

Superior performance of a trailing edge low-latitude population of an intertidal marine invertebrate

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ABSTRACT

The objective of this study is to compare ecologically relevant measures of performance over a broad range of latitude of a species subjected to climate change. Do populations change in relative function over a wide range of latitude? Are populations at the low latitude trailing edge in danger of extinction in the onset of thermal stress? Coastal marine species with planktonic larvae can range over an enormous span of latitude and thermal environments. The fiddler crab *Leptuca pugilator* extends from high-latitude (41.75°N) winter-frozen Massachusetts tidal flats in the north to subtropical low latitude flats in Florida (24.55°N), where they may be active at the surface over most of the year. We characterized the air environment for males at three sites (New York – latitude 40.0°N, Beaufort, North Carolina – latitude 34.7°N, Panama Florida, latitude 30.0°N) over the geographic-thermal range, and found major differences in temperature, wind speed, humidity, and vapor pressure deficit. Florida *L. pugilator* males preferred warmer sand than North Carolina and New York crabs. Local adaptation to latitude-dependent thermal conditions might suggest tradeoffs in performance as a function of temperature. We examined measures of predator escape performance (running speed and righting speed) and overall condition reflecting endurance rivalry success (endurance on a treadmill and major claw closing force) over a wide range of test temperatures. Predator escape rates increase steadily with increasing temperature, but endurance rivalry measures show an intermediate temperature peak of performance. We tested the hypothesis of tradeoffs, with expected local superiority of performance according to regional thermal differences. But instead, the trailing edge Florida males were superior to the higher latitude populations, over a broad range of temperature, but especially at higher temperatures, for all four types of performance measures. The trailing edge population of *L. pugilator*, in thermal terms, is therefore likely not vulnerable to near future further effects of warming in terms of performance measures related to male reproductive and feeding activities and escape from predators. Fiddler crabs appear to display niche conservatism for stronger performance at tropical temperatures. Such a natural tropical superiority in performance might have to be accommodated in future conceptions of response of marine species to climate change with broad latitudinal distributions in the tropics.

1. Introduction

The broad thermal-latitudinal range of coastal marine species places populations in a thermally graded series presumably living under different selection regimes, which are all subjected to climate change (Levinton, 1983; Bennett et al., 2019). Latitudinal genetic clines have been associated with natural selection (Levinton and Suchanek, 1978; Sotka et al., 2004), and latitudinal intraspecific variation in physiologically related performance traits have also been described in marine invertebrate species as the result of adaptation to climate variation

related to latitude (Rao, 1953; Pickens, 1965; Levinton and Monahan, 1983; Lonsdale and Levinton, 1985; Stillman and Somero, 2000; Broitman et al., 2021).

Climate change, especially large-scale ocean warming trends, presents major challenges to the functioning and survival of coastal intertidal species. As warming occurs, species with high dispersal capability can extend their geographic ranges to higher latitudes, but they might also suffer strong thermal stress from increasing air and water temperatures at their respective lower latitude limits, causing high temperature stress and even truncation of the geographic range. It is therefore crucial

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to develop tools to understand performance of both larval and adults over a broad latitudinal range. While we expect a general warming to occur with decreasing coastal latitude, local differences in tidal periodicity and temporal changes of interactions with open-ocean climate owing to various climate oscillations might alter our conception of a smooth north-south trend in thermal conditions for coastal species (Helmuth et al., 2003). Strong seasonal temperature variation must also complicate responses to thermal regimes at different latitudes. Of equal importance may be adaptations of some phylogenetic groups to long-standing climatic conditions within which they have evolved.

With ocean warming (IPCC, 2022), despite complexities of marine communities (Poloczanska et al., 2016), the high-latitude geographic ranges of coastal species are expanding (Barry et al., 1995; Mieszkowska et al., 2006; Wetthey and Woodin, 2008; Johnson, 2014; Rosenberg, 2018), more so than many other biological groups (Helmuth et al., 2006; Wetthey and Woodin, 2008) creating opportunities for genetic differentiation and evolutionary change on range margins (Cahill and Levinton, 2016). On some coasts, spread to higher latitudes has not been observed (Rivadeneira and Fernandez, 2005). The apparent broad ranges of many marine species are complicated by a tendency to identify complexes of species under one broadly distributed species name, and by recent increases of global invasions facilitated by human activities (Carlton and Geller, 1993; Darling and Carlton, 2018).

Logic would predict that warming should be directly implicated in local extinctions related to climate change, but a broad investigation produced few cases where extinction could be explained by thermal stress, and other factors such as interspecific competition were instead implicated (Cahill et al., 2013). A broad pattern of niche conservatism suggests that climate change might negatively affect populations resistant to change in habitat selectivity and unable to adapt to environmental change (Lynch et al., 1993; Wiens and Graham, 2005). Along coasts following lines of longitude, it is widely expected that species at the low latitude limit, or trailing edge, would be most vulnerable to high temperature thermal stress, leading to conservation strategies for vulnerable species (Gilbert et al., 2020). Some evidence exists for such truncation of coastal marine species at the species (Jones et al., 2010; Cahill et al., 2014) and genotype (Nicastro et al., 2013) levels. A study of records of abundance changes of ca. 300 marine species (mainly fishes) demonstrated a significant trend over the past century, whereby declines were at low latitude ends of ranges, whereas population increases were at high latitude range boundaries (Hastings et al., 2020). There was considerable scatter in population changes, so vulnerability might be related to particular ecologies and taxonomic affiliations. Such generalities argue for more complete studies of individual species.

