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Caribbean king crab larvae and juveniles show tolerance to ocean acidification and ocean warming

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Abstract

Coastal habitats are experiencing decreases in seawater pH and increases in temperature due to anthropogenic climate change. The Caribbean king crab, *Maguimithrax spinosissimus*, plays a vital role on Western Atlantic reefs by grazing macroalgae that competes for space with coral recruits. Therefore, identifying its tolerance to anthropogenic stressors is critically needed if this species is to be considered as a potential restoration management strategy in coral reef environments. We examined the effects of temperature (control: 28 °C and elevated: 31 °C) and pH (control: 8.0 and reduced pH: 7.7) on the king crab's larval and early juvenile survival, molt-stage duration, and morphology in a fully crossed laboratory experiment. Survival to the megalopal stage was reduced (13.5% lower) in the combined reduced pH and elevated temperature treatment relative to the control. First-stage (J1) juveniles delayed molting by 1.5 days in the reduced pH treatment, while second-stage (J2) crabs molted 3 days earlier when exposed to elevated temperature. Juvenile morphology did not differ among treatments. These results suggests that juvenile king crabs are tolerant to changes associated with climate change. Given the important role of the king crab as a grazer of macroalgae, its tolerance to climate stressors suggests that it could benefit restoration efforts aimed at making coral reefs more resilient to increasingly warm and acidic oceans into the future.

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Introduction

The continued use of fossil fuels is increasing atmospheric carbon dioxide (CO_2) concentrations which is simultaneously resulting in decreased ocean pH, a process known as ocean acidification (Calderia and Wickett 2003). Current models (RCP 8.5, IPCC 2018) forecast that under the current rate of fossil fuel emissions seawater pH will likely decrease by ~ 0.35 units by 2100 (Meehl et al. 2007; IPCC 2018). In addition, many coastal habitats can experience high variability in seawater pH as a result of seasonal changes in biogeochemical cycles, daily biological activity, storms, and tidal cycles (Millero et al. 2001; Yates et al. 2007; Manzello et al. 2012; Enochs et al. 2019; Cyronak et al. 2020). Some nearshore coastal marine habitats are also experiencing acidification due to increased development and the associated runoff that is rich in organic matter (Bauer et al. 2013; Wallace et al. 2014; Ekstrom et al. 2015). As a result, some coastal habitats can experience daily or seasonal shifts in seawater pH that may exceed critical thresholds for some organisms (Yates et al. 2007; Harris et al. 2013; Zhang and Fisher 2014). In addition, rising atmospheric CO_2 concentrations has led to an increase in seawater temperatures and current models forecast average ocean temperatures to continue to increase by 2–4 °C (~ 10% increase) by the end of the century (IPCC 2018). The smaller volume of water within shallower coastal habitats, however, may result in more extreme increases in temperature and pH than what is projected for the end of the century in the open ocean (Yates et al. 2007; Wallace et al. 2014). The health of Florida's coral reefs are declining due to local and global stressors, including ocean acidification (OA, Muehllehner et al. 2016), disease outbreaks (Muller et al. 2020), coastal eutrophication (Burkepile et al. 2013), and warming temperatures (Smith et al. 2019). In fact, some nearshore coral reef habitats within the Florida Keys have already experienced an unprecedented increase in sea surface temperature of 0.8 °C over the last century (Kuffner et al. 2015). As a result, the relative abundance of non-reef building corals and other biota, such as macroalgae and sponges, may be increasing in some locations (Burman et al. 2012; Chavez-Fonnegra et al. 2017; Toth et al. 2014, 2019). Therefore, management efforts aimed at both restoring coral populations and reviving critical grazing processes should be considered a critical need for Florida reefs.

Spider crabs of the family Mithracidae, including the large Caribbean king crab, *Maguimithrax spinosissimus*, reside on Caribbean and Florida reefs, where they graze on algae (Windsor and Felder 2014; Klompmaker et al. 2015). Although the Caribbean king crab is an omnivore, benthic macroalgae and turf comprise the bulk of its diet,

including algae species that are known to be chemically defended and avoided by other herbivores (Winfree and Weinstein 1989; Guzman and Tewfik 2004; Butler and Mojica 2012). The grazing rates of the Caribbean king crab on macroalgae have been reported to exceed those of herbivorous fishes including parrotfish (Butler and Mojica 2012). Recent work by Spadaro and Butler (2021) showed that *M. spinosissimus* is highly effective at reducing algal cover (reduction by 50–80%) on patch reefs in the Florida Keys, resulting in a three–fivefold increase in coral recruitment, and an increase in both reef fish richness and abundance.

The entire lifecycle of the Caribbean king crab occurs within coral reef habits and so all life-stages experience coastal conditions. The Caribbean king crab has two larval stages (zoeae) and one postlarval stage (megalopa) before molting into a juvenile, an ontogenetic process that generally takes about 7 days (Provenzano and Brownell 1977; Baeza et al. 2019). After settlement, the Caribbean king crab tends to be solitary, dependent upon crevices within the reef for shelter, and exhibits relatively high site fidelity (Hazlett and Rittschof 1975; Spadaro and Butler 2021). The short larval duration of the Caribbean king crab likely limits the species' dispersal, and largely isolates Florida's king crab populations from the rest of the metapopulations throughout the greater Caribbean basin (Baeza et al. 2019).

