking eventually caused some of them to stay retracted. It was found that by controlling their behavior in this way, there was a more even distribution of behaviors during the experiment. After 10 min, the snails were lightly dried and weighed as in the previous experiment. We then placed the snails in the wind tunnel on top of a LEGO base plate with 1.5 cm diameter cylindrical LEGO "stems". The LEGOs simulated turbulence conditions and vertical structures for climbing as within a S. alterniflora canopy. Humidity and temperature levels were kept stable for each run, with an average RH ($\pm$ SD) of 50.8 $\pm$ 1.8% and average temperature of 25.5 $\pm$ 0.4 °C.

We placed snails in the wind tunnel for 20 min and recorded their behavior every 5 min. Snails were only observed for 20 min in order to record water loss due to a single behavior. If the snails were observed for longer periods, they were more likely to alter their behavior during that time. If they were crawling for at least 3 of the 5 min, they were identified as "crawling". Non-crawling snails were identified as either "attached" or "retracted" by turning them over at the end of 20 min to see if they were withdrawn into the shell or stuck to the base plate. The glued behavior was not observed, as conditions were minimally desiccating and not thermally stressful. If a snail was performing one behavior for 75–100% of the experiment, it was considered to be exhibiting that one behavior for the analysis; otherwise, its weight loss and behavioral information were not used. At the end of the experiment, the snails were immediately reweighed to determine their weight loss. We tested all three wind speeds within one day using a different set of snails for each speed, and repeated the experiment four times, using new snails each time.

As in the previous experiment, we measured weight loss as a proportion of original weight, and we assumed that weight loss was solely due to water loss. A multifactor ANOVA was used to test the interaction between the effect of behavior and wind speed on weight loss. Wind speed level and behavior were then combined as a single factor to further analyze their effects on weight loss. These comparisons were made with a single factor ANOVA and Bonferroni post-hoc tests.

2.3. Dry weights

We obtained dry tissue weights from 80 of the snails used in the experiments to calculate water loss in relation to the snails' water storage capacity. After the snail shells and tissues were separated, tissues were placed on pre-weighed aluminum foil pans, weighed, and dried at 65 °C until weight loss was no longer occurring. Shells were weighed after drying for one day. We then used a least-squares linear regression to compare the original weights of the snails taken at the beginning of the experiments to the dry tissue and shell weights. The original weight − (shell weight + dry weight) gave the value for the amount of water held in the tissue. Since we measured the original weights just after taking the snails out of water and extracting the excess fluid in their mantle cavities, we assumed that their tissues were fully saturated upon original weighing.

2.4. Snail temperature and movement due to time of day and emersion, field observations

We measured environmental conditions and snail responses in the field to determine how L. irrorata responds to microclimates in

the salt marsh. Field observations were made from July 2–8, 2010 at the high marsh site described previously, as well as 25 m away in the low marsh at 1.2 m above MLLW. We tagged twelve snails a day prior to the observation period with bee tags (Floy Tag Inc., Seattle, WA) for identification and with nail polish to make them conspicuous. Tagged snails were all within a meter of each other and were chosen based on a distribution of height in the S. alterniflora canopy. Four snails were selected for each height range of 0–4, 5–9, and 10 cm + in the high marsh, and 0–14, 15–29, and 30 cm + in the low marsh.

We made observations every 2 h during low tide and at 6:00, 18:00, and 24:00 h from 6:00 h on July 2 to 24:00 h on July 4, after which observations around low tides switched to 8:00, 18:00, and 22:00 h through July 8. During the low tide, a biomimic sensor was attached to a S. alterniflora stalk with a zip-tie at heights of 0 (on the soil), 5, 10, and 20 cm in the high marsh, and 0, 10, 20, and 40 cm in the low marsh. Thermocouples inserted into the biomimics were attached to a Campbell data logger contained in a cooler near the site. RH and air temperature were recorded during daytime measurements and in the vicinity of the snails with a HOBO logger (Onset Computer Corporation, Pocasset, MA) at heights of 10, 20, and 40 cm above the sediment in the high marsh, and 10, 30, and 80 cm in the low marsh. Measurements were also made at 1 min intervals during low tide at the same stalk heights for air temperature with a type T thermocouple connected to the Campbell data logger. We chose the vertical range of the biomimics based on the observed range of the live snails, whereas we picked the vertical range of the sensors to span the height of the S. alterniflora canopy.

We recorded snail temperature, substratum temperature (next to where the snails and biomimics were attached), vertical height, and behavior at every observation time. Snail temperatures were measured with an Omega infrared sensor (OS36-3 Omega Engineering, Inc., Stamford, CT) held close to the shell, and substratum temperatures were measured with a type K thermocouple connected to an Omega hand-held data logger. Lab simulations of live snails heated with a light-emitting heat lamp showed that snail body temperatures measured with thermocouples inserted through the shell were on average only 1.0 $\pm$ 1.2 °C off from the temperatures measured with the infrared sensor (n = 3 snails, 19 observations). We noted behavior as crawling, attached, or glued (retracted with mucus holdfast).

We analyzed the effect of the time of day on snail temperatures and vertical movement with a series of univariate analyses of covariances (ANCOVAs), with time of emersion as the covariate. The variables used were (1) the difference between snail and substratum temperature, (2) the difference between snail and biomimic temperature, and (3) vertical movement per hour. Observations on individual snails were averaged for each measurement time (n = 12), and measurements made at the same time of day were used as replicates (n = 5–7). We calculated snail-biomimic temperature using the biomimic closest to the same height in the canopy for each snail. A univariate ANOVA was used to compare snail-biomimic temperatures at 8:00 h between high and low marsh sites across 4 days. We selected this time for analysis because all other measurement times with more than two replicates (10:00, 12:00, 14:00, and 16:00 h) overlapped in the standard deviations from the means.

