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Lower seawater pH reduces the foraging activity of the Florida stone crab, *Menippe mercenaria* (Say, 1818) (Decapoda: Brachyura: Menippidae)

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ABSTRACT

Anthropogenic activities like habitat degradation, excess nutrient runoff, and sewage outfalls can decrease seawater pH in coastal environments. Coastal waters can also experience frequent fluctuations in seawater pH due to biological activity (i.e., photosynthesis and respiration). Commercially important species like the Florida stone crab, *Menippe mercenaria* (Say, 1818), inhabit coastal waters and experience fluctuations in seawater pH on both diurnal and seasonal scales. Organisms exposed to reductions in seawater pH may have difficulty sensing chemical cues due to physiological changes and the associated metabolic stress of compensating for a more acidic environment. Here we determined the foraging activity of the Florida stone crab when exposed to reduced pH conditions (control pH 7.8, reduced pH 7.6). The impacts of reduced pH on foraging activity were determined by monitoring activity time, stress, predation attempts, and handling time when crabs were exposed to lower seawater pH for 12 hrs. Crabs exposed to reduced pH conditions experienced elevated stress levels and reduced activity than crabs in the control pH treatment. These results suggest that exposure to more extreme pH conditions may limit the foraging activity of stone crabs.

KEY WORDS: coastal acidification, Crustacea, crustacean fisheries, foraging behavior

INTRODUCTION

Reductions in seawater pH threaten many marine ecosystems, with current models predicting a decrease of 0.10–0.40 units by the end of the century (Dodd *et al.*, 2015; Wu *et al.*, 2017). The main contributor to the reduction in pH is the increasing concentration of carbon dioxide (CO_2) in the Earth's atmosphere, which is partly being absorbed by the oceans, a phenomenon called ocean acidification. Some coastal habitats are already experiencing reductions in seawater pH at a rate faster than what is projected for the end of the century due to anthropogenic activities such as land-based runoff and habitat degradation (De Carlo *et al.*, 2007). Coastal areas that are impacted by these changes are usually bays and estuaries, where there is a high nutrient influx from land-based runoff and where biological activity can impact shallow water pH on both daily and seasonal scales (De Carlo *et al.*, 2007, Carstensen & Duarte, 2019; Gravinese *et al.*, 2020). These areas can also experience sporadic inputs of freshwater, which mixes with saltwater causing a further decrease in the pH buffering capacity of the environment, making coastal waters more vulnerable to changes in pH, therefore increasing the severity of acidification in those environments (Saba *et al.*, 2019).

Changes in seawater pH are known to impact the physiology of many marine species (i.e. metabolism, reproduction, and chemical processing; Briffa *et al.*, 2012; Jiahuan *et al.*, 2018; Gravinese *et al.*, 2019). One known disruption caused by reduced pH is the inability to process chemical cues (Briffa *et al.*, 2012; Gravinese *et al.*, 2020). Many marine crustaceans use sensory stimuli to process chemical cues that can be used for homing, prey detection and evasion, and foraging (de la Haye *et al.*, 2011; Ross & Behringer, 2019; Gravinese *et al.*, 2020). Several recent studies have shown that reductions in seawater pH can reduce activity and impair the ability of crustaceans to identify or locate chemical stimuli previously known to elicit a behavioral response (de la Haye *et al.*, 2011; Ross & Behringer 2019; Gravinese *et al.*, 2020). For example, reduced pH was shown to reduce and limit the foraging activity in the Japanese stone crab, *Charybdis japonica* (A. Milne-Edwards, 1861) (Wu

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et al., 2017). Ross & Behringer (2019) showed that the ability to locate shelters by the Caribbean spiny lobster, *Panulirus argus* (Latreille 1804), was disrupted when exposed to low pH conditions, while Gravinese *et al.* (2020) showed that the pueruli of the same species of spiny lobster that were conditioned in reduced pH seawater were less active and failed to select known positive settlement cues.