The early life stages of coastal crustaceans can be especially sensitive to reduced pH and elevated temperature. For example, postlarval spiny lobsters became disoriented and took longer to locate positive settlement cues after exposure to reduced seawater pH (Gravinese et al. 2020). Juvenile spiny lobsters, which are gregarious, lost their ability to orient toward conspecific chemical cues and avoid diseased conspecifics when exposed to reduced pH and elevated temperature (Ross and Behringer 2019). Stone crab larvae reversed their larval swimming direction in reduced pH conditions (Gravinese et al. 2019) and their embryos and larvae, exhibited a 28% reduction in hatching success and a 37% reduction in larval survival when raised in reduced seawater pH (Gravinese 2018; Gravinese et al. 2018). Simultaneous exposure to both reduced pH and elevated seawater temperature stressors resulted in 80% mortality in stone crab larvae (Gravinese et al. 2018). The aforementioned responses are likely due to physiological stress. For example, reduced seawater pH can in turn result in acidification of the haemolymph and possibly disrupt enzyme pathways or denature proteins, resulting in less efficient physiological responses under reduced pH and elevated temperature (Anger 1987; Somero 1995; Hofmann and Todgham 2010). Reduced seawater pH and elevated temperature stressors can also increase metabolism and limit oxygen supply at the cellular level, which can alter metabolic demands and disrupt hormones that regulate molting (Roberts 1957; Leffler 1972;

Anger 1987; Frederich and Portner 2000; Storch et al. 2011). Buffering for reductions in internal pH can result in sublethal physiological impacts which can be energetically costly (Somero 1986; Cameron 1985; Michaelidis et al. 2005), especially over the course of weeks to months (Whiteley 2011).

The effects of reduced pH and elevated seawater temperatures on the larval and juvenile development of the Caribbean king crab may represent a bottleneck to the species' recruitment on Florida's coral reefs as their early life stages may not have fully developed compensatory mechanisms to physiologically tolerate extremes in both temperature and pH. Therefore, we determined the effects of reduced seawater pH (control: 8.0 and reduced pH: 7.7) and elevated temperature (control: 28 °C and elevated: 31 °C) on the early life-history stages of the Caribbean king crab by monitoring (i) larval survival, (ii) juvenile survival, (iii) juvenile molt-stage duration, and (iv) juvenile morphology using a fully crossed laboratory experiment.

Materials and methods

Ovigerous female collection

Twenty-eight ovigerous female king crabs all with late-stage embryos (mean $\pm$ SD; 80.7 ± 6.4 mm carapace width; 80.9 ± 6.9 mm carapace length) were collected by hand near Key West, Florida during September–November 2019. Females were immediately transported to Mote Marine Laboratory's Elizabeth Moore International Center for Coral Reef Restoration and Research on Summerland Key, Florida, USA and were maintained in the Climate and Acidification Ocean Simulator (CAOS). Mote's CAOS system is an outdoor experimental facility that contains 18.9 L flow-through aquaria ($n = 10$–12) within temperature-controlled fiberglass raceways ($254 \times 101.6 \times 30.5$ cm) which allows for continuous seawater flow. Female crabs were held in ambient seawater conditions (28 °C, $pH_{total} = 8.0$, and pCO_2 of ~450 µatm) until larval release. During brooding, adult crabs were fed a

diet of various macroalgae species collected from nearshore seagrass flats and shrimp ad libitum.

Experimental design

All experiments consisted of two fully crossed treatments (i.e., temperature and pH), each with two levels (either ambient temperature or elevated temperature; either ambient pH or reduced pH), resulting in a total of four different treatments. The two temperature levels were set at 28 °C and 31 °C. The control temperature (ranged from 27.9 to 28.7 °C) was based on the 9-year mean (2009–2018) seawater temperature for Sombrero Reef, Florida for September–November (USGS Coral Reef Ecosystem Studies: https://coastal.er.usgs.gov/data-release/doi-F71C1TZK/; Kuffner et al. 2019), while the elevated temperature (ranged from 29 to 31.3 °C) was based on the 2–4 °C projected increase for sea-surface temperatures at the end of the century (IPCC 2018). The control pH was 8.0 (pCO_2 level ~450 µatm) and was within the range (325–700 µatm) of southeast Florida coastal habitats and reefs (see Millero et al. 2001; Manzello et al. 2012; Enochs et al. 2019). The reduced pH treatment was set to 7.7 (pCO_2 level ~1100 µatm), which was based on the IPCC (2018) projections (~1000 µatm) for the end of the century.

