

Energetic consequences of temperature and sequential autotomy for the stone crab, *Menippe* spp.

Eric R. Hancock^{1,*}, Blaine D. Griffen^{1,2}

¹Marine Science Program, University of South Carolina, Columbia, SC 29208, USA

²Department of Biological Sciences, University of South Carolina, Columbia, SC 29208, USA

ABSTRACT: Stone crabs of the genus *Menippe* are harvested in a claw-only fishery along the Gulf of Mexico and southeastern Atlantic US coasts. As climate change continues to warm these areas, crabs are forced to cope with higher water temperatures. Altered environmental conditions may influence crab energetics by influencing both energy intake and expenditure. To prepare for a potential range expansion of the crabs, we investigated the energetic intake and expenditure of individual stone crabs. Crabs were found to respire 80 and 69% more following the loss of major and minor claws, respectively. Q_{10} , the factor by which the mass-specific respiration rates change as temperature is increased by 10°C, was 1.54. Mass-specific consumption of oysters in field cages increased by 15.8% for every 10°C increase in water temperature. Ingestion efficiency did not significantly vary with crab size, water temperature, or claw loss. We hypothesize that the ingestion efficiency of soft tissue did not change with the loss of the claws due to the unique feeding behavior of stone crabs. The front 4 walking legs were used more in food manipulation than both major and minor claws. Although current regulations were designed to promote sustainability and allow for the possibility of previously harvested crabs to reenter the commercially available stock, our results suggest that stone crabs may struggle to cope with fishery-style claw loss in warming conditions that are expected with continued climate change, especially in areas that are O₂-depleted.

KEY WORDS: Respiration · Ingestion efficiency · Temperature · Autotomy · Sustainability

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INTRODUCTION

The world's oceans are experiencing increased water temperatures due to global climate change (Bindoff et al. 2007). Over the past 100 yr, the global mean surface temperature has risen by approximately 0.6°C and is projected to continue rising for several centuries (IPCC 2001). Although regional climate patterns are often dynamic and heterogeneous (Burrows et al. 2011), this study focuses on the western north Atlantic along the US coast where ocean warming trends are projected to be among the strongest in the world (IPCC 2013). The temperatures

within a region influence the ecological processes that occur there, such as mortality (Hallett et al. 2004), nutrient cycling, and productivity (Allen 1995), as well as specifics of both animal behavior and physiology (Holtby 1988). Ectotherms are particularly sensitive to temperature changes because of the influences on individual development, energetics, physiology, and behavior in this group of organisms (Precht et al. 1973, Wieser 1973).

Temperature shifts associated with climate change have caused many marine ectothermic organisms to begin shifting their ranges towards the poles (Southward et al. 1995, Walther et al. 2002, Helmuth et al.

*Corresponding author: ehancoc@gmail.com

2006, Last et al. 2011). However, range shifts are often hard to quantify. For marine invertebrates, Cheung et al. (2009) reported an average rate between 45 and 59 km decade⁻¹, whereas Burrows et al. (2011) reported the rate between 14 and 38 km decade⁻¹. Rather than only studying the rate at which a species may shift its range, it is important to understand the energetic processes that drive an organism's physiology throughout a range of temperatures. Such a mechanistic understanding enables us to better describe a species' response to climate change throughout its range and may also help us to understand potential mechanistic drivers that underlie range shifts. This understanding may be particularly important for commercially harvested species. The regulations and harvesting zonations of a fishery are often indirectly determined by the temperature ranges that dictate where harvested species are successful (Mellin et al. 2012). Shifts in a commercial stock's range or physiology could lead to a need for altered regulations or a shift in the primary location of the fishery.

One commercial stock that appears to be experiencing a poleward range expansion is the Florida stone crab *Menippe mercenaria* and the Gulf stone crab *M. adina* (Rindone & Eggleston 2011). These crabs are naturally found in the North Atlantic from North Carolina to Mexico and throughout the Caribbean (Bert 1986). While the fishery within the USA exists in all coastal southeastern states in some capacity, it is most prominently found on the west coast of Florida, which has accounted for 97.1% of landings since the 2000–2001 season (NMFS 2016). Recently, blue crab fishermen have reported higher bycatch, and research divers have observed stone crabs in waters previously thought to be north of the crabs' natural range (Rindone & Eggleston 2011). Moreover, commercial landings in North and South Carolina have increased in recent years (NMFS 2016), suggesting the beginning of a poleward range expansion.