3. Results

3.1. Behavioral responses and tolerance levels of thermal and desiccation stresses

For the duration of the experiments, we maintained RH levels of 93.7 $\pm$ 3.8% (VD deficit of 2.9 $\pm$ 2.2 g/m^3) in the high humidity treatments and VD rate change differences between high and low RH treatments of 16.6 $\pm$ 3.4 g/m^3. There was no significant interaction between treatment conditions and time ($F_{27,574} = 0.933$, p = 0.564),
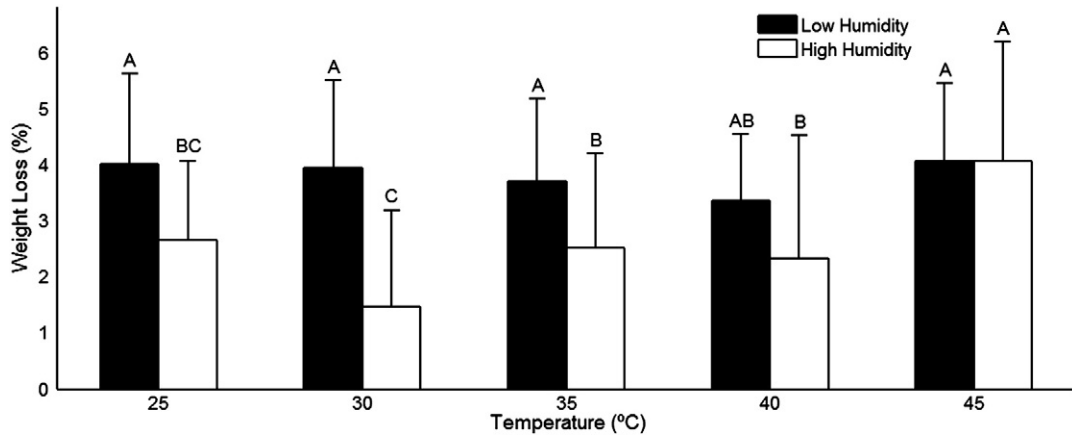
Fig. 2. Percent weight loss ($100*$weight loss /original body weight) of *Littoraria irrorata* in high (vapor density deficit $= 2.88 \pm 2.22$ g/m^3) and low (16.59 ± 3.39 g/m^3) humidity treatments after 9 h at biomimic temperatures from 25 to 45 °C. Data are averages $+1$ SD and letters indicate significant differences in weight loss ($p<0.05$).

so treatments were analyzed independently with Bonferroni post-hoc tests. RH and temperature had a significant effect on snail water loss ($F_{9,574} = 16.786$, $p<0.001$), though the effect of temperature was different depending on the RH. Snails in low RH treatments lost a consistent amount of water throughout the temperature range, and lost more water than snails in high RH treatments at all temperatures except 45 °C ($p<0.05$; Fig. 2). Snails in high RH treatments lost a similar amount of water from 25–40 °C, though at 45 °C, their water loss significantly increased to the same level as snails in low RH treatments ($p=0.001$).

Snail water loss increased throughout the duration of the experiments ($F_{3,574} = 49.750$, $p<0.001$). After 9 h at 45 °C, snails lost approximately $24.6 \pm 8.3\%$ of their water capacity in high RH treatments and $21.3 \pm 4.7\%$ in low RH treatments. At the lower temperatures in high RH treatments, snails lost from $12.8 \pm 6.9\%$ to $18.2 \pm 10.6\%$ of their water capacity. We were able to calculate water capacity after finding a linear relationship between the original weights and dry tissue weights (dry weight $= 0.085*$original weight $- 0.033$, adj r$^2 = 0.56$, $p<0.001$) and between the original weights and shell weights (original weight $= 0.673*$shell weight $+ 0.061$, adj r$^2 = 0.916$, $p<0.001$).

The mode behavior exhibited at 1.5, 3, 6, and 9 h was the same throughout the experiment for most treatments. However, in 45 °C and 40 °C low RH treatments, 47% of the snails were attached after 1.5 h, but by 3 h, the predominant behaviors were retracted (60% at

3 h) and glued (60% at 3 h), respectively, for the duration of the experiment. The other exception was in 35 °C high RH treatments, where the snails were mostly attached for the first 6 h (60–100%) but were glued after 9 h (53%).

Snails exhibited glued, retracted, gaping, and attached behaviors with different frequencies depending on the RH and temperature level. The overall frequencies of certain snail behaviors in low RH treatments was similar from 25 to 40 °C, but at 45 °C, the snails went from >60% gluing behavior (at 25–40 °C) to only 17% glued, with 45% retracted, 27% gaping, and 12% attached (Fig. 3). In the high RH treatments, snails were mostly attached (59–93%) from 25 to 40 °C, with a slight increase in the other classified behaviors as temperatures increased. By 45 °C, 25% of snails were retracted and 75% were gaping. Gaping was largely a response of the snails to the temperature treatment, and in some cases, it was an indication of heat coma.