Ocean acidification (OA) system setup

The CAOS facility pumps seawater from the Atlantic side of the Florida Keys through 20 µm particulate filters before entering 3800 L header tanks, where pH is manipulated through the injection of CO_2 gas using a high precision dosing apparatus (Walchem controllers that regulate solenoids). The CAOS facility uses 6 different header tanks that can be interchanged and randomized to avoid pseudoreplication among treatments. The CAOS dosing system records pH (Walchem W900 probes; Iwaki America, Inc., Hopping Brook Park Holliston, MA, USA) every 2 s and will trigger (i.e., turn off and on the flow of CO_2 gas) CO_2 manipulation within ± 0.01 of the target pH value. Ambient seawater pH (control) was maintained at 8.0 ± 0.05 (mean $\pm$ SD; Table 1). The reduced pH treatment

Table 1 Mean ($\pm$ SD) temperature (°C), total alkalinity (A_T; µequiv kg^{-1}), dissolved inorganic carbon (DIC; µmol kg^1), pCO_2 (µatm), spectrophotometric pH (Total), and salinity during experimentation

Treatments	Temperature (°C)	A_T (µequiv kg^{-1})	DIC (µmol kg^1)	pCO_2 (µatm)	pH (Total)	Salinity
Control	28.1 ± 0.16	2278.1 ± 81.4	1949.5 ± 90.1	410.3 ± 61.7	8.080 ± 0.053	35.5 ± 0.81
Reduced pH	28.1 ± 0.19	2256.3 ± 102.4	2113.8 ± 101.4	1014.3 ± 162.7	7.742 ± 0.060	35.5 ± 0.74
Elevated Temperature	30.7 ± 0.39	2283.5 ± 74.1	1953.6 ± 78.1	446.2 ± 51.9	8.085 ± 0.044	35.3 ± 0.84
Combined	30.6 ± 0.42	2273.5 ± 83.7	2104.4 ± 99.1	1020.6 ± 216.9	7.781 ± 0.085	35.5 ± 0.72

pCO_2 values were estimated with CO2SYS software using the TA and DIC. Samples ($n = 13$) were collected during the day between 08:00 and 12:00

was maintained at 7.7 ± 0.06 (Table 1), which mimics pH conditions projected for 2100 under "business-as-usual" CO_2 emission scenarios (RCP 8.5; IPCC 2018). Temperature was controlled using Walchem temperature probes connected to heaters, which were submerged in each experimental raceway.

Ovigerous females ($n = 7$ broods per treatment; 28 total) were independently held in control conditions until larval release (~ 72 h after collection). Immediately following larval release, newly hatched larvae were collected and randomly assigned into each of the experimental treatments. Larvae from the same brood were divided among the treatments. A total of 72 larvae were randomly harvested from each brood. Those 72 larvae were then randomly assigned as 18 individuals per treatment level. Larvae came from 7 independent broods (replicates) per treatment. To avoid shock to the larvae, the elevated temperature and pCO_2 levels were gradually increased (~ 0.25 °C and ~ 40–60 μatm per hour) to the experimental set-points over the first 10–12 h ("ramp-up period") for each experimental replicate.

Seawater carbonate chemistry

To monitor the carbonate chemistry of the CAOS system, a seawater sample was collected every 3–8 days from a randomized subset of the replicate experimental aquaria ($n = 13$ samples per treatment). The seawater samples were collected in 500 mL borosilicate bottles, and were immediately fixed with 200 μL of saturated mercuric chloride. Total alkalinity (A_T), and dissolved inorganic carbon (DIC) were measured at NOAA's Atlantic Oceanographic and Metrological Ocean Acidification Laboratory using Apollo SciTech instruments (AS-ALK2 and AS-C3, respectively) as described by Enochs et al. (2015). Alkalinity and DIC samples were checked for accuracy with certified reference materials (Dickson et al., 2003, Scripps Institution of Oceanography, La Jolla, CA). The total pH scale (pH_T) within each experimental aquarium was also monitored daily using a handheld pH meter (Orion Star A221, ThermoFisher Scientific) and Ross triode (Orion 8302BNUMD, ThermoFisher Scientific), which was calibrated at temperature daily using Tris buffer (Dickson et al. 2003; Scripps Institution of Oceanography, La Jolla, CA). The A_T and DIC values were then used to calculate pCO_2 using CO2SYS 2.1 using dissociation constants of carbonic acid (K_1 and K_2 from Mehrbach et al. 1973; Robbins et al. 2010; Table 1). Temperature and salinity of each experimental aquarium were also monitored twice daily during the experiment (Orion Star A222, ThermoFisher Scientific).