Understanding the physiological performance of this stock is particularly important not only due to the range expansion of the genus *Menippe*, but also because it is harvested in a claw-only fishery. Claw-only fisheries aim to lessen the impact on populations by harvesting only the claw(s) and releasing the individual crabs alive, thereby reducing overall mortality of the commercial stock. Stone crab regulations are mostly uniform across state lines except the number of claws a fisherman can take from a single crab. In the Florida discard fishery, both claws can be harvested from non-ovigerous individuals if propodus lengths are >70 mm. To promote sustainability, every

other state limits harvest to the larger of the 2 claws. The return of harvested crabs alive to the water allows for an individual's continued contribution to the fishery through both the potential reentry to the commercial stock by regeneration and the continued spawning before natural mortality (Costello et al. 1979). However, analysis of stridulation ridges (Simonsen 1985) have shown long-term trends of regenerated claws representing only 9.5–13% of total Florida landings (Savage et al. 1975, Wilber 1995, Muller et al. 2006, 2011, Gandy et al. 2016). These results suggest that many stone crabs may not be able to contribute to the fishery a second time. The low landing rates of regenerated claws can be attributed to numerous factors. First, the fishery technique used to remove claws often results in breaks that are not along the natural autotomy-fracture plane, causing wounds correlated to mortality (Davis et al. 1978, Savage & Sullivan 1978, Sullivan 1979, Simonsen & Hochberg 1986, Duermit et al. 2015). Also, adult stone crabs are generally only able to regenerate a lost claw to its previous size or greater after 2 or more years in ideal conditions (Savage & Sullivan 1978, Restrepo 1989). However, a 2 yr regeneration period is not likely to occur before many crabs reach their terminal molt (Cheung 1973). Furthermore, regeneration frequencies are lower in field populations (Savage et al. 1975). Claw regeneration to the size of fishery eligibility likely requires major energetic investment (Niewiarowski et al. 1997, Naya et al. 2007) and, due to the ectothermic nature of crabs, may be strongly reliant on the crabs' temperature-dependent energetic processes.

To fuel these energetic processes, the crabs must eat. The primary diet for adult stone crabs is hard-shelled bivalves (Gunter 1955, Menzel & Nichy 1958); however, Hogan & Griffen (2014) found that 1-clawed stone crabs consume 50% fewer bivalves than those with 2 claws, and crabs that had lost both claws generally did not consume any hard-shelled prey. Similarly, feeding on hard-shelled bivalves was virtually eliminated for *Cancer pagurus* after claws were autotomized. Autotomized *C. pagurus* also demonstrated significantly higher consumption of fish flesh compared to 2-clawed individuals (Patterson et al. 2009). Although fish flesh consumption has not been quantified with clawless stone crabs, Bender (1971) suggested they are able to alter their diet to consume more macroalgae after claw loss. Hogan & Griffen (2014) found no evidence of algal consumption, but did find that stone crabs would consume polychaete worms regardless of the number of claws present. This suggests the potential ability of stone

crabs to shift to soft-bodied prey after claw loss if such prey is readily available. Regardless of food type, ingestion efficiency has rarely been studied in any crab species with or without the influence of claw loss. Additionally, the influence of temperature on consumption rates and ingestion efficiency has yet to be addressed for stone crabs. Since most crabs use exclusively claws in feeding (Elner & Hughes 1978, Smallegange & Van Der Meer 2003), it is logical to assume that ingestion efficiency, like consumption rates (Hogan & Griffen 2014), would decline following claw loss. Stone crab feeding behavior has not yet been quantified to investigate this potential mechanism of decreased consumption and efficiency. However, the compensatory use of walking legs has been observed when declawed stone crabs are opening and manipulating oysters (Savage & Sullivan 1978). The reduced energy intake associated with potentially altered diets or decreased ingestion efficiency may impact the energetic processes dictating claw regeneration.