Live snail body temperatures were lower than biomimic temperatures in both high ($\chi^2 = 121.949$) and low RH conditions ($\chi^2 = 367.653$; $p<0.001$; Fig. 4). This was consistent throughout the experiment, except in 35 °C high RH treatments where they were only 0.1 ± 0.9 °C hotter. In the rest of the treatments, biomimic-snail temperatures ranged from 1.4 ± 1.1 °C in 30 °C low RH to 0.0 ± 1.3 °C in 45 °C high RH treatments, respectively. The body temperatures of the snails were also higher in the high RH treatments than in the low RH treatments in all temperature treatments (45 °C $\chi^2 = 909.123$,
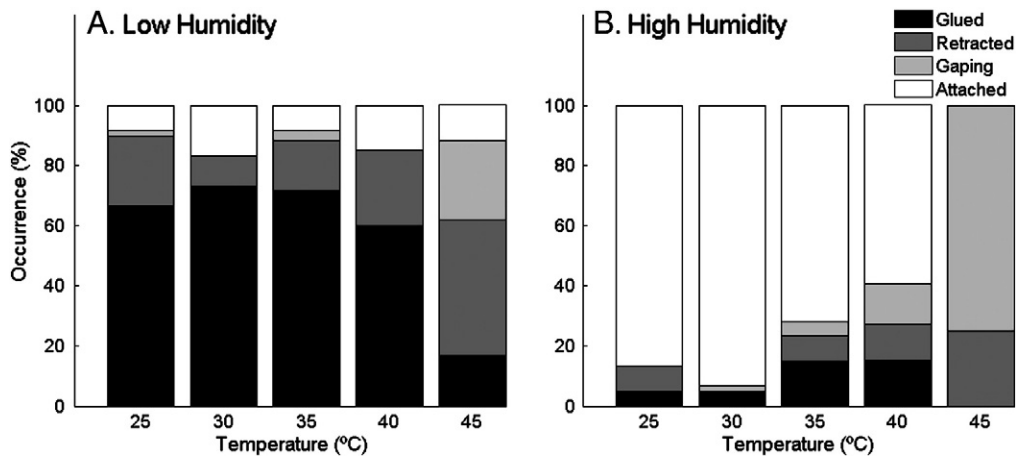
Fig. 3. Percent occurrence of *Littoraria irrorata* behavior throughout the duration of the three trials combined and at biomimic temperatures from 25 to 45 °C. Snails were identified as glued, retracted, gaping, and attached, based on the position of their foot with respect to their shell (retracted, gaping, or attached) and whether or not dried mucus was observed at the lip of the shell (glued). Graphs are separated by a) low relative humidity (RH; vapor density (VD) deficit $= 16.6 \pm 3.4$ g/m^3) and b) high RH (VD deficit $= 2.9 \pm 2.2$ g/m^3).
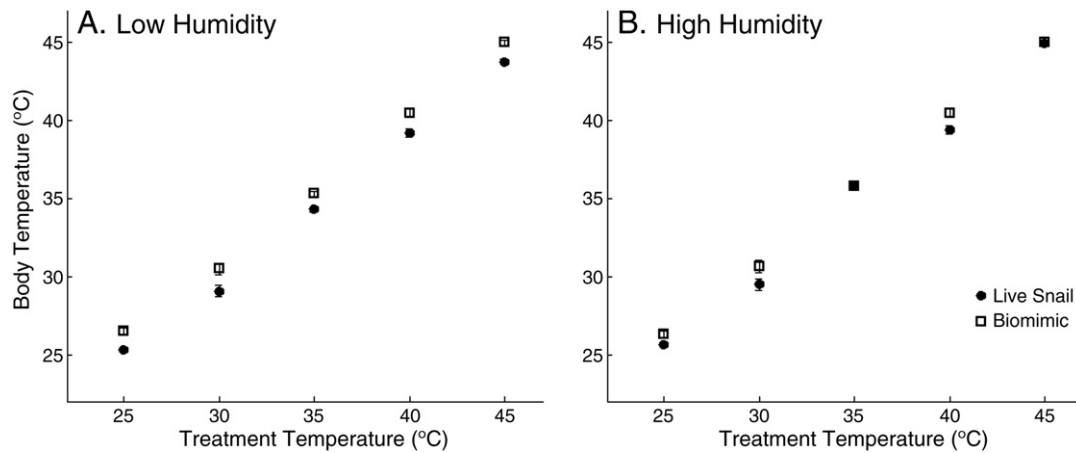
Fig. 4. Body temperatures of *Littoraria irrorata* (circles) and biomimics (squares) in treatment temperatures from 25 to 45 °C. Graphs are separated by a) low relative humidity (RH; vapor density (VD) deficit $= 16.6 \pm 3.4$ g/m^3) and b) high RH (VD deficit $= 2.9 \pm 2.2$ g/m^3). Data are averages ± 1 SD.

40 °C $\chi^2 = 50.83$, 35 °C $\chi^2 = 1735.044$, 30 °C $\chi^2 = 126.936$, p<0.001), except 25 °C ($\chi^2 = 5.563$, p=0.018). Differences between body temperatures in the high and low RH treatments ranged from 0.2 ± 0.9 °C in 40 °C to 1.6 ± 1.2 °C in 35 °C treatments.

The mortality rate was higher in the high RH treatments than in the low RH treatments. Average mortality in high RH treatments was $38 \pm 8\%$ at 45 °C, $8 \pm 3\%$ at 40 °C, $7 \pm 3\%$ at 35 °C, and $2 \pm 3\%$ at 30 °C. Average mortality at 45 °C in low RH treatments was $3 \pm 3\%$, with 0% mortality in the rest of the low RH treatments.

Snails weighed for mantle cavity fluid were found to hold $0.2 \pm 0.3\%$ of their total water content (tissue water + mantle cavity fluid without rehydration) in their mantle cavities at the beginning of a low tide cycle. Ambient air temperature was 16 °C and RH was 58% at the time of collection (cdmo.baruch.sc.edu), so desiccation potential when the snails were removed the stalks was relatively low. Rehydrated snails held $3.3 \pm 1.5\%$ of their total water content (tissue water + mantle cavity fluid with rehydration) in their mantle cavities.