Survival and molt-stage duration of larval and juvenile King crabs

To determine the effects of elevated temperature and reduced pH on larval and juvenile king crab survivorship and molt-stage duration (MSD), individuals were reared within clear acrylic compartmentalized boxes (100 ml), with the plastic bottoms replaced with nylon mesh (190 μm), similar to methods reported in Gravinese et al. (2018) for stone crabs. Each box was held within its own water bath to maintain experimental temperatures within a narrow range in the CAOS flow-through system. All compartmentalized boxes were elevated on a PVC platform so that an aquarium pump could be positioned to direct flow through the mesh. Larvae from seven independent broods were used during survival and MSD experiments with each brood serving as a replicate. After hatching, larvae ($n = 72$ per brood, 18 individuals per treatment level) from each ovigerous female ($n = 7$ independent broods) were placed within a compartmentalized box and were monitored to determine the treatment effects on survival and MSD (Gravinese et al. 2018). Due to the species' rapid larval development, larval survival and MSD were monitored by counting exuvia (i.e., molts) and dead larvae every 6 h for the first 24 h. After the first 24 h, individuals were monitored daily from the postlarval stage (megalopae) until reaching the third juvenile stage (J3). *M. spinosissimus* have lecithotrophic larvae and do not feed until juvenile stages and, therefore, were not fed during these experiments. Previous work has indicated that food availability had no effect on *M. spinosissimus* survivorship for the first day after hatching (Tunberg and Creswell 1988). Juveniles were fed a diet of *Dasycladus vermicularis* (~ 5 mm length; ~ 0.4–0.5 mm^2), a frondose green alga and small pieces of shrimp, twice per week. The CAOS system is a shaded outdoor facility, and thus ovigerous females, larvae, and juveniles were all maintained under a natural photoperiod. Ovigerous females were only used once in our experiments (e.g., no subsequent clutches were used).

Juvenile King crab morphology

The effects of elevated temperature and reduced pH on juvenile king crab morphology were determined using similar methods to those described in Long et al. (2013). Upon molting, a digital image was taken at $15 \times$ magnification using a stereomicroscope (Amscope with digital camera with MU130 digital mount). Juveniles were photographed dorsally so that the carapace width (CW), carapace length (CL), carapace length to the rostrum (CLR), rostrum length (RL), and orbital spine width (OW) could be measured from the digital micrographs (ImageJ software, similar to Long et al. 2013). Prior to measurement, digital images of juvenile crabs were calibrated in ImageJ by determining the number of pixels within the micrometer scale provided by the microscope.

Statistical analysis

The effect of the different treatments on larval survival and juvenile survival was determined using a Cox proportional hazard model, with death serving as the 'event', and time, since the beginning of the experiment as the 'time until an event occurs.' The Cox regression coefficients (i.e., hazard ratios) were used to estimate the likelihood an individual would die under the experimental treatments with a hazard ratio > 1 indicating an increased effect of being exposed to the treatment. To control for variation among broods, individuals from the same female were treated as covariates in the analysis.

Differences among treatments in the molt-stage duration (MSD) for megalopae, stage-1 juveniles (J1), and stage-2 juveniles (J2) were determined using a linear mixed effect model with temperature and reduced pH serving as the main effects, and brood as a random factor. The statistical results were Bonferroni corrected to the alpha level of 0.01, because the MSD comparisons required three separate tests.

Because of the high degree of shared variability among morphological features, a principal component analysis (PCA) was used to establish a new set of orthogonal variables that were compared among the treatment groups. The contribution of the new variables was then determined based on the largest factor loadings for each principal component (PC). The point of inflection on the scree-plot was used to determine the number of PCs to retain. The derived component scores were then analyzed using separate linear mixed effect models with brood as a within subject factor to determine if larval morphology differed among treatments. The statistical results for morphology were also Bonferroni corrected to the alpha level of 0.01, because the PCA comparisons required separate tests for each juvenile stage. All experiments were replicated using larvae from seven independent broods ($n = 7$). All statistical analyses were performed using R (R Core Team 2021).

Results

Larval King crab survival

The absolute percentage of larval survival to the megalopal stage was 67.9% in the control. The reduced pH and elevated temperature treatments were comparable to the control with both treatments resulting in 64.2% and 63.5% absolute survival to the megalopal stage, respectively. Survival in the combined treatment was the lowest among the treatments with only 54.3% of the larvae surviving to the megalopal stage: a 13.5% decrease in survival relative to the control. A Cox proportional hazard model indicated there was a statistically significant difference in the survival probability among
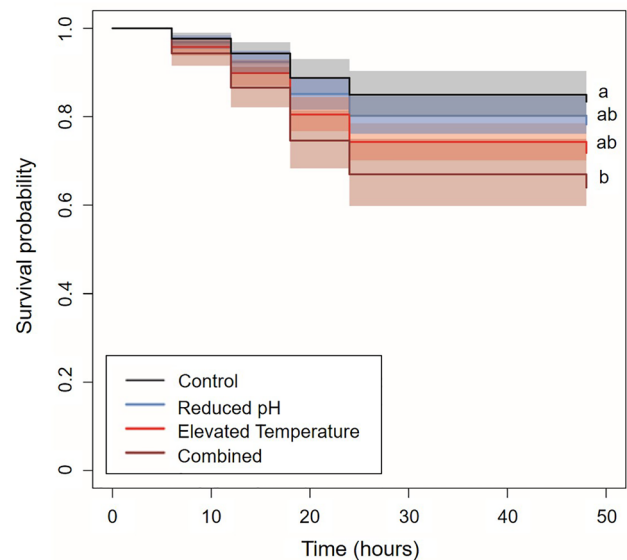