An understanding of genetic diversity and capacity for adaptation at range boundaries will be crucial for understanding the evolutionary potential of marine populations at range edges (Cahill and Levinton, 2016; Vranken et al., 2021). It is equally possible that adaptation to changing thermal conditions at different parts of the latitudinal range (Levinton, 1983; Lonsdale and Levinton, 1989) might make trailing edge populations adapted to the changing thermal conditions found at different latitudes, reducing their vulnerability to thermal stress accompanying climate change. This prediction should apply especially to species living in strongly seasonal environments with frequent high temperature peaks in typical summers. Adaptation to these extremes might select for broadly thermally adapted species that are less vulnerable to high temperature stress from climate change. Mobile air-breathing intertidal poikilotherms might be vulnerable to thermal and hydric stress, but behavioral responses such as strategic retreats to shade and moist microhabitats might ameliorate stress (Allen and Levinton, 2014), even in trailing edge environments.

The objective of this study is to compare ecologically relevant measures of performance over a broad range of latitude of a species subjected to climate change, to test the hypothesis that thermal sensitivity to a range of environmental temperatures varies with latitude of origin. We have chosen fiddler crabs (Decapoda, family Ocypodidae) as

a model system to study thermal-related performance in the context of ocean warming and global climate change. Marine species are anticipated to be more vulnerable to reaching thermal limits of stress, relative to terrestrial species (Pinsky et al., 2019). Currently, 106 named species of fiddler crabs (Rosenberg, 2014) exist in typically intertidal habitats throughout tropical and temperate shores, with a biphasic adult occurrence in open air (sun and shade) and in moist burrows (Crane, 1975). Species diversity, despite regional biogeographic subdivisions (Rosenberg, 2020), is uniformly strongly correlated positively with summer air temperature (Levinton and Mackie, 2013), perhaps suggesting that hot low latitude warm environments actually promote biodiversity in this group. Fiddler crab species ranges are commonly broad (Crane, 1975; Rosenberg, 2014) and overlap of species within biogeographic regions is usually broad (J. Levinton, unpublished). High latitude range limits are associated with larval survival at low temperatures (Sanford et al., 2006; De Grande et al., 2021). While intertidal, species may range over broad salinity zones (Thurman, 1998; Thurman et al., 2010), and extend from dry, sunny and high intertidal sites to low intertidal zones, with attendant differences in resistance to desiccation stress (Levinton et al., 2015a; Capparelli et al., 2021). Most importantly, a series of methods have been developed to study adult fiddler crab performance (e.g., Levinton et al., 1995; Allen et al., 2012; Levinton et al., 2015a; Darnell and Darnell, 2018; Pena and Levinton, 2021; Jimenez et al., 2022). A number of studies have made comparisons among fiddler crab species living in different major habitats (Thurman et al., 2010; Levinton et al., 2015b; Faria et al., 2017; Capparelli et al., 2021) or climate zones (Jimenez et al., 2022).

Studies of thermal preference and natural occurrence demonstrate that male fiddler crabs may often occur in far more thermally stressful microhabitats than they would prefer (Allen and Levinton, 2014; Munguia et al., 2017; Levinton, 2020). Species living in shady sites enjoy far less thermal stress than in open sunny sites (Nobbs, 2003; Darnell et al., 2015; Chou et al., 2018), and species with males displaying in open sunny sites retreat to burrows and even to the low shore periodically to restore hydric state and lower body temperature (Christy, 1978; Allen and Levinton, 2014).

We employed four different measures of performance, that capture different aspects of successful behavioral response of males at mating areas to different real-world challenges, including (1) escape from and response to predators (Bildstein et al., 1989) and (2) maintenance of continuing activity under conditions of heating while males are feeding and wave-displaying to attract females to mating burrow areas. The latter traits reflect endurance rivalry success (Darnell et al., 2013). These measures are complements to field experiments where thermal stress has been manipulated by field shading to investigate behavioral responses (Allen et al., 2012). Our multi-performance approach complements the need for consideration of multiple stressors, which may act in variable combinations to exert physiological stress (Gunderson et al., 2016). Previous studies have incorporated components of performance related to energy budgets (Lonsdale and Levinton, 1985, 1989) or tolerance of physiological extremes, such as CT_{max} , tolerance of desiccation, measure of heartbeat rate, acclimation ability, and respiration rate (Thurman, 1998; Stillman and Somero, 2000; Stillman, 2003; Darnell and Darnell, 2018; Levinton et al., 2020; Jimenez et al., 2022). This study instead incorporates measures of performance more closely related to crucial functions performed regularly in air during the hot intertidal mating season. We believe that this is the most complete study done to date using multiple measures of performance of populations from a wide latitudinal range of natural populations of a coastal marine species, all related to the crucial element of male success in a stressful mating arena.

2. Materials and methods

2.1. Collecting sites

Leptuca pugilator males were collected from three sites (Fig. 1),



Fig. 1. Map of eastern North America showing collection sites.

ranging from Long Island, New York, USA to the panhandle of Florida, USA from June–July 2019. These sites nearly encompass the latitudinal thermal range of maximum summer temperatures (Darnell and Darnell, 2018). The three sites were: (1) West Meadow Creek, Old Field, New York, 40.935°, −73.144167°; (2) Rachel Carson Reserve near Beaufort North Carolina, 34.711096°, −76.677762°; (3) Porter Island near Panama, FL, within the St. Marks National Wildlife Refuge. 30.015889°, −84.368736°. All sites were intertidal sand flats near *Spartina alterniflora*-dominated salt marshes. Males were collected by hand, and about

300–400 individuals were placed in an insulated container in a plastic bag with sand and ca. 500 ml of seawater. The container was shipped overnight to a laboratory in Stony Brook NY. Stony Brook crabs were collected, treated in the same way, and kept overnight in the container at room temperature. Unpacked crabs were transferred to seawater and kept for 7–8 days at ca. 20 °C in a salinity of 30, and fed TetraMarine fish flakes (Tetra, Blacksburg, VA) every other day ad libitum. Before experiments were performed. Crabs were kept on a 12 h light/dark cycle.