3.2. Desiccation as a function of behavior and wind speed

The multifactor ANOVA testing the interaction between the effect of behavior and wind speed on weight loss gave a significant interaction (p<0.001), though the profile plot of estimated marginal means versus wind speed showed only a slight difference in slopes. Water loss varied with wind speed and behavior ($F_{8,205} = 73.834$, p<0.001; Fig. 5). Snails

lost the most amount of water while crawling, an intermediate amount of water when attached, and the least amount of water when retracted (p<0.05; except there was no significant difference in water loss between retracted and attached at 0.5 m/s). Crawling snails lost more water in 1–1.5 m/s wind speeds ($17.1 \pm 4.8\%$ at 1.5 m/s) than in 0.5 m/s wind speeds ($11.7 \pm 3.1\%$; p<0.05). The attached behavior also had slight increases in water loss from $5.7 \pm 2.6\%$, $8.1 \pm 3.5\%$, to $10.2 \pm 4.6\%$ as wind speeds increased from 0.5 to 1.0 to 1.5 m/s, though this was not significant (p>0.05). Water loss in retracted snails did not change due to wind speed and averaged $2.4 \pm 3.1\%$.

3.3. Environmental conditions in the high and low marsh

There was a neap tide during the time that environmental measurements were made, and the high marsh site was not tidally inundated at all between ~6:00 h on July 3 rd and ~17:00 h on July 7th. Therefore, the high marsh snails were emerged for approximately 112 consecutive hours. In the low marsh site, there was a consistent tide such that the snails were only emerged for periods of up to 6 h. Verified tides at Oyster Landing, a site ~1.5 km away, indicated emersion at the elevation of our high marsh site (1.4 m above MLLW) for 93 h. Verified neap tides (emersion longer than 2 days at elevations ≥1.4 m above MLLW) from May–September 2010 lasted 136 ± 54 h (n=4), with the longest emersion period of 155 h from June 1–7 (Station 8662245, www.tidesandcurrents.noaa.gov).
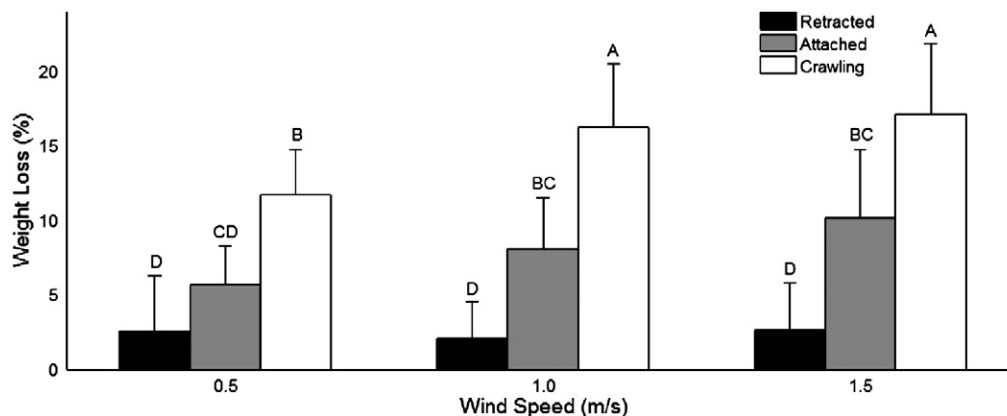
Fig. 5. Percent weight loss (100*weight loss/original weight) of *Littoraria irrorata* in wind speeds of 0.5, 1.0, and 1.5 m/s as function of behavior (retracted, attached, and crawling). Data are averages $+ 1$ SD. A single factor ANOVA was run with wind speed and behavior as a combined factor and proportion weight loss (weight loss/original weight) as the variable. Letters indicate significant differences in weight loss (p<0.05).
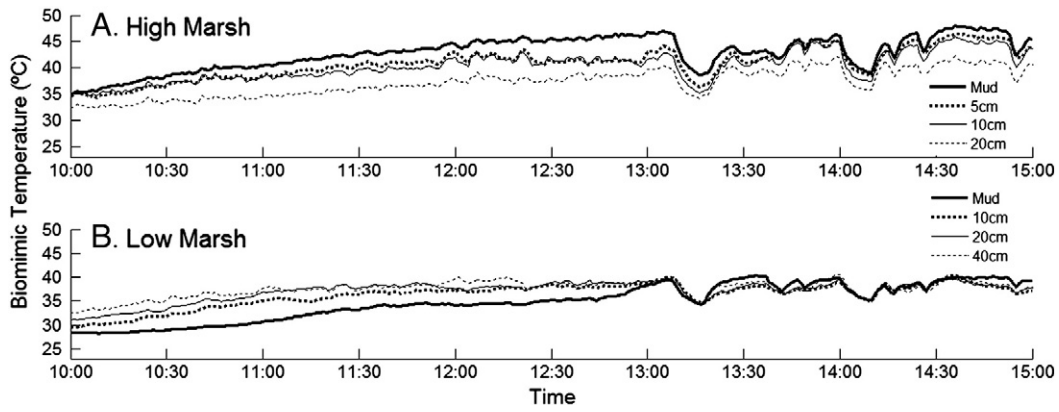
Fig. 6. Biomimic temperatures of *Littoraria irrorata* on July 7 from 10:00–15:00 h during low tide in the a) high marsh and b) low marsh. Biomimics were placed in the mud and on *Spartina alterniflora* at 5, 10, and 20 cm in the high marsh. In the low marsh they were placed in the mud and at 10, 20, and 40 cm.