To prepare for the expected continued range expansion of stone crabs, we aimed to understand the individual energetics and feeding processes of these crabs. In this study, we tested the following hypotheses: (1) the stone crabs' respiration rates will increase with temperature, claw loss, and crab size; (2) food consumption will increase with claw loss when soft tissue is readily available; (3) the consumption of bivalves will increase with temperature and crab size; (4) the ingestion efficiency will increase with temperature and crab size, and will decrease with claw loss; and (5) the use of walking legs in feeding behavior will increase with claw loss.

MATERIALS AND METHODS

We conducted 5 experiments to test our hypotheses. The first experiment examined the influence of sequential autotomy on mortality and how respiration rates changed (acclimated) over a 3 wk time period in the lab, with and without the influence of claw loss. The second examined the influences of temperature and sequential autotomy on respiration rates. All crabs used in the first 2 experiments were collected from the Stono River in Charleston, SC ($32^{\circ}45'31''$ N, $80^{\circ}00'16''$ W). The third experiment examined the influence of temperature on the consumption of oysters in field cages. The fourth examined the influences of temperature and sequential autotomy on ingestion efficiency in the lab. The fifth experiment quantified feeding behavior of

stone crabs on single oysters to investigate the mechanistic use of walking legs versus claws. All crabs used in the third, fourth, and fifth experiments were collected from Town Creek in the North Inlet-Winyah Bay National Estuarine Research Reserve near Georgetown, SC ($33^{\circ}19'57''$ N, $79^{\circ}11'17''$ W). The stone crab populations in these 2 areas include *Menippe mercenaria*, *M. adina*, and their hybrids (Bert 1985, 1986, Williams & Felder 1986, Bert & Harrison 1988, Rindone & Eggleston 2011). Previous work has demonstrated differences between the 2 species and their hybrids in genotype and shell coloration (Bert & Harrison 1988), resting metabolic rate and ammonia excretion ability (Combs et al. 1997), and juvenile tolerance to temperature and salinity (Brown & Bert 1993). However, because stone crabs are managed as a single stock in commercial fishing, we did not distinguish between these species or their hybrids for the purposes of this study, similar to more recent work studying the influence of temperature on the mortality of stone crabs after claw loss (Gandy et al. 2016). We assume that our samples are therefore representative of the stone crab population found in South Carolina. Also, approximately 38% of the stone crabs in the first 2 experiments and 39% of the crabs in the last 3 experiments had left-handed crusher claws, similar to what has been previously reported (Cheung 1976). Stone crabs are naturally right-claw dominant (Cheung 1976, Davis et al. 1978), becoming left-claw dominant only after claw loss. We included both left- and right-handed crabs haphazardly in the following experiments. All data analyses were performed in R (R Core Team 2016).

Mortality and acclimation experiment

We collected a total of 16 legal-sized stone crabs during the summer of 2015 (6 females and 10 males; carapace width [CW] \pm SD, 89.5 ± 6.35 mm) for use in the first experiment. The crabs were transported to the University of South Carolina and placed in recirculating tanks of approximately 0.155 m^2 at $25 \pm 0.5^{\circ}\text{C}$ with normoxic conditions. Tanks were supplied with an ASM G-2 in-Sump protein skimmer and live rock to maintain water quality. A 10×30.5 cm PVC pipe was provided to each crab for use as a false burrow (Beck 1995). We fed each crab 20 g wet mass of tilapia (*Oreochromis* spp.) every other day. Crabs were split into 2 blocks for feeding, with half of the crabs being fed on any given day. Crabs were given 4 h to consume this food before any uneaten food was removed. The respiration rates described below were

measured 24 h after feeding, ensuring that these measurements reflected resting rates and not specific dynamic action (Secor 2009).