2.2. Climate characterization

We characterized the climate at each of the three sites using Niche-Mapper software (niche-mapper.com). The Global Climate Extractor module was employed to characterize air properties corresponding to the coordinates of the three collecting sites at zero altitude, including monthly average temperature, monthly minimum humidity (we did not use maximum humidity because it reached 100% at all three sites and provided no differentiation among sites), monthly average wind speed, and monthly vapor pressure deficit (the vapor pressure at 100% relative humidity minus the vapor pressure corresponding to the monthly minimum humidity). Vapor pressure deficit was taken as a measure of a crab's relative ability to reduce body temperature by means of evaporation (Wilkins and Fingerman, 1965; Thurman, 1998; Allen et al., 2012).

2.3. Temperature preference

A thermal gradient was created by circulating water from a cold (5 °C) water source and a warm (40 °C) water source (Forma Scientific water baths, Marietta, OH) combining along an aluminum block 1.8 m in length. Mounted on the block was an open Plexiglas raceway (1.2 m long, by 0.10 m wide x 0.10 m high) with a layer of sand ca. 5 mm in depth, kept moist with seawater. This created a linear thermal gradient, following methods reported previously (Allen et al., 2012). Males were placed successively at 30, 60, and 90 cm locations, left to right. After 15 min, we measured the sand temperature at the location of the crab (T_e) with an Oakton model WD 39642 infrared thermometer and used a penetrating thermocouple thermometer with a 0.34 mm diameter hypodermic probe, coupled to an Omega K-type digital thermometer to measure body temperature (T_b). The probe was inserted ca 5 mm into the ventral body cavity. Body temperatures after 15 min in the gradient were used as a measurement of the temperature setpoint, T_{set} (Hertz et al., 1993). During the run the investigator was invisible to the crab on the other side of a large baffle. Sand temperatures ranged from ca. 8–40 °C, over the length of the sand raceway.

2.4. Performance measures

2.4.1. Performance and temperature

Using collected male fiddler crabs from the three localities, we measured various aspects of performance, over a range of body temperatures, in an environmental chamber with a relative humidity of 50–60%. In all cases, males were removed from seawater, and placed in the test temperature on a moist paper towel for 20 min before measurements were made which allowed body temperature, T_b to equilibrate with the chamber air temperature (Allen et al., 2012), although body temperature likely lagged at higher chamber temperatures (Levinton et al., 2020).

2.4.2. Treadmill endurance

Treadmill endurance was used as a measure of general ability of males to maintain activity, displaying and feeding on an open sandflat. We used a previously described treadmill (Allen et al., 2012), with speed set at 4 m min⁻¹ (0.24 km h⁻¹), which was a mid-range of running speeds used in past work (Full and Herreid, 1984), designed to bring crabs to inability to keep pace on the treadmill, after a period of time. Failure to keep pace was identified by dragging of the abdomen and failure to respond to prodding. *L. pugilator* was kept for 20 min in the chamber before measurements (time to failure to keep pace with treadmill in seconds) were conducted at 10, 15, 20, 25, 30, 35 °C. In all temperatures, $N = 10$. Fiddler crabs even under modest running conditions derive the majority of ATP through anaerobic metabolic pathways (Full and Herreid, 1984).

2.4.3. Major claw closing force

Closing force of the major claw is a measure of ability to succeed in intermale combat, but also is a useful measure of overall male vigor, during the time it is at its burrow, engaging in reproductive activities, including display, mating, and combat (McLain et al., 2015). The chela-closer muscle operates through a fulcrum than can readily be used to measure closing force in fiddler crabs (Levinton and Judge, 1993). We used a closing apparatus modeled after a battery-operated device using a force transducer connected to two compression plates, adaptable to laboratory and field conditions (McLain et al., 2015), but modified using a slightly different apparatus (Levinton and Arena, 2021). Measurements of maximum closing force (N) at claw tips were conducted at 20, 25, 30, 35, 40, 45, 50 °C; at each temperature, $N = 15$.

2.4.4. Sprint speed

Running speed was used as a measure that might correspond to escape from mobile predators, especially birds (Riegner, 1982; Land and Layne, 1995; Koga et al., 2001), but we have observed male *L. pugilator* also running from and captured by approaching blue crabs, *Callinectes sapidus*. Indirect evidence of scat composition also shows the importance of raccoons as predators at the New York locality. Male fiddler crabs were blotted dry and kept for 30 min at the test temperature before the sprint speed measure was made. A male was placed at the end of a running track that was 180 cm long and 14 cm wide, with ca. 1 cm of dry sand, and males were encouraged to continue running to the end of the track. Measurements (made with an electronic stopwatch, and converted to sprint speed: cm/s) were conducted at 15, 20, 25, 30, 35, 40, 45 °C, with 25 males tested at each temperature.

2.4.5. Righting time

Righting time can also be critical in escape from attacking predators (Pena and Levinton, 2021). We placed males upside down and measured time the crab took to return to fully standing position with a hand-held stopwatch, in seconds, following a published method (Pena and Levinton, 2021). Crabs were kept at experimental temperature for 20 min, and measurements of righting time (seconds) were conducted at 10, 15, 20, 25, 30 °C; at each temperature, $N = 15$.

2.4.6. Body size measures

We measured carapace width and length as a measure of body size. We report overall mean carapace width for the three sites, averaged over the individuals used in the performance experiments.