Measurements beginning July 2nd were preceded by a few days of rain, and air temperatures were cooler, with a high of 25.4 °C. There was no rain for the duration of the observation period though, and air temperatures steadily increased throughout the week, peaking on July 7th at 33.0 °C (Oyster Landing, North Inlet Winyah Bay, SC, cdmo.baruch.sc.edu). The environmental measurements of air temperature, *S. alterniflora* temperature, and RH all decreased from the base of the canopy to the top, and the gradient appeared to become stronger as the day progressed. (Supplementary Figs. 1–3). The parameters also reflected a diurnal pattern of increasing until ~14:00 h, then decreasing with sunset.

Biomimic temperatures in the high marsh generally decreased with height in the canopy, but there was less of a consistent pattern in the low marsh (Fig. 6). Before 10:00 h in the high marsh, the pattern was less clear or sometimes opposite, but became more pronounced as the sun rose and temperatures increased. On July 7th at 14:30 h, high marsh biomimic temperatures peaked at 48.0, 46.4, 45.9, and 42.2 °C on the mud (0 cm) and on *S. alterniflora* at 5, 10, and 20 cm, respectively. At the same time in the low marsh, temperatures were lower, ranging from 39.6 to 40.0 °C, and did not exhibit a gradient. Until 13:00 h, biomimics placed in the low marsh mud remained cooler than those on the stalks, whereas biomimics in the high marsh mud were hotter by 10:00 h.

While RH was generally higher at lower heights in the canopy, the difference between saturated VD at the temperature of the snails and air VD was usually higher at lower heights by midday. Before 10:00 h, biomimic temperatures were often slightly higher at 20 cm than at 10 cm, which led to greater VD differences at 20 cm than at 10 cm. As the day proceeded, and biomimic temperatures became hotter lower in the canopy, VD differences became higher at 10 cm than at 20 cm. For instance, on July 7th at 12:00 h, the VD difference was 34.5 g/m^3 at 10 cm and 25.3 g/m^3 at 20 cm.

3.4. Snail responses to environmental conditions

During field observations, *L. irrorata* was always found on *S. alterniflora*, with the exception of relatively few cases (79/1027 individual observations in the high and low marsh) where the snail was on the sediment or on top of another snail. After 6:00 h on July 3rd in the high marsh, the beginning of the 112-hour emersion period, snails were always found below 5 cm on the stalks. Before 10:00 h on July 3rd, 73% of observed snails (n = 98) were attached, but after 10:00 h, only 7.7% were attached (n = 389). Snails in the low marsh were on average ~20 cm high on the stalk. Of the snails observed, 65% were attached or crawling at 6:00 h and 8:00 h (n = 71), but 68% were glued for the rest of the day (n = 362). Snail temperatures were lowest at 17 °C on July 3rd at 24:00 h and at 14 °C on July 3rd at 6:00 h in the high and low marsh, respectively. Their temperatures peaked at 14:00 h on July 7th at 46 °C and 36 °C in the high and low marsh, respectively. One of the two snails that reached 46 °C expired and was cleaned out of its shell within two days.

The difference between snail and substratum temperatures was affected by the time of day in the high marsh ($F_{8,41} = 10.612$, $p < 0.001$) but not in the low marsh ($F_{8,42} = 1.757$, $p = 0.131$; Fig. 7).
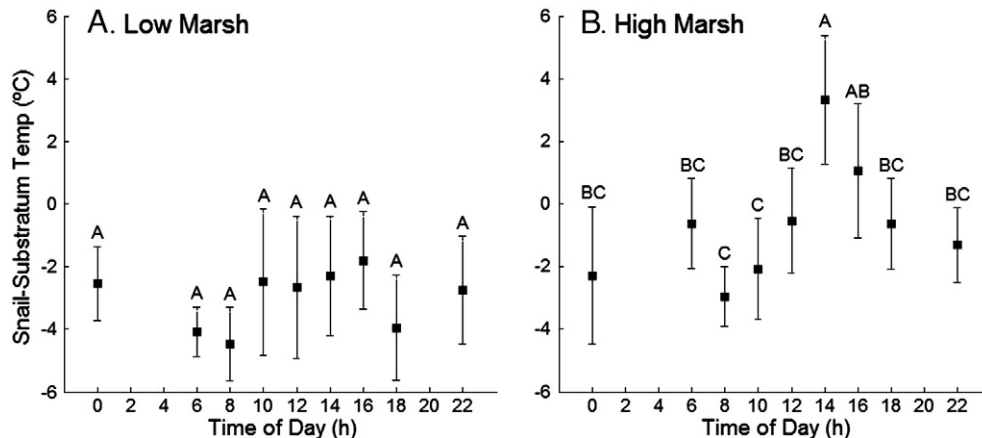
Fig. 7. Difference in *Littoraria irrorata* and substratum (primarily *Spartina alterniflora*) temperatures throughout the day from July 2–8, 2010 at a) low marsh and b) high marsh sites. Time of day had a significant effect on snail-substratum temperatures in the high marsh ($F_{8,41} = 10.612$, $p < 0.001$), but not in the low marsh ($p > 0.05$). Letters indicate which times were significantly different ($p < 0.05$).

Snails were hotter than the substratum in the high marsh at 14:00 h and 16:00 h, with a peak difference of 3.3 ± 2.0 °C at 14:00 h. At all other times in the high marsh, snails were cooler than the substratum. In the low marsh, snails were on average cooler than the substratum at all of the times measured and were up to 4.5 ± 1.2 °C cooler at 8:00 h. Snail-substratum temperatures were not different from each other even at midday in the low marsh. Also, time of emersion did not have an effect on snail-substratum temperatures in either the high or low marsh.