Crabs were split into 2 treatments: experimental crabs that sequentially lost their claws throughout the experiment, and control crabs that retained both claws throughout the experiment. The sequence of the experiment proceeded as follows. After an initial minimum 6 d acclimation period, we observed 4 crabs d^{-1} (2 experimental and 2 control) in respiration chambers until all 16 crabs had been observed. Respiration chambers consisted of an air-tight 12.2 l tank that was filled with sea water and partially submerged in a water bath at 25°C. Water in the experimental chamber was mixed throughout the measurement period using a magnetic stir bar located below a perforated subfloor so as to not disturb the animal whose respiration rate was being measured. After placing a single crab into the chamber, we measured dissolved O₂ (ppm) every 10 min for 2 h using a Hanna Instruments HI9146-10 dissolved O₂ meter. Crabs were fed according to their normal feeding schedule immediately after these respiration measurements. Following this feeding period, we triggered autotomy of crabs in the experimental group by applying mechanical stress until they autotomized the larger, crusher claw. To induce autotomy through mechanical stress, we clamped the merus and applied repeated point pressure just beyond the coxa. We used this method rather than traditional declawing methods used by the fishery in order to reduce injuries that may lead to mortality (Davis et al. 1978). Mortality measured in this experiment is therefore not representative of the declawing methods of the fishery but rather the minimized injuries caused by natural autotomy. We allowed the crabs 7 full days after autotomy to acclimate before being handled again, while continuing the regular feeding cycle during this time. On the eighth day, we again measured their respiration rates. This was followed by removal of the second claw, again by applying mechanical stress until the crab autotomized its own smaller, cutter claw. We again gave the crabs 7 full days after autotomy to acclimate before being handled again, while continuing to feed them. This was followed by a final respiration rate measurement. Claws removed throughout the experiment were frozen for later measurements.

Following the experiment, we measured the volume of the body and each claw by water displacement. We used these volumes to account for water displacement by crabs in the respiration rate cham-

bers. We then dried the body and each claw at 70°C for 5 d and determined their dry mass. The respiration rate for each 10 min interval throughout each 2 h measurement period was calculated and converted to ml O₂ g⁻¹ dry mass h⁻¹ for analysis. We analyzed respiration rates using a mixed-effects linear model with the number of claws, measurement week, and gender treated as fixed categorical factors, the initial O₂ concentration for each 10 min interval and crab size as continuous variables, and crab ID as a random factor to control for repeated measurements of the same individuals.

Temperature-respiratory experiment

We collected a total of 32 legal-sized stone crabs during the summer of 2015 (10 females and 22 males; CW ± SD, 91.8 ± 6.48 mm) for use in the second experiment. The crabs were again transported to the University of South Carolina and placed in the same recirculating tanks as described above. However, in this experiment, all crabs experienced sequential autotomy, and water temperature was manipulated as the experimental treatment and was maintained at approximately 15, 20, 25, or 30°C. Eight crabs were used at each of these 4 experimental temperatures, and temperatures in each tank were constantly maintained within 0.5°C of the target values. All other aspects of the experimental setup and maintenance were identical to those described above for the first experiment. However, in this experiment, we also quantified the amount of food consumed in order to determine how claw loss and temperature influenced the consumption of fish flesh. At the end of each 4 h feeding period, the uneaten food was collected, dried at 70°C for 3 d, and weighed in order to determine the amount consumed.

As with the first experiment, we held crabs for at least 6 d of acclimation before observing 8 crabs d^{-1} (2 from each temperature) in respiration chambers until all 32 crabs had been observed. Respiration chambers were the same as described in the above experiment, with the water bath temperature corresponding to the holding tank temperature so that individual crabs experienced the same constant temperature throughout the duration of the experiment. We conducted respiration rate measurements and triggered claw loss as described in the first experiment.

Following the experiment, we measured the volumes and dry mass of the body and each claw as described in the previous experiment. We calculated the mass-specific respiration rate for each 10 min

interval throughout the 2 h measurement period and converted this to ml O₂ g⁻¹ dry mass h⁻¹ for analysis. We analyzed these mass-specific respiration rates using a mixed-effects linear model with the number of claws and temperature treated as fixed categorical factors, the initial O₂ concentration for each 10 min interval as a continuous variable, and crab ID as a random factor to control for repeated measurements of the same individuals. We used z-scores to scale water temperature and initial O₂ concentration. The use of z-scores allowed us to make direct comparisons from the linear regression between the parameter estimates for different explanatory variables, without affecting the t- or p-values. Q₁₀, the factor by which the respiration rates change as the temperature is increased by 10°C, was calculated using the equation $Q_{10} = (R_H/R_L) (10/(T_H - T_L))$, where T_H and T_L are the average high and low temperatures during the 2 h measurement period, and R_H and R_L are the average respiration rates measured at the high and low temperatures. Since the respiration rates varied with initial O₂ concentrations, and the initial O₂ concentrations varied with temperature, the average R_H and R_L values were only calculated from the 10 min intervals whose initial O₂ concentrations were found at each of the temperatures. We analyzed consumption rates of tilapia using a mixed-effects linear model with the number of claws and temperature treated as fixed categorical factors, crab size as a continuous variable, and crab ID as a random factor to control for repeated measurements of the same individuals.