2.5. Statistical analyses and experimental setup

Comparisons were first made on graphs of performance measures, as a function of temperature and locality. Initial comparisons were made by simply comparing means and standard errors across the temperature spectrum. For temperature preference experiments, analyses involved ANOVA among groups, and mean preferences were compared by multiple-mean comparisons with Bonferroni correction. For performance measures, treadmill endurance and major claw closing force had peaks of performance at intermediate temperatures, so multiple comparisons among localities were done by multiple comparisons of means using standard ANOVA, with Bonferroni correction, where appropriate. By comparison, sprint speed and righting time displayed monotonic changes with increasing temperature. Sprint speeds among localities were analyzed using standard ANOVA techniques, and specific multiple comparisons with Bonferroni corrections were performed. A similar analysis was done for righting time comparisons. All analyses were performed using JMP, version 14 (SAS Institute, Cary, North Carolina, USA).

All experiments were performed in an environmental chamber with relative humidity of 50–60%. Temperature range endpoints differed among performance measures (see methods above), according to past experience of extremes where animals performed poorly or data

collection was too erratic to obtain predictable measurements. All differences were reckoned over broad ranges of temperatures within each performance measure.

3. Results

3.1. Climate comparisons

Overall, monthly mean maximum (Fig. 2a) and minimum (Fig. 2b) temperatures were lowest at the NY site but were strongly overlapping from June–September between the NC and FL sites. Higher temperatures in FL lingered through December, and on warm days, crabs could be found foraging at the FL site into December. Minimum humidity (Fig. 2c) was strikingly higher at the NC site during the period of May–August, with similar and lower humidity at that time at the FL and NY sites. Average monthly wind speed (Fig. 2c) was distinctly lower in FL, relative to the NC and NY sites. The higher summer humidity in NC confers a lower potential for water loss in NC in summer, but the high humidity also reduces the potential for evaporative cooling via water loss. The combination of temperature and humidity variation results in vapor pressure deficit (difference of vapor pressure in air and maximum

vapor pressure at 100% relative humidity) (Fig. 2d) being ordered from lowest to highest from NY to FL for all months of the year, with a peak in July–August. FL and NC vapor pressure deficits were similar through May, and then FL was the highest through December. NY values were distinctly lower than the other two sites throughout the year, suggesting a lower stress with regard to water loss than the other two lower-latitude sites.

3.2. Body size differences

Males used in performance experiments were collected in the field at the three sites to represent the larger males found at breeding burrows. Individuals were haphazardly chosen from aquaria for experiments. We found a significant size difference of males used in performance experiments: males from Beaufort NC (carapace width = 15.10 ± 0.065 mm [mean \pm SE], $N = 415$) were significantly smaller than either Stony Brook NY (carapace width = 18.33 ± 0.052 mm, $N = 415$), or Panacea FL (carapace width mean = 18.37 ± 0.073 mm, $N = 415$). A multiple comparison of means with Bonferroni correction shows that NY and FL mean carapace width do not differ from each other, but both each differ significantly and are larger than NC ($p < 0.0001$).