The Florida stone crab, *Menippe mercenaria* (Say, 1818), lives in shallow coastal habitats that can experience shifts in seawater pH due to processes associated with coastal acidification. The crab is a commercially important species in Florida, where fishermen harvest one or both claws and return the body to the water allowing the claws to regenerate. The fishery is valued at ~$30 million annually. The crabs use their large claws to crush the shells of bivalves and other gastropods and feed on the tissues inside the shells (Brown & Haight, 1992; Rindone & Eggleston, 2011).

We aimed to determine if reduced seawater pH would alter the foraging activity of the Florida stone crab. We conducted a laboratory experiment to determine whether activity time (minutes), stress level, handling time (minutes), and predation attempts would be negatively impacted during exposure to a reduced seawater pH.

MATERIALS AND METHODS

Animal collection and care

Individuals of the Florida stone crab (mean 50.93 mm ± 6.07 SD carapace width) were collected by snorkeling and from the Florida Fish and Wildlife's Independent Stone Crab Monitoring Program in Tampa Bay, Florida from October 2021 to February 2022. After collection, crabs were transported to the ocean acidification laboratory at Florida Southern College, Lakeland, FL. Crabs were placed into 19-l aerated aquaria filled with seawater (temperature 26.5 °C ± 1.1 SD, salinity 38.33 ppt ± 2.53 SD) and were acclimated to laboratory conditions for 72 h. Crabs were not fed during this 72 h acclimation period. Individuals were randomly assigned into one of two treatments: the control (N =10, pH 7.86 ± 0.08 SD) or reduced pH (N =11, pH = 7.6 ± 0.08 SD). The control pH was based on the range of pH conditions that can be experienced within stone crab habitats that includes the U.S. Geological Survey's monitoring platform, Loboviz, (http://tampabay.loboviz.com/) located in the middle of Tampa Bay along with historical data from some parts of Florida Bay (Millero *et al.* 2001), and was within the range of seawater pH during the time of collection (temperature 19.75 °C± 3.45 SD; salinity 28.22 ppt ± 5.69 SD; pH 7.96 ± 0.20 SD). The reduced seawater pH was based on the Intergovernmental Panel on Climate Change end of century predictions (Masson-Delmotte *et al.*, 2018).

Experimental design and manipulation of seawater pH

We manipulated the pH of the laboratory seawater according to ocean acidification best practices (Riebesell *et al.*, 2010) by aerating header tanks with atmospheric air and CO_2 gas, which was controlled using a mass flow controller (model GFC17; Aalborg Instruments & Controls, Pearl River, NY, USA,). Temperature and salinity were recorded at the start of each trial using a conductivity thermometer probe (YSI, Yellow Springs, OH, USA) calibrated to manufacturer guidelines. Seawater pH was determined using a glass electrode probe (Thermo Fisher Scientific, Waltham, MA, USA) (Table 1) that was calibrated daily using tris buffer. Seawater samples were collected and were immediately preserved with 100 μ l of saturated mercuric chloride during each trial for measuring total alkalinity (A_T). Total alkalinity was measured using an automated total alkalinity titrator (model AS-ALK2; Apollo SciTech, Newark, DE, USA) that was calibrated with Dickson certified reference standards (Scripps Institution of Oceanography, La Jolla, CA, USA).

After acclimating to the laboratory environment, both control and reduced pH crabs were placed into the experimental chamber 12 h before a foraging trial began to acclimate to pH conditions. During each trial, the crabs were presented with seven live littleneck clams (*Protothaca staminea* (Conrad, 1837)), and were allowed to forage overnight to mimic foraging behavior observed in the wild. Foraging activity was video-recorded continuously using a GoPro Series 8 video camera (GoPro Inc., San Mateo, CA, USA) for a 13-h period. The experimental chambers were illuminated with dim red light during foraging trials. Each video was then analyzed for handling time (minutes spent handling a prey item), predation attempts made (number of times a crab touched a prey item), and total time actively moving within the chamber. No crab was used more than once, and the chambers were given a 100% water change after each trial to remove metabolic wastes and residual chemical cues from prey items.