Consumption experiment

We collected a total of 41 legal-sized stone crabs between 22 October 2015 and 23 September 2016 (13 females and 28 males; CW ± SD, 90.6 ± 11.6 mm) for use in the third experiment. Experimental periods consisted of 7 separate week-long trials performed between October 2015 and October 2016 (Table 1). The number of replicate crabs included in each trial varied based on the number of healthy stone crabs successfully captured prior to the start of each trial. During preliminary experiments with water temperatures as low as 15°C, we observed drastically reduced feeding. Thus, we elected to not measure consumption rates during the winter months because water temperatures in the field reached weekly averages as low as 8°C (NOS/CO-OPS 2016).

For each of the 7 trials, the sequence of the experiment proceeded as follows. Crabs were held for a

Table 1. Dates of week-long experimental periods from the consumption experiment with stone crabs (*Menippe* spp.). Temperature and salinity measurements were recorded in 15 min intervals and averaged for the entire week. Data are mean ± SD

Experimental date	Temperature (°C)	Salinity	No. females	No. males
24–31 Oct 2015	21.3±1.03	31.3±2.16	7	2
14–21 Nov 2015	17.8±1.36	24.0±3.10	6	3
23–30 Apr 2016	23.7±2.24	34.1±0.48	4	2
14–21 May 2016	23.7±1.22	34.3±0.39	2	3
8–15 Jul 2016	30.9±1.39	34.9±0.36	1	3
7–14 Aug 2016	30.9±1.33	34.0±1.27	3	0
24 Sep – 1 Oct 2016	27.7±0.81	29.2±3.74	3	2

24 h starvation period in individual porous tanks (circular with a diameter of 26.24 cm; water height 30 cm) submerged in a flow-through tank (circular with a diameter of 1 m; water height 30 cm), that was supplied with raw seawater from the estuary. Completely enclosed cages with dimensions 61 × 46 × 30.5 cm (length × width × depth) and 7 mm Vexar mesh were used for both experimental and control measurements. Experimental cages held a single stone crab, 3124 ± 122 g (mean ± SD) of live eastern oyster *Crassostrea virginica* clumps, and a 10 × 30.5 cm PVC pipe for use as a false burrow (Beck 1995). Control cages held 3137 ± 161 g of live oyster clumps and a 10 × 30.5 cm PVC pipe, but no crab. Oyster clumps were gathered from a tidal creek (33° 21' 53" N, 79° 10' 6" W), washed clean of mud, cleared of mud crabs (*Panopeus herbstii* and *Eurypanopeus depressus*) and ribbed mussels *Geukensia demissa*, sundried, and weighed to the tenth of a gram before placement in cages. Cages were then positioned at least 1.5 m apart and within 150 m of the Oyster Landing Station (NOAA Station ID: 8662245) such that at the lowest tide during the week-long experimental period, cages were still fully submerged under at least 30 cm of water. Following the week-long experimental period, cages were collected and crabs were immediately separated from oysters. All live oysters and shell fragments (≥7 mm) from both experimental and control cages were collected, washed clean of mud, sundried, and weighed to the tenth of a gram. The difference in oyster mass in experimental cages between the beginning and end of the experimental period was considered the amount of oyster consumed by the stone crab assuming 100% ingestion efficiency. The average difference in oyster mass in control cages was used as correctional value for

experimental cages. A minimum of 3 control cages were present in each trial, and their mass differences (before – after) were averaged for a correctional value for each trial separately. Meteorological and water quality data were collected in 15 min intervals for the duration of each week-long trial from NOAA Station 8662245 (NOS/CO-OPS 2016) and averaged for the entire week.