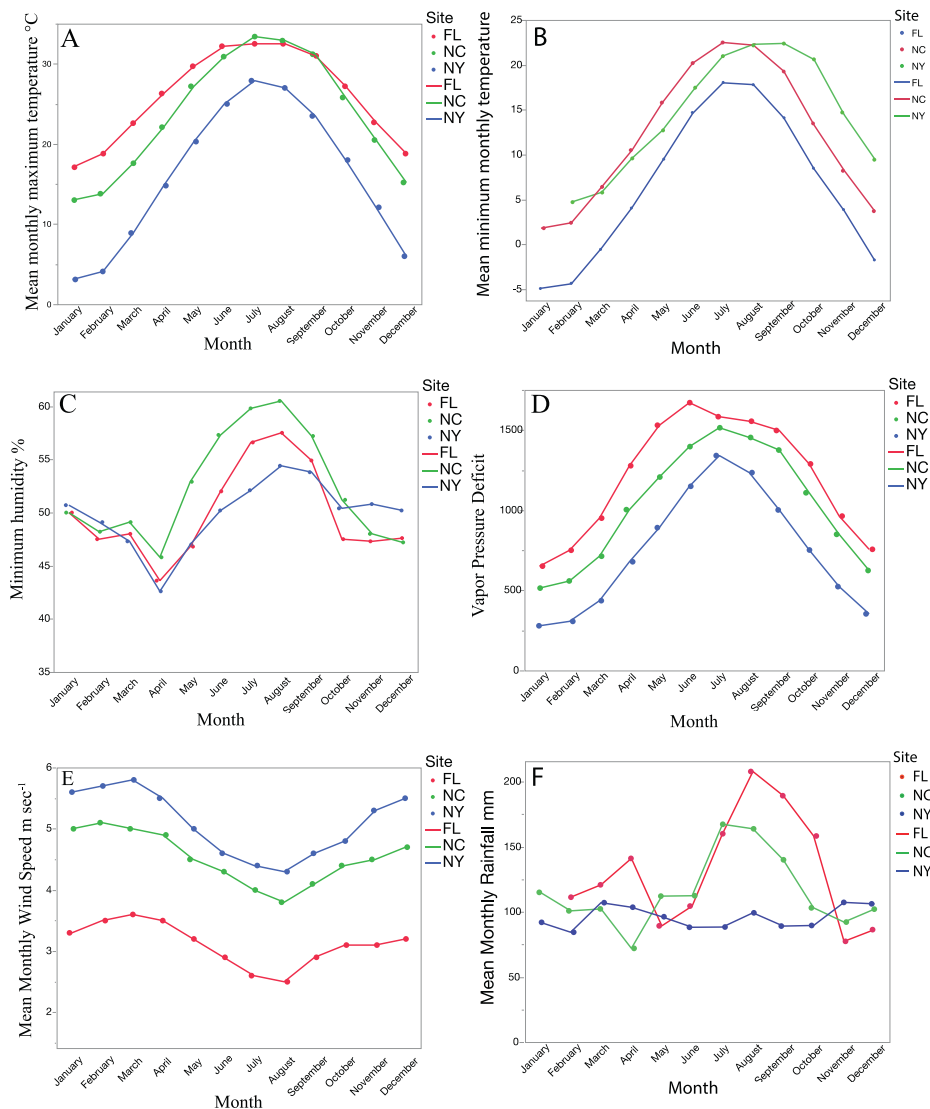


Fig. 2. Climate characterization of *Leptuca pugilator* sites using Niche Mapper (FL = Panacea, Florida; NC = Beaufort, North Carolina; NY = West Meadow Creek, New York): (A) Mean monthly maximum temperature; (B) Mean monthly minimum temperature; (C) Mean minimum percent humidity; (D) Mean monthly wind speed; (E) Mean monthly vapor pressure deficit.

3.3. Temperature preference

The sand temperature selected by male crabs from the three sites showed a strong among-site heterogeneity (Fig. 3); analysis of variance among groups was significant ($F_{2,87} = 5.03$, $p \sim 0.0086$). Multiple-mean comparisons with Bonferroni correction showed that FL crabs were located at a mean sand temperature significantly greater (ca. 30 °C) than NY = NC crabs (ca. 25–26 °C). This demonstrated that FL crabs preferred higher T_e than NY or NC crabs. T_b data however, showed no significant difference in body temperatures among crabs from the three sites (ANOVA, $F_{2,87} = 0.54$ ns). This may be due to the relatively short time of the experiment (15 min), precluding adjustment of internal body temperature (Levinton et al., 2020) or it may reflect frequent movement among sites in the gradient. It may be that even shorter times are relevant for temperature preference of males at or near their breeding burrows. Based on observations of 161 male *L. pugnator* in the high-intertidal mating area in Panacea, FL, surface time ranges from 0.4 to 48.4 min, with an average of 6.5 ± 6.8 (S.D.) minutes (M.Z. Darnell, unpublished data). Future studies of preference will have to take such short excursion times into account.

3.4. Performance measures

3.4.1. Treadmill endurance

For all three localities (Fig. 4a), time to endurance increased from 10 °C to a peak at 30 °C, with a decline to 35 °C. A complete linear model analysis showed a strong effect of temperature ($F_{2,2} = 127.4$, $p < 0.0001$), with a significant contribution of variation by the Florida site (t ratio = 2.03, $p \sim 0.04$), which is reflected in its great peak at 30 °C. When comparing 95% confidence limits of mean endurance, the Florida male crabs clearly had significantly greater endurance time at 30 °C, over North Carolina and New York. NC mean endurance time was consistently intermediate between NY and FL over the 25–35 °C temperature range, although mean NY and NC values were overlapping in 95% confidence limits over the entire range of experimental temperatures.

3.4.2. Major claw closing force

FL males (Fig. 4b) displayed increasing closing force from 20 °C to a peak temperature of 35 °C, with a decline to 45 °C. Closing force for NC increases to a peak of 30 °C with a gentle decline with increasing

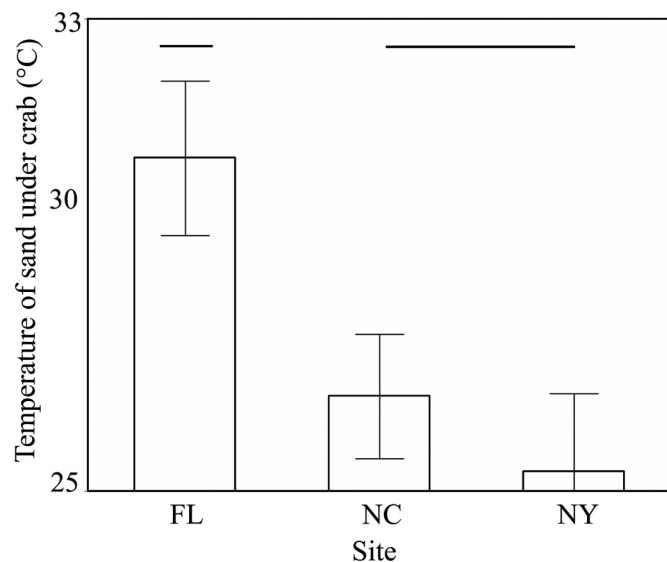


Fig. 3. Temperature of sand, where males were found after being placed 15 min at varying sites on a spatial-temperature gradient (mean \pm s.e.). Horizontal lines designate statistically homogeneous groups.

temperature. NY closing force was more flat with changing temperature and distinctly less than for the other two localities. Closing force of the FL males was distinctly greater than that of both NY and NC males over the range of 20–35 °C. FL closing force then declines above 35 °C and converges with measurements from the NC and NY sites, except at 50 °C, where FL closing force was higher than NC and NY, which overlapped. An ANOVA considering closing force by site and temperature shows a significant intersite effect ($F_{2,2} = 10.92$, $p < 0.0001$) and a significant temperature effect ($F_{2,2} = 18.97$, $p < 0.0001$), with no significant interaction effect ($F_{2,2} = 0.66$, $p \sim 0.52$). Over the entire temperature range FL closing force individual data shows significantly greater closing force than NC (Tukey HSD Bonferroni-corrected multiple comparison: t ratio = 3.53, $p \sim 0.001$) and NY (Tukey HSD Bonferroni-corrected multiple comparison: t ratio = 4.42, $p < 0.0001$) closing forces. NY and NC total individual data over all temperatures are not significantly different (t ratio = 0.89, $p = 0.646$). Data at 50 °C probably reflects significantly lower T_b , as we have found a lag time in environmental chambers between T_e and measured T_b (Levinton et al., 2020).