The stress levels of stone crabs were determined using Florida Fish and Wildlife's reflex action mortality predictor (RAMP) described by Kronstadt *et al.* (2018) before and after each trial. The test includes an assessment of several involuntary reflexes in the crabs' bodies. The presence of these reflexes indicates low stress levels (i.e., score of 0), whereas the absence of these reflexes indicates higher stress levels (i.e., score of 6; see Table 2).

Statistical analysis

All data were tested for normality using a Shapiro-Wilk test. The number of predation attempts made on prey items, total time active, and handling time between treatments was analyzed using a Mann-Whitney U test. A Wilcoxon signed rank test was used to compare the difference in stress levels before and after each trial (Conover & Iman, 1981). All statistical tests were conducted using R Studio (version 4.1.2) (R Core Team, 2022).

Table 1. The environmental conditions during foraging activity trials where stone crabs (*Menippe mercenaria*) were exposed to a control pH and reduced pH. Mean daily seawater temperature (± SD), total alkalinity (A_T), and salinity.

Treatment	Temperature (°C)	pH_{total}	A_T (equiv kg^{-1})	Salinity (ppt)
Control pH	26.11 ± 1.22	7.86 ± 0.08	2050.87 ± 603.48	39.32 ± 3.53
Reduced pH	26.83 ± 0.79	7.65 ± 0.08	1908.127 ± 558.04	39.20 ± 3.77

Table 2. A description of the reflexes tested on stone crabs (*Menippe mercenaria*) used to assess stress level. Reflex tests were performed on crab individuals in the order they are listed. A reflex was considered absent when there was no reaction/response. This test assessed the presence or absence of a reflex to determine overall stress level and was modified from Kronstadt *et al.* (2018).

Reflex	Test	Presence of reflex	Absence of reflex
Leg retraction	Squeeze the walking legs gently with forceps.	The leg is pulled towards the body and out of the grip of forceps quickly.	The leg is not pulled away.
Joint reaction	Gently poke the soft tissue in the elbow with tweezers.	Legs and claws are quick to react to push the pressure away.	There is no movement from the crab after or during pressure.
Abdominal turgor	Pull open the abdominal flap with tweezers.	Retraction of the flap to the body immediately after being opened.	The flap remains open and hanging after being opened.
Abdomen reaction	Open abdominal flap with tweezers.	Chelipeds and legs become agitated and move.	There is no movement from the crab.
Mouth closure	Open the 3rd maxilliped with tweezers.	Maxillipeds close tightly while the smaller mouthparts continue to move. If the mouth is already closed, it will be difficult to open.	Maxillipeds do not retract and remain open.
Eye retraction	Use a blunt probe and touch the eyestalk	Eye is retracted under the carapace hood.	The eye does not retract and remains extended out of the carapace.