The difference between snail and biomimic temperatures was not affected by time of day (low marsh: $F_{5,24} = 2.066$, $p = 0.12$; high marsh: $F_{5,24} = 2.333$, $p = 0.08$) or emersion (low marsh: $F_{1,24} = 0.773$, $p = 0.391$; high marsh: $F_{1,27} = 3.565$, $p = 0.074$), though snails in the low marsh were cooler than their respective biomimics compared to snails in the high marsh at 8:00 h ($F_{1,8} = 46.532$, $p < 0.001$). At this time, snails in the high marsh were on average 2.0 ± 0.5 °C cooler than the biomimics, and in the low marsh were 4.7 ± 0.5 °C cooler. Snails at both sites were on average cooler than the biomimics for all of the measurement times during the low tide. In the high marsh, snails ranged from 1.2 to 5.0 °C cooler than the biomimics and in the low marsh they ranged from 3.9 to 6.9 °C cooler.

Hourly snail movement was affected by time of day ($F_{8,41} = 2.880$, $p = 0.016$) and duration of emersion ($F_{1,41} = 9.436$, $p = 0.004$) in the low marsh, but not in the high marsh (time of day: $F_{8,41} = 1.243$, $p = 0.308$; duration of emersion: $F_{1,41} = 3.089$, $p = 0.089$). The main difference in the low marsh was around 16:00 h, when snails moved up the stalk at a rate of 3.6 ± 2.3 cm/h. During the rest of the time, snails moved from 0.2 ± 1.9 cm/h to 0.8 ± 1.3 cm/h (<0 cm/h indicates downward movement). Snails in the high marsh moved from 0 cm/h to 0.5 ± 0.9 cm/h throughout the day. In terms of emersion time, snails in the low marsh moved up the stalk 0.7 ± 4.1 cm/h at 0 h of emersion and down the stalk from 0.4 ± 2.5 cm/h to 0.7 ± 4.1 cm/h during the rest of the emersion period (Fig. 8). Snails in the high marsh moved the most after 2 h of emersion at an average of 1.6 ± 2.0 cm/h down the stalk, but they did not move more than 0.1 ± 0.2 cm/h after 6 h. They stopped moving on average after 16 h and were entirely stationary from 32 h to the end of the 112-hour emersion period.

4. Discussion

The effect that retracting behaviors have on the fundamental niche spaces (using the definition of climate space; Porter and Gates, 1969) of snails exemplifies the importance of including behavior as a functional trait in mechanistic approaches to ecology (McGill et al., 2006). Furthermore, the response of snails introduced to simultaneous thermal and desiccation stresses elucidates more about their avoidance strategies than solely measuring responses to the individual stresses. Snails are adept at avoiding thermal and desiccation stresses separately (McMahon, 1990), but the synergistic effects of multiple stressors create trade-offs in avoidance that influence behavior and performance. The salt marsh is a very heterogeneous environment, with thermal and desiccation stresses varying between both the high and low marsh (Baxter, 1983) and within the *S. alterniflora* canopy (Gómez-Cornejo, 1993). While snails experience different degrees of thermal and desiccation stresses depending on their location and the tidal cycle, our hypothesis that *L. irrorata* moves vertically on the stalk to avoid environmental stressors was not supported. However, the results of our study confirmed the hypothesis that retracting behaviors are effectively employed by *L. irrorata* to alter its tolerance range when introduced to high temperatures, low humidity, or emersion, but that it is limited in its capacity to avoid thermal stress when also under desiccating conditions. By analyzing the effect of retracting behaviors individually, we were able to reveal how the fundamental niche of snails is modified differently by each behavioral response.

The retracting behaviors that snails employ alter the degree of thermal and desiccation stresses that they experience (McMahon, 1990), and thereby shift their temperature and humidity tolerance ranges. However, their ability to avoid thermal stress is limited by their capacity to tolerate desiccation, because an increase in the tissue surface area for evaporative cooling also increases exposure to desiccation (Campbell and Norman, 1998). For instance, at 45 °C in high RH treatments, *L. irrorata* did not have to cope with the same level of desiccation stress as in low RH treatments due to a lower VD difference (2.9 ± 2.2 g/m^3 in high RH vs. 16.6 ± 3.4 g/m^3 in low RH), but had limited use of evaporative cooling. However, the snails still lost more water at this temperature, while maintaining body temperatures equivalent to the biomimics and higher than snails in low RH conditions. While snails in the low RH treatments were better able to use evaporative cooling due to a greater VD difference, they also had to control their water loss and thus were not always able to avoid mortality from high temperatures.

L. irrorata's capacity for avoiding thermal stress by evaporative cooling is closely connected with desiccation, but its ability to avoid desiccation is only affected by thermal stress when close to its thermal tolerance limits. Without thermal stress, snails are able to effectively avoid desiccation by retracting into their shell. As determined from the wind speed experiments, water loss increased the more that snails exposed their tissue, but was only affected by wind speed when the snails were crawling. Snails were not affected by wind speed when retracted and also lost the least amount of water. Therefore, snails have the ability to avoid desiccation stress effectively when there is no thermal stress, but as thermal stress increases,
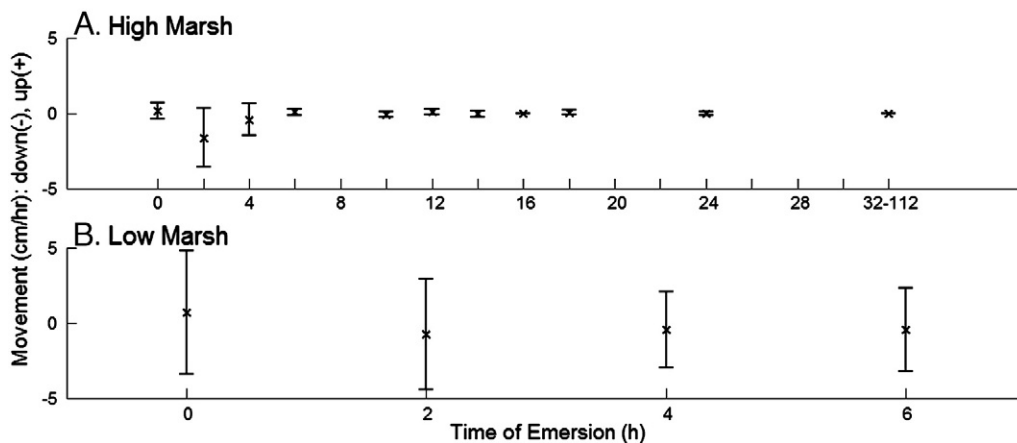