3.4.3. Sprint speed

Overall, sprint speed (Fig. 4c) for all three sites increased with increasing temperature from 5 to 40 °C and then reached a maximum from 40 to 50 °C (as in other measures in this study, body temperatures did not reach 50 °C, see Levinton et al., 2020). Males from all three localities (Fig. 4a) overlapped strongly at 15 °C, but crabs from the FL site had consistently highest sprint speeds at all temperatures of 20–45 °C, with the largest mean difference at 40 °C. NC was intermediate, and NY crabs had the lowest apparent sprint speeds at temperatures above 15 °C. An ANOVA shows a strongly significant intersite difference ($F_{2,2} = 34.56$, $p < 0.0001$) and a significant site \times temperature interaction ($F_{2,2} = 49.19$, $p \sim 0.007$). A multiple comparisons test over all temperatures (Tukey HSD test, Bonferroni corrected) showed that FL sprint speed was greater than NC (t ratio = 5.74, $p \sim 0.0001$) and greater than NY (t ratio = 8.08, $p < 0.0001$), but NC vs NY failed to demonstrate a significance at $p \sim 0.05$ (t ratio = 2.34, $p \sim 0.08$). Experimental temperatures of 50 °C appear to surpass the CT_{max} for populations of this species (Darnell and Darnell, 2018), but the time of exposure to this temperature in the environmental chamber did not allow for T_b to exceed CT_{max} (Levinton et al., 2020).

3.4.4. Righting time

For all three sites, righting time (Fig. 4d) decreased with increasing temperature from 15 to 25 (ANOVA Effect Test of all temperature data: $F = 26.99$, $p < 0.0001$). Mean righting times were close in value among sites. However, even though the curves overall for the three sites were not significantly different among sites (ANOVA on differences by site: $F = 1.43$, $p \sim 0.24$), there was a consistent ordering of mean righting time over all the temperatures: FL < NC < NY. At 30 °C righting time distinctly slowed for NY crabs, and two of the three sites at that temperature were significantly different ($p < 0.05$) with FL < NY (Tukey HSD comparison with Bonferroni correction, $p \sim 0.01$).

3.4.5. Was there an effect of among-site body size differences?

In section 3.2 we noted that body size (carapace length) of NC males was somewhat smaller than NY and FL, which do not differ from each other. This raises the question of whether this size difference had any impact on our overall results. We addressed this question with linear analysis of the sprint speed data, which are simplest to analyze, owing to the monotonic relation of sprint speed to temperature and the approximately parallel plots of sprint speed \times temperature, among localities (Fig. 4c). A linear model with two-way interaction effects was calculated (analysis available on request). Carapace length was not a significant contributor to sprint speed as an individual effect ($p \sim 0.06$) and the effect size of carapace length was the smallest of all measured effects ($< 1\%$ of total logworth values, involving temperature and site and 2-way interactions). This result is clearly reflected in the sprint speeds

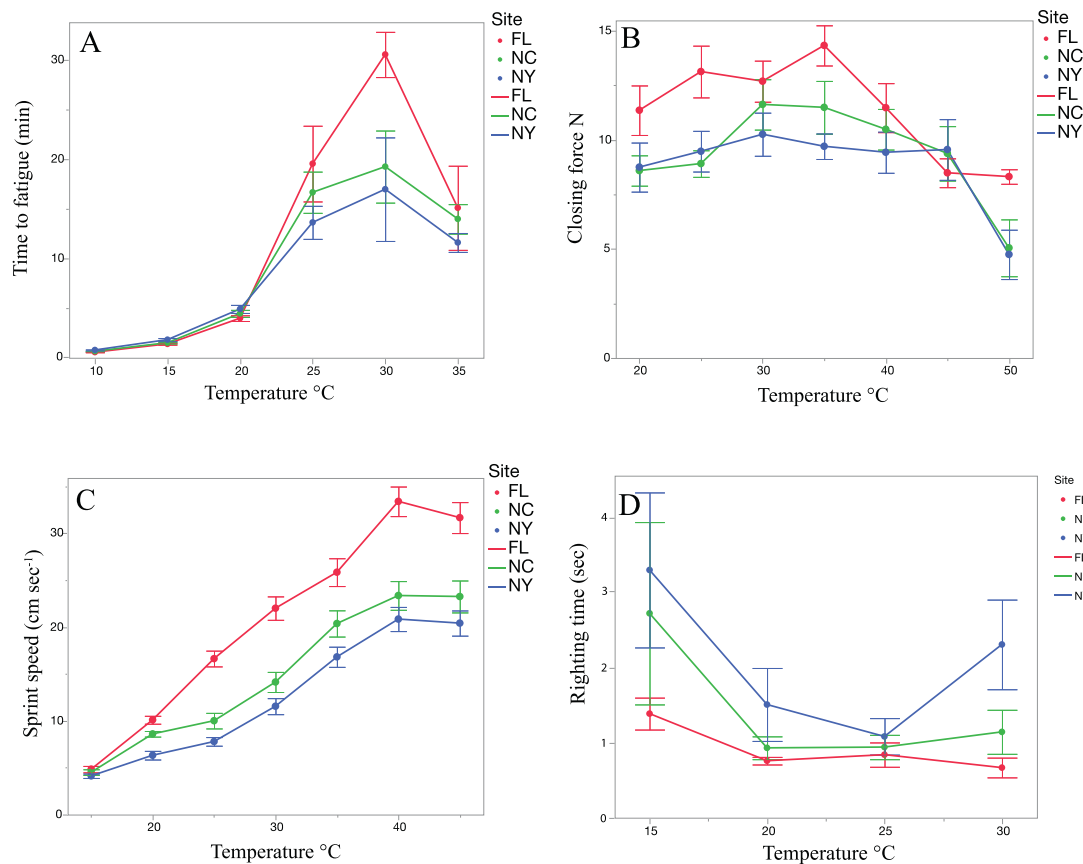


Fig. 4. Performance measures of *Leptuca pugilator* by site: (A) Sprint speed (cm sec^{-1}) over a 1.8 m sand track; (B) Endurance time to fatigue (min) on treadmill; (C) Closing force (N) of the major claw tip; (D) Righting time (sec).

shown in Fig. 4C, where NY speeds are the lowest, and FL speeds are clearly the highest, despite essentially identical body size distributions. We conclude therefore that size is not an important contributor to the major performance superiority of the FL crabs in sprint speed found in this study.