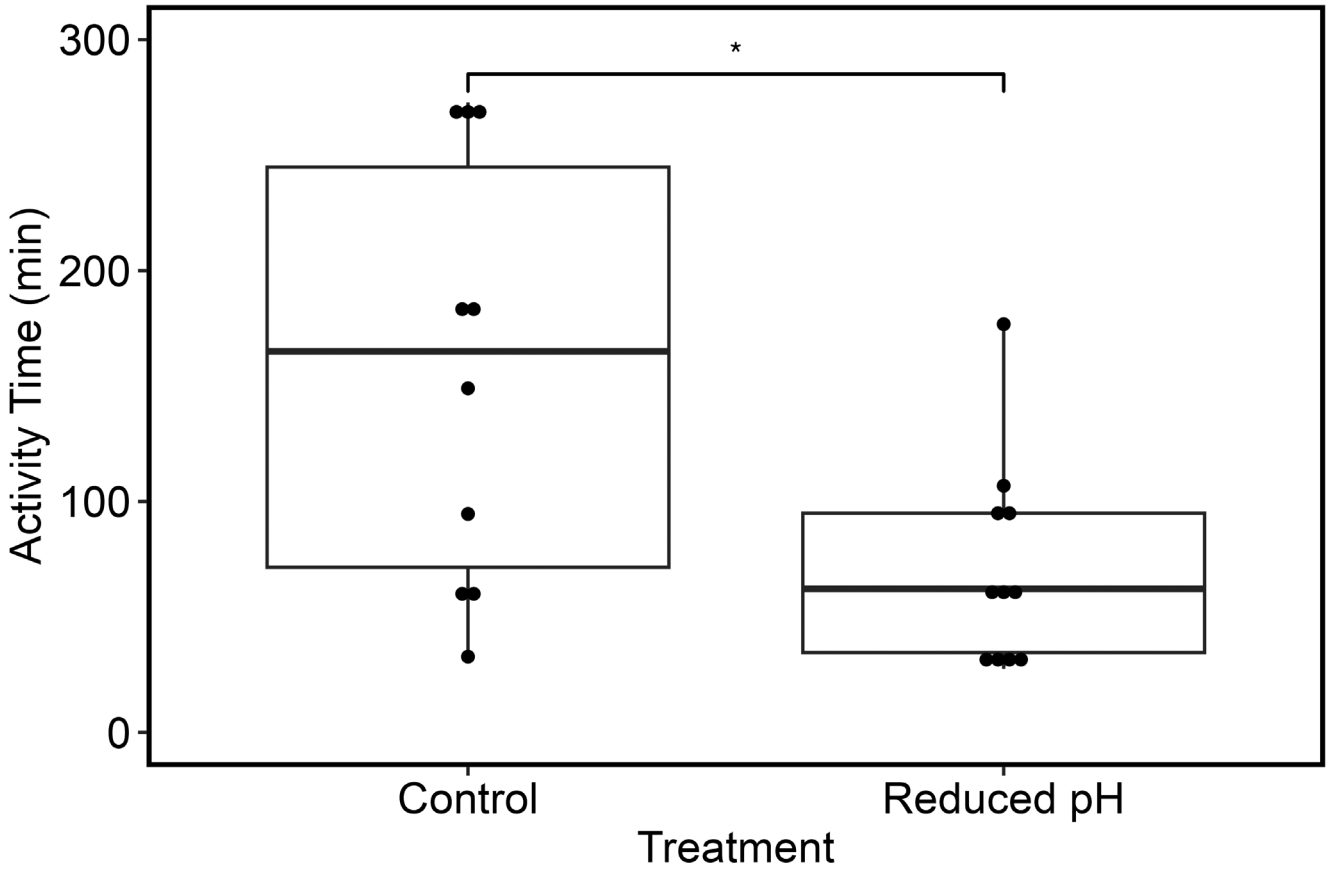

Figure 1. Box plot depicting the activity time of the crabs in control-pH and reduced-pH treatments. The dots represent the distribution of individual activity times (minutes); the horizontal line within the box the median; the lower and upper horizontal lines the first and third quartile, respectively; the vertical lines the range of the data. The asterisk indicates a significant difference at the alpha $P < 0.05$ level.

RESULTS

Crabs in the control treatment on average attempted to consume prey 18.1 times per trial ± 5.48 SE, whereas predation attempts in the reduced-pH treatment were 19.27 ± 3.46 SE. There was no significant difference in the attempts made on prey between the control pH and the reduced-pH treatments ($t = -0.18$ $df = 15.4$, $P = 0.86$). There were, however, no prey items consumed in the reduced-pH treatment and a total of three were consumed across all individuals in the control.