Fig. 8. Hourly movement of *Littoraria irrorata* up (+) and down (−) *Spartina alterniflora* stalks in the a) high marsh and b) low marsh in relation to the time of emersion. Data are averages ± 1 SD.

desiccation has to be balanced with the need for evaporative cooling. At extreme air temperatures (45 °C and above), the snails suffer heat coma (Gòmez-Cornejo, 1993) and are not able to retract into their shells, so they can experience a combination of water loss and thermal stress even in conditions with low VD deficits.

L. irrorata responded to desiccation more consistently and immediately than to rising temperatures, which may be a result of the desiccating consequences of evaporative cooling. The finding that snails in low RH treatments were largely glued up to 40 °C and lost the same amount of water at every temperature (regardless of behavior) indicated that they were responding to desiccation stress at all temperatures. At 45 °C, when the snails were highly thermally stressed, those in low RH treatments were trying to cope with both thermal and desiccation stresses. Unlike the snails in the high RH treatments that were either gaping or retracted, snails in the low RH treatments were still exhibiting all four behaviors. The fact that there was more of a spread in behavior at 45 °C indicated that the snails may not be well-adapted to cope with both stresses simultaneously. It appeared that some primarily avoided desiccation by gluing, or thermal stress by attaching, while others may have tried to avoid both by gaping. Rocky intertidal snails have been found to gape during periods of long emersion (McMahon and Britton, 1991), though this may be primarily to increase aerial metabolic gas exchange (McMahon, 1988). Snails may also use gaping to increase evaporative cooling, though at highly stressful temperatures, snails can exhibit gaping due to heat coma. During these studies, gaping was observed both as a responsive behavior and as a result of heat coma.

Despite the associated trade-off in desiccation, retracting behaviors that allowed for evaporative cooling in high temperature, low RH treatments increased the snails' thermal tolerance range. Snails that were only able to use evaporative cooling to a small extent in the high RH conditions had higher body temperatures than those in low RH conditions at all temperature treatments. Even though evaporative cooling only reduced body temperatures of snails in low RH treatments by ~1 °C (compared to biomimic temperatures), at higher temperatures they expired much less frequently than did snails in the high RH treatments.

Oxygen limitation may set the range of ectotherms' thermal tolerance windows (Pörtner, 2010), and specifically, snails have been found to be oxygen-limited at temperatures close to their thermal tolerance (Sokolova and Pörtner, 2003). When snails employ behaviors that reduce their body temperatures and increase air flow to their tissues, they may increase their ability to aerobically respire (McMahon, 1988). Conversely, behaviors that reduce water loss may decrease the snails' ability to exchange oxygen. While this study did not examine the trade-offs between body temperature, desiccation, and oxygen stress, this is an avenue for fruitful research. The results of this study do suggest, however, that while the use of behaviors that increase evaporative cooling is limited by desiccation, they can still be effectively employed to shift the snails' fundamental niche with respect to temperature.

Upon tidal emersion, *L. irrorata* was found to contain little water in its mantle cavity compared to the amount it contains in its tissues, even though desiccation stress was relatively low. This could be due to water loss from crawling up the stalks at high tide to avoid predators (Vaughn and Fisher, 1992; West and Williams, 1986). Even after snails were rehydrated, they still contained relatively little water in their mantle cavities compared to water storage in their tissues. During the experiments, snails were predominantly active in conditions with low desiccation stress, even though their mantle cavity fluid had been extracted. Therefore, it is unlikely that extracting mantle cavity fluid before the experiments to standardize water content (Henry et al., 1993) had a significant effect on the responses observed in the experiments.

The difference in thermal and desiccation stresses found between the high and low marsh allowed for a comparison of snail responses across a gradient of environmental conditions. Snails were consistently hotter in the high marsh (some even reaching lethal temperatures), while snails in the low marsh remained several degrees below lethal temperatures at all times. The high marsh also had a vertical gradient in heat stress, with higher air, biomimic, and *S. alterniflora* temperatures lower in the canopy at midday due to very low wind speeds close to the ground. The low marsh did not show the same gradient, because the mud and lower heights of the canopy were continuously cooled by tidal inundation. Also, snails in the high marsh reached higher temperatures than the substratum at midday, whereas snails in the low marsh remained cooler than the substratum and were unaffected by the time of day. Overall, snail temperatures in the high marsh were greatly affected by the microclimate throughout the day and reached thermally stressful levels, while snail temperatures in the low marsh were relatively stable and non-stressful.

Conditions in the high marsh were also much more desiccating than in the low marsh since the high marsh site was not tidally inundated during the neap tide. During this time, the soil went from a muddy consistency to dry pellets that provided little-to-no moisture for the snails. The verified tides at Oyster Landing (Station 8662245, www.tidesandcurrents.noaa.gov) indicated that at the elevation of our high marsh site (1.4 m above MLLW), emersion periods lasting several days were common during summer neap tides in 2010 (4 times from May–September). In the low marsh, the tide inundated the site every 6 h, which allowed the snails to rehydrate their tissue regularly and provided the soil with continuous moisture.