Fig. 1 Survival probability of *M. spinosissimus* throughout larval development during exposure to the control (black line), reduced pH treatment (blue line), elevated temperature treatment (red line), and the combined treatment (maroon line). The 95% confidence intervals are indicated by the shaded regions. Larvae were used from seven independent broods in the analyses, which served as the replicates. Curves with different letters are significantly different at the $\alpha = 0.05$ level

the treatments ($LR_4 = 22.1$, $P = 0.0001$). The survival probability was significantly lower in the combined treatment relative to the control (Wald $X^2 = 3.14$, $P = 0.001$; Fig. 1). There were no other statistically significant differences among treatments relative to the control. The Cox regression coefficients (i.e., hazard ratios) were used to quantify the likelihood that an individual would die under the treatment conditions. The hazard ratios (HR) indicated that larvae in the combined treatment were 2.38 times more likely to die than animals in the control. The HR for the reduced pH and the elevated temperature treatment were 1.20 and 1.57, respectively, supporting the conclusion that the effect of these treatments on larval survival was minimal relative to the combined treatment. Female brood, which was used as a covariate in the Cox model, was observed to have a significant effect on larval survival (Wald $X^2 = -3.11$, $P < 0.001$), suggesting that some broods may be more acclimatized to the experimental treatment levels than others.

Juvenile King crab survival

The survival probability to the third juvenile stage (J3) was not significantly different among any of the treatments (Cox proportional hazard model: $P > 0.05$ for all comparisons). The control had the greatest absolute survival with 24.3% of the individuals reaching the J3 stage. The reduced pH and

elevated temperature treatments were again comparable to the control and resulted in absolute survival of 23.6% and 20.8%, respectively, to the J3 stage. The combined treatment experienced the lowest absolute survival of 16.6% survival to the J3 stage. Although we still observed decreases in juvenile survival, the HR's for all treatments indicated that elevated temperature (HR = 0.93), reduced pH (HR = 0.76), and the combined treatment (HR = 1.1) all had a minimal effect on the probability of survival in juvenile king crabs. Female brood, which was used as covariates in the model, was also significant, indicating a high degree of brood variability (Wald $X^2 = 3.37$, $P < 0.0001$).

Molt-stage duration

The MSD of megalopae ranged from 3.1 to 3.5 days regardless of treatment. There was a statistically significant effect of elevated temperature on the megalopal molt-stage duration ($t_{1,253} = -3.05$, $P = 0.002$; Fig. 2). This resulted in individuals in the elevated temperature and combined treatments molting faster than individuals in the control by 0.37 and 0.27 days, respectively. We did not observe a statistically significant difference in the J1 MSD among individuals within the reduced pH treatment ($t_{1,253} = -0.44$, $P = 0.65$), nor was there an interactive effect between temperature and pH ($t_{1,253} = 1.25$, $P = 0.21$).

Stage-1 juveniles in the control treatment had a mean MSD of 8.5 ± 3.0 days ($\pm$ SD). J1 crabs in the reduced pH treatment experienced a statistically significant delay in their MSD and molted on average ~ 1.46 days later than individuals raised in the control ($t_{1,188} = 3.5$, $P = 0.0006$; Fig. 2). There was no statistically significant effect of temperature on the J1 MSD ($t_{1,188} = -0.25$, $P = 0.80$). Individuals in the elevated temperature treatment molted (8.3 ± 2.3 days) and combined (8.5 ± 2.3 days) treatment had MSDs comparable to the control. There was also no statistically significant interaction ($t_{1,188} = -2.3$, $P = 0.018$).

Stage-2 juveniles in the control on average had a MSD of 14 ± 2.7 days ($\pm$ SD). There was no statistically significant difference in the reduced pH treatment for MSD in J2 crabs ($t_{1,108} = -1.09$, $P = 0.27$) with individuals molting on average in 12.9 ± 4.4 days ($\pm$ SD). J2 crabs molted significantly faster in the elevated temperature and combined treatment with individuals molting on average 3.0 and 1.8 days, respectively, than individuals in the control ($t_{1,108} = -3.29$, $P = 0.001$; Fig. 2). There was no statistically significant interaction effect ($t_{1,108} = 1.72$, $P = 0.08$).