4. Discussion

Because our world coasts are so dominated by north-south orientations, latitude has become a touchstone context for the understanding of thermal adaptation and the possible impact of climate change on coastal species. As discussed above, coastal marine species can respond biogeographically to ocean warming by extending biogeographic range to higher latitudes, suffer extinction at the low-latitude “trailing edge” owing to extreme thermal stress that outpaces local adaptation, or (for non-obligatory intertidal and estuarine species) by extending range to cooler deeper waters, if suitable habitats exist. These predictions are at biogeographic boundaries and ignore the wide range of thermally variable habitats that extend throughout the interior biogeographic range of a coastal-intertidal species. They also ignore larger biogeographic issues. Fiddler crabs, for example, occur throughout the world tropics and subtropics, and diversity seems to increase directly with temperature (Levinton and Mackie, 2013), suggesting a niche conservatism (Wiens and Graham, 2005) for tropical adaptation.

Adaptive thermal performance responses to climate change within a range are liable to be complex: (a) Tradeoffs may exist between thermal responses such as the ability to acclimate to short term thermal change and the survival from extreme temperature stress (Stillman, 2003), or greater tolerance to high temperatures at the cost of tolerance to low temperatures; (b) Local adaptation to thermal conditions at a given

latitude-thermal regime might involve compensation in response to energy budget constraints that could be costly as climate changes (Levinton, 1983; Lonsdale and Levinton, 1985), making it unclear whether local adaptation of marine species reduces the capacity to spread to new thermally extreme habitats; (c) Responses to thermal and thermal-hydric stress, might involve complex responses, dependent upon microhabitat distributions such as the presence of local refuges (Allen, 2007; Allen et al., 2012; Darnell et al., 2019); (d) Thermal responses might vary extensively with life history stage, e.g. differential thermal adaptations of planktonic larvae, recruiting juveniles, and adults (Sinclair et al., 2016). Thus, we would expect different measures of performance to have differing thermal response curves, simply owing to their adaptive value in differing ecological contexts (Levinton et al., 2020).

Temperature and desiccation stress strongly influence physiological adaptations relating to performance of intertidal animals (Hochachka and Somero, 2002; Helmuth et al., 2005). But many mobile organisms must carry out feeding and mating behavior under such stressful situations. In this study, we have chosen a species with broad latitudinal occurrence, and focused upon measures of performance that relate to success in mating behavior on a thermal-hydric stressful area of sand associated with a fiddler crab male’s breeding burrow (Christy, 1978; Allen et al., 2012; Allen and Levinton, 2014; Levinton et al., 2015a), which also places male fiddler crabs at risk of predation by mobile predators, especially shorebirds (Petit and Bildstein, 1987; Bildstein et al., 1989; Backwell et al., 1998). We selected two measures, sprint speed and righting time, which directly measure performance related to predator escape. Treadmill endurance at 0.24 km h⁻¹ requires mainly an anaerobic pathway to produce most energy (Full and Herreid, 1984), and we believe reflects energy consumed during mating display-related

locomotion and feeding movements around the mating burrow. Claw closing force reflects performance potential for combat and burrow defense. Energy for both these activities likely becomes less available as the male spends more days at its mating burrow where physiological stress is great and food is scarce (Christy, 1978; Allen and Levinton, 2014; McLain et al., 2015). Evidence suggests that closing force declines over several days when the male is active near a mating burrow, reflecting gradual overall weakening (McLain et al., 2015). Thus, our four measures capture various aspects of performance related to a stressful time for males, that eventually requires desertion of the burrow and periodic return to moist and more food-rich creek edge sites (Hernkind, 1968; Crane, 1975; Salmon and Hyatt, 1983).

Our multiple estimates of performance as a function of temperature clearly have strongly different responses with increasing temperature. Sprint speed increases monotonically with increasing temperature, to a peak of 40 °C. This response is generally consistent, with righting speed, our other measure of response to predators, which generally increases with increasing temperature (Fig. 4D). But at 30 °C, NY righting time is strongly negatively affected, which may be consistent with adaptation to lower temperatures at higher latitude. The measures of endurance rivalry success by contrast appear to display peaks around 30–35 °C. Treadmill endurance time reaches a clear peak at 30 °C for fiddler crabs from all three latitude-sites. Closing force also appears to gradually increase or be flat with increasing temperature and then decline as temperatures exceed 35 °C, suggesting negative effects under typical summer conditions on New York sand flats (Levinton, 2020), whose near surface air temperatures are cooler than the NC and FL sites (Fig. 2). Declining closing force is known to occur as fiddlers move from water-side sites to intertidal reproductive sites near breeding burrows after several days of activity in air near breeding burrows (McLain et al., 2015). Thus, our performance data reveals a complexity of responses that might show different thermal performance curves for two classes of behaviors. If these measures apply to field conditions, then continuing activity associated with feeding and display appears to occur at a lower peak temperature than the ability to escape predators.