Although the predation attempts were comparable among treatments, the activity time of crabs exposed to the reduced-pH treatment was significantly different than those in the control treatment ($W = 85$; $P = 0.03$) (Fig. 1). Crabs in the reduced-pH treatment were active for a mean of 71.04 min ±

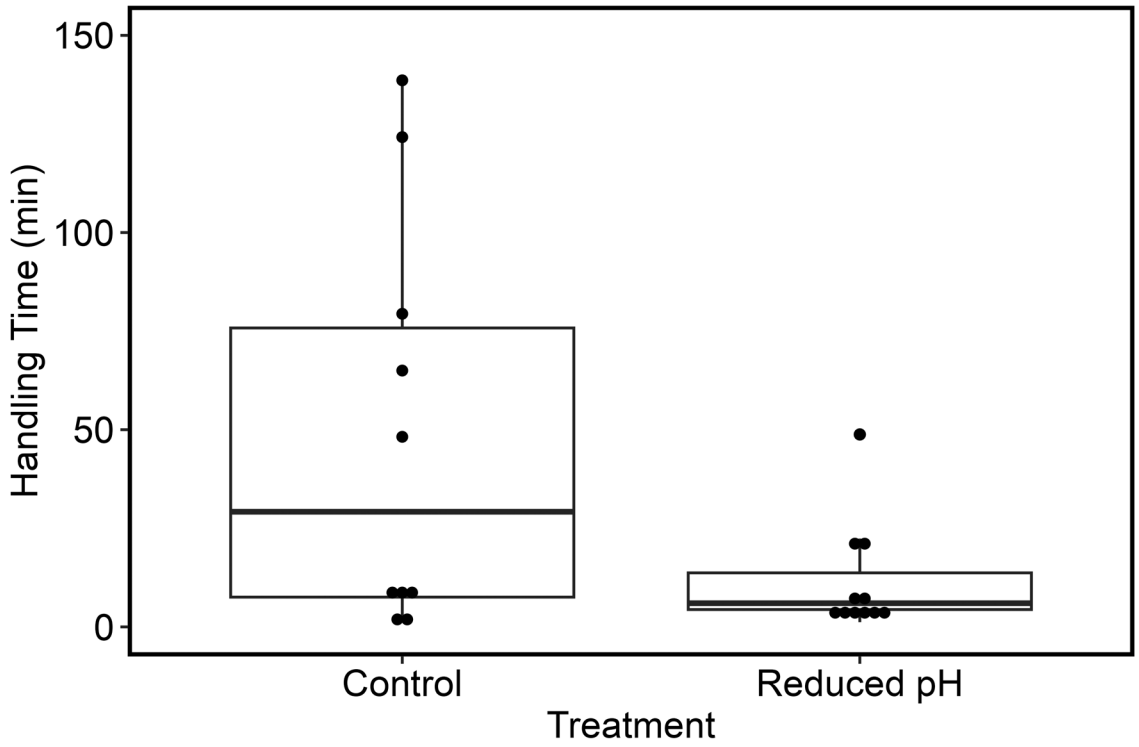

Figure 2. Box plot of handling time of the crabs in control-pH and reduced-pH treatments. The dots represent the distribution of individual handling times (minutes); the horizontal line within the box plot the median; the lower and upper horizontal lines the first and third quartile, respectively; the vertical lines the range of the data.

29.35 SE, whereas crabs in the control pH were two times more active (157.1 min ± 13.62 SE).

Handling time between the two treatments was not significantly different ($W = 79$; $P = 0.09$), although there appears to be a trend toward reduced-pH treatment crabs having a lower handling time. Control crabs had a mean handling time of 53.71 min ± 52.15 SE, whereas it was 11.74 min ± 4.23 SE in the reduced-pH treatment (Fig. 2).