Juvenile morphology

Principal component analysis on the morphological measurements of J1 and J2 crabs resulted in two principal
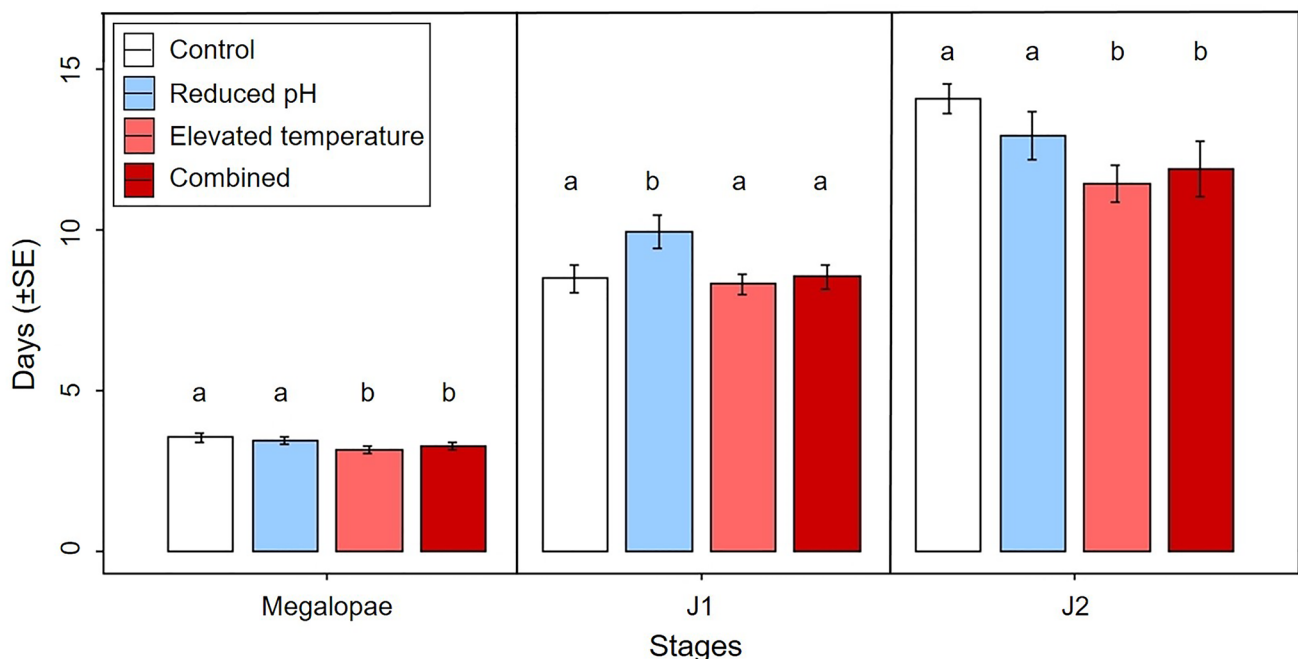

Fig. 2 Mean (days, $\pm$ SE) molt-stage duration of *M. spinosissimus* megalopae and juveniles during exposure to reductions in seawater pH and elevated temperature. Juveniles from seven different broods were used in the analysis (i.e., $n = 7$ replicates). Letters above the bars represent statistically significant differences among treatments at $\alpha = 0.01$ for each stage. An α of 0.01 was used as the statistical threshold, because a separate test was performed within each developmental stage to test for differences among treatments and so the results were Bonferroni corrected. Comparisons were not made between different stages

components (PCs) being retained representing 74.3% and 73.7% of the variation in the data, respectively. The loadings for PC1 in both juvenile stages were positively associated with CL. The loadings for PC2 were negatively associated with CW in J1 crabs and positively associated with CW in J2 crabs. The J1 and J2 component scores were then compared among the main effects using a linear mixed effect model with brood as a random factor and showed no significant difference in CL or CW ($P > 0.05$ for all J1 and J2 comparisons; Tables 2 and 3). The PCA analysis for J3 crabs also resulted in two PCs being retained, representing 72.3% of the total variation (Table 4). The loadings for PC1 were negatively associated with CL, while the loadings for PC2 were associated with CW in J3 crabs. Comparisons of the J3 component scores showed no significant difference in PC1 or PC2 for CL or CW among the treatments.

Discussion

Caribbean king crab larvae raised in the combined treatment (reduced pH + elevated temperature) had 2.3× greater mortality than those in the control treatment; however, there

Table 2 Results of the principal component analysis on morphological characters of J1 *M. spinosissimus* crabs

PC	Eigenvalues	% Variation	% Cumulative variation	
1	1.59	50.6	50.6	
2	1.09	23.7	74.3	
Variables		Loadings		
		PC1	PC2	
Carapace width		0.45	− 0.47	
Carapace length		0.50	0.33	
Carapace length to rostrum		0.52	0.36	
Rostrum length		0.41	0.20	
Orbital spine width		0.32	− 0.71	
Variable	Factor		t	P
Mixed effect model				
PC 1	Temperature		0.39	0.69
	pCO_2		− 0.05	0.95
	Temperature * pCO_2		0.91	0.35
PC 2	Temperature		− 0.37	0.70
	pCO_2		− 0.85	0.39
	Temperature * pCO_2		0.29	0.76

Two orthogonal principal components (PCs) representing 74.3% of the total variation were retained by the analysis. The derived component scores were analyzed using separate linear mixed effect models to test for the main effects on juvenile morphology. The largest factor loadings were used to determine each variables contribution to each PC. Morphology analyses used juveniles from 7 independent broods

were no effects on survival when larvae were exposed to reduced pH and elevated temperature independently. This suggests that Caribbean king crab populations may be somewhat tolerant to elevated temperature and reduced seawater pH after their short (24 h) larval stages given the lack of any significant reduction in survival or any changes in morphology when juvenile stages were exposed to the same treatment conditions. However, the species may still show susceptibility to reduced pH and elevated temperature for other important biological factors that were not measured in this study, such as changes in calcification or behavior. Nevertheless, the tolerance of juvenile crabs to these stressors is encouraging for the potential use of the Caribbean king crab as a target for mariculture given their role as a macroalgal grazer which could potentially aid coral recruitment and restoration efforts within the western Atlantic, including the Florida Keys (Spadaro and Butler 2021).