Even though the low marsh was a much wetter environment, both sites had more desiccating conditions (up to 2× more in the high marsh) at midday than those used for the low RH treatments in the laboratory. Also, in the early morning, desiccation stress in the high marsh was lower closer to the ground, but by midday conditions, were more desiccating at lower heights. This shift in potential for desiccation with height was not evident in RH values, because RH was often higher closer to the ground. The discrepancy between RH and the VD difference between the snail's tissue and the air exemplifies the importance of determining desiccation levels by taking into account the snails' body temperatures.

L. irrorata responded to thermal and desiccation stresses similarly in the field as in the laboratory. Despite the relatively low levels of desiccation stress in the low marsh compared to the high marsh, snails at both locations primarily exhibited desiccation avoidant behaviors during aerial exposure. The finding that at 8:00 h, when thermal stress was low, snails in the low marsh were reducing body temperatures through evaporative cooling more than snails in the high marsh indicated that they were not as consistent in avoiding water loss. Snails in rocky intertidal habitats have also been found to lose more water when located lower on the shore due to prolonged activity during low tide (McMahon and Britton, 1991). However, the differences between high and low marsh snails in behavior and physiological condition relative to the surrounding microclimate were comparatively minimal.

The effect of time of day and emersion on snail movement in the low marsh was primarily due to the incoming tide. As has previously been found, the snails moved down the stalk to re-wet their tissue (Gòmez-Cornejo, 1993), then immediately climbed back up the stalk to avoid predation (Vaughn and Fisher, 1988). Furthermore, when the tide did not come in after the first 6 h of emersion in the high marsh, the snails moved very little and remained glued for the rest of the emersion period. While on average the snails in the low marsh were moving very little after the tide went out, there was much more variability in their movement than snails in the high marsh. A study on *L. irrorata's* vertical migration in Galveston Bay, TX found that during warm weather, the snails only climbed grass stalks with tidal inundation and were otherwise found foraging on the sediment (Vaughn and Fisher, 1992). Conversely, a study in Dauphin Island, AL observed *L. irrorata* climbing stalks during periods of

low tide in July (McBride et al., 1989). The snails in both of these studies may have been experiencing less stressful microclimate conditions than the snails in this study, and therefore were able to exhibit more active behaviors. In both the high and low marsh of South Carolina, *L. irrorata* responded to potential desiccation stress when emerged, though snails in the high marsh were much more consistent and rigorous in avoiding desiccation.

As in the laboratory experiment, snails that simultaneously experienced thermal and desiccation stresses had difficulty in balancing the two through retracting behaviors. Despite potential desiccation, snails were maintaining a low level of evaporative cooling by mostly gaping while glued to the stalk (as demonstrated by lower snail temperatures than biomimic temperatures). However, when conditions were both dry and hot (e.g. July 7th in the high marsh), the snails were unable to increase evaporative cooling, and thus a few reached potentially lethal temperatures (~45 °C), though only one expired. As they had been emerged for over 100 h by this time, the snails may have been unable to afford further desiccation by exposing their mantle tissue in order to increase evaporative cooling. In rocky intertidal habitats, limpets were found to live closer to their desiccation tolerance limit in places where their range was surrounded by adequate food resources (Wolcott, 1973). The observation that *L. irrorata* can reach its tolerance limits when experiencing both thermal and desiccation stresses at this site may indicate that it has spread to its range limit in order to exploit energy resources within the *S. alterniflora* canopy.

Snails in the high marsh were found low in the *S. alterniflora* canopy during the emersion period, even though temperature and VD measurements indicated that conditions were more stressful there at midday. Field observations at a high marsh site within 250 m of ours found that *L. irrorata* was more frequently low on *S. alterniflora* when temperatures were hotter (Gòmez-Cornejo, 1993). Lack of movement appeared to be due to avoidance of desiccation from crawling, which would prevent *L. irrorata* from using vertical migration to change its microclimate. Snails in the low marsh also did not vertically migrate in response to abiotic conditions, though their microclimates were minimally stressful. While snails in the high marsh experienced much greater thermal and desiccation stresses, they do not migrate from the high to low marsh (Hamilton, 1978) in part due to heightened predation in the low marsh (Baxter, 1983). The marsh is a very heterogeneous environment, but *L. irrorata* is too constrained by predation and desiccation to take advantage of movement as a way to avoid abiotic stresses.

4.1. Conclusions

L. irrorata is able to perform several different retracting behaviors that alter its functional niche and allow it to withstand higher temperatures or VD deficits. When the snails simultaneously experience both thermal and desiccation stresses, they have to either tolerate both at a lesser degree, or heighten one stress while avoiding the other. The snails generally respond to tidal emersion and high VD differences between their tissue and the air by withdrawing into the shell soon after exposure. Under conditions of interacting thermal and desiccation stresses, they exhibit a distribution of behaviors and less effective avoidance. Since desiccation stress in the high marsh can be severe during neap tides in summer months, the snails may occasionally be unable to avoid reaching potentially lethal temperatures of 45 °C and above. However, high marsh snails appear to be much more limited by environmental conditions than those in the low marsh. While snails in the low marsh respond to potential desiccation stress, their daily movement and behavior is also likely to be affected by predator avoidance. *L. irrorata's* use of different retracting behaviors to shift its fundamental niche (climate space) may affect interactions such as predation and herbivory in its realized niche space. The behavioral responses of *L. irrorata* as a function of its realized niche in the marsh have a strong impact on the species' individual

ecology, and are therefore important to consider in salt marsh community ecology.

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Acknowledgments

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