There was no significant difference ($W = 5$, $P = 0.14$) in the stress level before (mean stress level of 0.6 ± 0.22 SE) and after (mean stress level of 1.3 ± 0.37 SE) experimental trials in control crabs (Fig. 3a). There was a significant difference, however, in the before (mean stress level of 0.36 ± 0.20 SE) and after (mean stress level of 1.55 ± 0.25 SE; $W = 2.5$, $P = 0.018$) of crabs in the reduced-pH treatment (Fig. 3b).

DISCUSSION

Stone crabs exposed to the reduced-pH treatment experienced elevated stress levels, which was accompanied by an overall lower activity level. These results suggest that acidification may reduce crab foraging activity at least until individuals are able to physiologically compensate for the reduction in seawater pH.

The crabs that were in the reduced-pH treatment spent less time moving during the experiment relative to crabs in the control. The stone crabs in the control had nearly double the activity time as crabs in the reduced-pH treatment. Studies have shown that short-term exposure to acidic conditions can cause temporary shifts in energetic and metabolic demand (de Andrade *et al.*, 2022), which can result in changes in movement resulting in an effect on foraging activity (Harms *et al.*, 2014; Watson *et al.*, 2017). Shifts in the metabolic demand and activity level in decapod crustaceans are likely the result of the animal reaching a pH threshold where metabolic stimulation can trigger metabolic depression (Harms *et al.*, 2014). Metabolic depression is common in crustaceans and is a strategy used to slow the animals' metabolism in response to a stress stimulus, often leading to a sacrifice of reproduction and predatory behavior (Guppy & Withers, 1999; de la Haye *et al.*, 2011). The lack of a difference in handling time between reduced pH and control treatments is likely the result of our small sample size and the lower handling time exhibited by a few of the control individuals. Despite this result, other mud crabs, including *Panopeus herbstii* H. Milne Edwards, 1834 and *Charybdis japonica,* are reported to experience a decrease in handling time and feeding behavior respectively when exposed to reduced seawater-pH conditions (Dodd *et al.*, 2015; Wu *et al.*, 2017).

Stone crabs in our experiment were overall less active and thus encountered fewer prey items, which likely explains the observed result. We were not able to identify the specific mechanism involved in this response; however, it is also important to consider the ability of acidic conditions to disrupt or alter olfaction. The impairment in the ability of the crab to sense a prey cue can be triggered by a reduced pH altering the function of neurotransmitters (Jiahuan *et al.*, 2018). For example, decreases in olfactory sensing under reduced pH has been documented in hermit crabs, where their antennules move more slowly, reducing their ability to process chemical cues