Larval and juvenile survival

Caribbean king crab larvae raised in the combined reduced pH and temperature treatment experienced a 13.5% decrease in survival. There was no significant effect of elevated temperature or reduced pH as independent stressors on larval survival, nor did we observe any significant treatment effects on juvenile survival, suggesting that the species is capable of physiologically tolerating singular stressors throughout development. This result aligns with what has been reported for related species, such as the Tanner crab (*Chionoecetes bairdi*), which lives in variable pH habitats, and shows no reduction in larval survival when exposed to reduced pH (Long et al. 2017). The adults of many crustacean species are able to regulate their acid–base equilibrium better than many other taxa during short-term (hours to days) exposure to reduced seawater pH (Whitely 2011). However, acid–base regulation may become affected during exposure to thermal extremes and simultaneous stressors, especially during earlier-life stages as larvae and juveniles are still developing the physiological ability to tolerate changes in abiotic factors (Portner 2005). These earlier life stages dedicate energy toward growth, molting and frequent changes in morphology, and thus may be more sensitive to environmental changes that can alter their physiological homeostasis (Anger et al. 1989; Walther et al. 2010; Schiffer et al. 2013). For example, reductions in seawater pH can result in sublethal or lethal metabolic costs during earlier crustacean life-stages, such as a depletion of energy stores that may be needed for later growth (Byrne 2011; Schiffer et al. 2013), or a decrease in the extracellular pH (Pane and Barry 2007), or a limited ability to regulate haemolymph ions (Pane and Barry 2007) all of which could result in negative

Table 3 Results of a principal component analysis on morphological characters of J2 *M. spinosissimus* crabs

PC	Eigenvalues	% Variation	% Cumulative variation
1	1.54	47.5	47.5
2	1.15	26.4	73.8

Variable		Loadings	
		PC1	PC2
Carapace width		0.31	0.61
Carapace length		0.53	−0.17
Carapace length to rostrum		0.59	−0.19
Rostrum length		0.49	−0.18
Orbital spine width		0.15	0.73

Variable	Factor	t	P
Mixed effect model			
PC 1	Temperature	− 0.30	0.76
	$p\mathrm{CO_2}$	− 1.46	0.14
	Temperature * $p\mathrm{CO_2}$	0.67	0.50
PC 2	Temperature	− 1.66	0.09
	$p\mathrm{CO_2}$	−1.23	0.21
	Temperature * $p\mathrm{CO_2}$	0.45	0.64

Two orthogonal principal components (PCs) representing 73.8% of the total variation were retained by the analysis. The derived component scores were analyzed using separate linear mixed effect models to test for the main effects on juvenile morphology. The largest factor loadings were used to determine each variables contribution to each PC. Morphology analyses used juveniles from 7 independent broods

biological effects for a species, especially when coupled with ocean warming.

Elevated temperatures can also affect larval physiology by increasing metabolic activity and accelerating both growth and gill ventilation (Frederich and Portner 2000; Arnberg et al. 2013; Storch et al. 2011). While we were not able to identify the exact physiological mechanism that contributed to the decreased larval survival in the combined treatment, some studies have suggested that exposure to thermal stress can cause individuals to switch to anaerobic metabolic pathways, thus limiting oxygen at the cellular level and resulting in acidosis (Frederich and Portner 2000; Portner et al. 2006; Storch et al. 2011; Rastrick et al. 2014). We would expect, however, a higher mortality in the elevated temperature treatment as well if this were the case. The elevated temperature treatment may, therefore, still be within the thermal window for the Caribbean king crab as a singular stressor, which would explain why we did not observe significant mortality in the high temperature treatment. The thermal tolerance of a species can be reduced when elevated temperature is coupled with reduced pH. For example, the spider crab (*Hyas araneus*) and the brown crab (*Cancer pagurus*) both experienced a reduction in their thermal sensitivity when simultaneously exposed to elevated temperature and

reduced pH suggesting that their physiological tolerance was under stress as evidenced by increased heart rates and reduced oxygen partial pressure in the haemolymph with increasing CO_2 concentration (Metzger et al. 2007; Walther et al. 2009).

Molt-stage duration and morphology

Elevated temperature accelerated molt-stage duration (MSD) during the megalopal stage, albeit only by 0.27 and 0.37 days in the combined and elevated temperature treatments, respectively, which might reduce some predation during the planktonic megalopal stage. While there was no effect of reduced pH on juvenile king crab survival, there was an effect of pH on juvenile molt-stage duration (MSD). Juvenile king crabs experienced a longer MSD by 1.4 days during exposure to reduced pH, which could subject individuals to additional post-settlement predation pressure; however, this longer time to molt was only observed during the J1 crab stage. The longer MSD observed in J1 king crabs may have been the result of individuals having difficulty osmoregulating or maintaining their acid–base balance, and thus experiencing an energetic deficit, which is reported to result in sublethal effects such as reduced growth or an individual experiencing a delay in molting when exposed to reduced pH (Portner et al. 2004; Whitely 2011). Reduced pH conditions resulted in a similar delay in MSD in the juvenile red king crabs (*Paralithodes camtschaticus*) which was attributed to crabs expending energy to maintain calcification, thus decreasing growth (Long et al. 2013). Other crustacean species, such as the portunid crab *Necora puber*, buffer their hemolymph during exposure to reduced seawater pH, resulting in a decrease in metabolic performance and reduced growth (Small et al. 2010). Despite the longer MSD in J1 crabs, we did not observe any changes in juvenile morphology among the treatments, similar to that of red, blue, and golden king crabs (Long et al. 2013, 2017, 2021). The rapid development for juvenile king crabs results in less exposure time to reduced pH and thus might not affect calcification. In contrast, longer exposure (30 weeks) in some crustacean species (*Palemon pacificus*) were shown to experience a disruption of their acid–base balance which resulted in dissolution of calcium carbonate (Kurihara et al. 2008).