Such differential responses of multiple performance measures suggest that a simple comparison of temperature preference to a single-type performance peak (Martin and Huey, 2008) tends to ignore the diverse thermal-related behaviors required for function and survival of a mobile organism living in a thermally stressed habitat. Sprint speed and righting time are instantaneous responses relating to a need for rapid escape from predators. Male *L. pugilator* run as fast as females with the same carapace size (Allen and Levinton, 2007). Surprisingly, presence of the male's giant cheliped imposes no cost on righting time (Pena and Levinton, 2021). In both cases, increasing temperature appears to allow faster response, which might be expected for a poikilotherm with adequate aerobic scope. In air, oxygen delivery scope might be far greater than in water, allowing fiddlers to respond rapidly with ample oxygen delivery (Fusi et al., 2016; Levinton et al., 2020), and gill structure of *L. pugilator* is adapted for efficient oxygen uptake in air (Rabalais and Cameron, 1985). But endurance measures of performance such as treadmill endurance time and claw closing force might reflect overall condition, based on cumulative stress as a male spends time in mating activities in the poor food conditions and stressful temperatures in which males live while in or near high and dry mating burrows (Allen and Levinton, 2014).

Despite the differences in performance measures, there is a consistent ordering of performance for sprint speed, endurance time, and closing force. Florida crabs are superior over NC and NY, over broad ranges of temperature. For sprint speed, FL crabs are faster at all temperatures. This is of special interest since mean minimum air temperature in NY is ca. 15 °C in May–June (Fig. 2), when males have emerged and are feeding in large droving groups (personal observations, JL). Righting speed results are consistent with sprint speed (with admittedly more overlap in experimental results), suggesting that FL *L. pugilator* enjoy a consistent advantage in predator avoidance relative to crabs

from higher latitudes over a wide range of temperatures. Consistent with these results is a relative preference of FL males for sediments warmer than NC or NY. Our results therefore suggest that the trailing edge population is thermally superior, and might survive considerable further warming.

It is true, however, that northern New York populations of *L. pugilator* have a lower CT_{max} than more low-latitude populations (Darnell and Darnell, 2018), indicating regional thermal evolutionary differentiation. This difference suggests adaptation to the lower temperature thermal regime in higher latitudes. But the overall superiority of Florida-low latitude populations is consistent with the notion that *L. pugilator* shares niche conservatism with fiddler crabs, whose overall species diversity correlates strongly with summer air temperature, irrespective of biogeographic region (Levinton and Mackie, 2013). Such a natural tropical superiority in performance might have to be accommodated in future conceptions of response of marine species to climate change with broad latitudinal distributions in the tropics. Our results are consistent with an interspecies study that demonstrates the relative superior survival and performance of tropical species to high temperature environmental extremes, relative to subtropical species (Jimenez et al., 2022).

Climate comparisons among the sites demonstrate a consistent ordering of increasing vapor pressure deficit with decreasing latitude, which suggests that lower latitude populations live under higher evaporative stress. This might result in stronger selection at lower latitudes for water retention and resistance to the effects of evaporation. While it is known that CT_{max} is greater for Florida populations (Darnell and Darnell, 2018), we are only beginning to understand adaptive responses relevant to more typical temperatures that males experience. A study of color response demonstrated that Florida males respond more in dorsal color to heat stress of 35 °C, whereas North Carolina males respond more to cold temperatures (15 °C), which may suggest differential adaptation in an important parameter relating to absorption and reflection of heat by adjustments of the dorsal carapace (Munguia et al., 2013).

A disadvantage of our approach is to use measures in the lab instead of directly in the field. It would be possible to study some of these measures in the field (e.g., closing force – (McLain et al., 2015), but our laboratory work shows strong variation in performance over a wide temperature range, which cannot be studied easily under field conditions. Classic studies of heartbeat performance of stationary intertidal mollusks over a wide range of latitudes is an important contribution to this field, showing strong variation in responses over a broad thermal range (Burnett et al., 2013; Seabra et al., 2016), but the measures we selected are diverse, and more closely connected to ecological challenges faced by male fiddler crabs, such as mating success and predation, in the context of thermal variation in a dynamically changing habitat, on a daily and seasonal scale. The ability to study these diverse responses, makes the laboratory approach powerful in dissecting the range of thermal adaptations required for successful male functioning in such a high and dry environment, ideal for mating success but in a thermally stressful microhabitat.

5. Main conclusions

Our study of populations of the fiddler crab *Leptuca pugilator* over a wide range of latitudes demonstrates the utility of studying a range of performance measures that reflect crucial thermal responses to focal individual performance challenges such as response to predators and endurance rivalry success in mating. The performance measures show strikingly different responses to temperature: predator escape measures show increasing performance with increasing temperature, whereas endurance rivalry success measures show intermediate temperature peaks. Our diverse performance measures demonstrate consistent superiority of the lowest latitude population over a wide range of temperatures, suggesting a thermal superiority and a likely resilience to future warming. This might reflect a general niche conservatism for tropical performance or perhaps local selection for performance over a

wide range of temperatures at the lowest latitude site.

Author statement

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Brook University, Stony Brook NY 11794-5245 USA., M. Zachery Darnell, Division of Coastal Sciences, School of Ocean Science and Engineering, The University of Southern Mississippi, Ocean Springs, Mississippi 39564 Levinton wrote the entire paper, designed the experiments, used Niche Mapper to analyze climate data, and analyzed the data emerging from performance comparison experiments.

M. Zachary Darnell contributed to the overall design of performance comparisons and selection of localities in order to perform comparative studies over the geographic range. Brooke Arena and Riley Pena performed most of the performance experiments and organized the data output for analysis.

Declaration of Competing Interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Jeffrey Levinton reports financial support was provided by National Science Foundation. Jeffrey Levinton reports a relationship with Stony Brook University that includes: employment. There are no other relationships or activities to declare.

Data availability

Data will be made available on request.

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