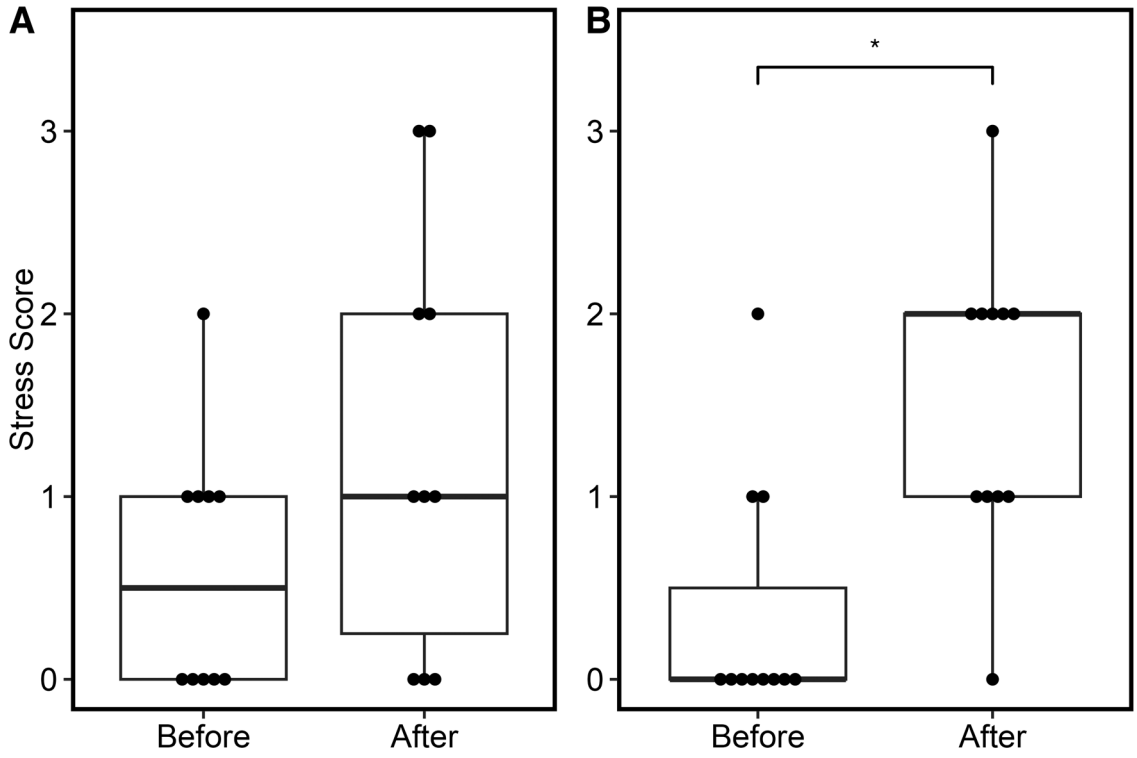

Figure 3. Box plots of the stress test results before and after experimental trials for control-pH treatment (**A**) and reduced-pH treatment (**B**). The dots represent the distribution of individual stress scores; the middle horizontal line representing the median stress score; the lower and upper horizontal line the first and third quartile, respectively; the vertical lines the range of the data. The asterisk indicates a significant difference at the alpha $P < 0.05$ level.

necessary to detect prey and new shells (de la Haye *et al.*, 2011; Briffa *et al.*, 2012). While we did not observe changes in antennule movement, lower activity could also correlate with a reduction in antennule movement, but this would require further study. The observed increase in stress levels under reduced seawater pH indicates that these crabs were likely attempting to compensate for a physiological change (an acute response). The stress levels of crustaceans are driven by physiological processes such as acid-base and temperature regulation (Harms *et al.*, 2014; Bednaršek *et al.*, 2021). When marine crustaceans are exposed to conditions outside their preferred range, their physiological processes become unbalanced, contributing to increased stress levels (Harms *et al.*, 2014). The ability of crustaceans to regulate their stress response relies on the pH buffering capacity of hemolymph (Pörtner, 2008; Harms *et al.*, 2014; Bednaršek *et al.*, 2021). For example, during exposure to reduced seawater pH the great spider crab, *Hyas araneus* (Linnaeus, 1758), was unable to compensate for changes in environmental pH due to limitations of the animals' acid-base regulation and oxidative stress caused by metabolic down regulation (Harms *et al.*, 2014). The hemolymph of decapods can regulate internal pH, but there is a threshold level when regulation becomes less efficient. An increase in stress levels could result in disruptions in pH regulation, which can impact the animals' response to their environment (i.e., foraging) when that threshold is reached.

Our experiment highlights the potential impacts of reduced seawater pH on the foraging activity and stress response of the Florida stone crab but does not identify how chronic exposure (long term) may impact the species. While we did observe greater stress levels in the reduced-pH treatment, there was also more variability in the stress response at lower seawater pH. Further, we did not observe mortality during the experiments. This variability among individuals may be related to the environmental history (pH variable habitat) experienced by the crabs, which can change spatially and temporally within the habitats of stone crabs (Millero *et al.*, 2001; Dufroe, 2012), suggesting that acclimatization is possible over longer temporal scales. Future work should therefore consider long term foraging (exposure for months or years) responses to reduced seawater pH.

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