A different trend was observed in J2 crabs, with individuals molting 3 and 1.8 days faster in the elevated temperature and combined treatments, respectively. A shortened MSD was expected with an increase in temperature and has been reported for several crustacean species including blue crabs (Leffler 1972), the Atlantic rock crab (Johns 1981), the Dungeness crab (Kondzela and Shirley 1993), and the Florida stone crab (Gravinese et al. 2018). The accelerated MSD at elevated temperatures in these species is attributed to an increase in metabolic processes resulting in individuals

Table 4 Results of a principal component analysis on morphological characters of J3 *M. spinosissimus* crabs

PC	Eigenvalues	% Variation	% Cumulative variation	
1	1.51	45.5	45.5	
2	1.16	26.8	72.3	

Variable		Loadings		
		PC1	PC2	
Carapace width		− 0.45	0.51	
Carapace length		− 0.47	− 0.32	
Carapace length to rostrum		− 0.55	− 0.40	
Rostrum length		− 0.41	− 0.19	
Orbital spine width		− 0.33	0.66	

Variable	Factor	t	P
Mixed effect model			
PC 1	Temperature	0.28	0.77
	pCO$_2$	− 0.76	0.44
	Temperature * pCO$_2$	0.97	0.33
PC 2	Temperature	− 1.56	0.11
	pCO$_2$	0.41	0.68
	Temperature * pCO$_2$	0.02	0.97

Two orthogonal principal components (PCs) representing 72.3% of the total variation were retained by the analysis. The derived component scores were analyzed using separate linear mixed effect models to test for the main effects on juvenile morphology. The largest factor loadings were used to determine each variables contribution to each PC. Morphology analyses used juveniles from 7 independent broods

progressing through each stage more quickly than individuals at the lower temperature treatment. Elevated temperature can increase metabolic rate but it can also destabilize proteins and decrease oxygen concentration (Frederich and Portner 2000; Storch et al., 2011). An accelerated metabolic rate could account for the shorter MSD observed in J2 crabs; however, we did not observe a significant decrease in survival during any juvenile stage, suggesting that king crab juveniles (J2) were not experiencing changes in protein stability or oxygen availability that were lethal. The faster MSD could still manifest developmental challenges or other sublethal effects in later juvenile stages as energy reserves can become depleted during periods of faster growth (Kurihara et al., 2008).

Conclusions

The observed variability among broods in these experiments supports the hypothesis that the environmental history of some females to these stressors may indeed influence larval and juvenile tolerance to both stressors and could represent the potential for acclimatization among populations and/or tolerant genotypes to target for restoration purposes (Sibert et al. 2004; McCormick and Gagliano 2008; Parker et al.

2012). While the future of coral reefs still remains uncertain, our research suggests that brood variability within Caribbean king crab populations may allow the species to continue to serve as a viable tool for reef restoration under future climate scenarios. In addition, the lack of significant differences in mortality among juvenile stages and the lack of any change in juvenile morphology suggests that *M. spinosissimus* may be tolerant to reductions in seawater pH and elevated temperature during some stages of their development.

Species vulnerability to elevated temperature and reduced seawater pH can vary with latitude or be habitat specific. For example, species with broad latitudinal ranges may have a wider thermal tolerance, but when exposed to reduced pH their thermal window may narrow (Walther et al. 2009, 2010). Alternatively, crab populations from shallower coastal habitats that experience more variable pH conditions from diel biological activity, upwelling, or eutrophication have been identified to have a greater tolerance during exposure to reduced seawater pH relative to a deep-sea species (Pane and Barry 2007). Therefore, the variation in environmental factors experienced during a population's environmental history could provide the capacity for phenotypic plasticity and those populations could be ideal targets for restoration efforts associated with the Caribbean king crab (Gaitan-Espitia et al. 2017; Byrne and Hernandez 2020). The tolerance of juvenile king crabs to future climate stressors coupled with their rapid larval development (Tunberg and Creswell 1988), and ease of laboratory spawning further suggests that this species can be an excellent candidate for stock enhancement aimed at reducing macroalgae cover on reefs, especially as reef managers work to prepare reefs for future changes in seawater temperature and pH.

Data availability The data sets generated during and/or analyzed during the current study are available from the corresponding author on reasonable request.

Declarations

Conflict of interest The authors have no relevant conflicts of interest to declare.

Compliance with ethical standards All applicable international guidelines for sampling, care, and experimental use of organisms for the study were followed and all necessary approvals were obtained.

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