We analyzed consumption using a linear regression model with the water temperature, salinity, and crab mass as continuous variables and gender as a fixed categorical variable. Other water quality parameters were measured on site but were not used in the model based on strong covariance with salinity or temperature. We again used z-scores to scale crab mass and water temperature in the linear regression because the range of crab mass measured was over 33 times greater than the range of water temperatures. The use of z-scores therefore allowed us to make direct comparisons between parameter estimates for different explanatory variables without influencing the *t*- or p-values.

Ingestion efficiency experiment

We collected a total of 14 legal-sized stone crabs during the summer of 2016 (17 females and 9 males; CW \pm SD, 93.5 \pm 10.3 mm) for use in the fourth experiment. The crabs were transported to the University of South Carolina and placed in recirculating tanks of approximately 0.31 m² held at either 18 or 28°C (temperature was consistently maintained within 0.5°C of the target value). Tanks were again supplied with an ASM G-2 in-Sump protein skimmer and live rock to maintain water quality. A 10 × 30.5 cm PVC pipe was provided to each crab for use as a false burrow (Beck 1995). In this experiment, all crabs experienced sequential autotomy while water temperature was manipulated as the experimental treatment.

After an initial 7 d acclimation and starvation period, we observed 4 crabs d⁻¹ (2 from each temperature treatment) in measurement tanks until all crabs had been observed. Measurement tanks were 32.4 l flow-through tanks supplied with normoxic water at 10 l min⁻¹ from the recirculating tanks used to hold crabs. Water leaving the measurement tanks was filtered through grade 50 cheesecloth to catch all large food particles. After placing a single crab and a single piece of tilapia (22.3 \pm 2.16 g) into the tank, the tank was covered with an opaque plastic film to provide a dark environment and left

undisturbed for 24 h. Immediately following the end of the 24 h measurement period, crabs were removed from measurement tanks and tanks were drained through the cheesecloth filter. Any uneaten tilapia was washed from the measurement tank into the filter. Filters and all food particles not ingested by the crabs were dried at 70°C for 5 d. Following the 5 d drying period, we measured the total mass of all food with the filter; any uneaten food that was too big to have been carried away by the water current was then removed and weighed separately. Following the measurement period, we triggered autotomy as described in the first experiment. We gave the crabs 8 full days after stimulating claw loss to acclimate before being handled again. We did not feed crabs during this 8 d period. On the ninth day, we again measured the crabs' ingestion efficiency following the same protocol as the first measurement. This was followed by autotomy of the second claw using the same methods, and another 8 d acclimation period. This was followed by a final ingestion efficiency measurement period.

Ingestion efficiency was calculated as follows: $E_I = 1 - [T - (U + F)]/M - U \times 100$, where E_I is the ingestion efficiency, T is the total mass of the filter and all food particles after drying and removing fecal pellets, U is the dry mass of uneaten food too big to have been taken by the water current, F is the mass of the filter, and M is the dry mass of the initial meat provided to the crabs. T , F , and U were measured to 0.01 g, and M was calculated as follows. We weighed pieces of tilapia (22.3 \pm 5.15 g) before placing them directly into the drying oven at 70°C for 5 d. After the drying period, we weighed the tilapia and performed a regression of the dry mass with respect to the wet mass ($R^2 = 0.968$). We then used this regression to calculate the initial dry mass of tilapia from the initial wet mass. Mass of the food the crab attempted to eat was defined as the difference between the mass of the initial meat provided to the crabs and the mass of uneaten food too big to have been taken by the water current ($=M - U$). We analyzed ingestion efficiency using a general additive model with CW and mass of the food the crab attempted to eat as smoothed parameters and temperature, number of claws present, and gender as categorical parameters. A general additive model was used to account for the nonlinear relationship between mass of the food the crab attempted to eat and the ingestion efficiency. CW and mass of the food that the crab attempted to eat were smoothed using a smoothing spline fit.

Feeding behavior experiment

We collected a total of 5 stone crabs during the fall of 2016 (2 females and 3 males; CW \pm SD, 88.3 \pm 11.1 mm) for use in the fifth experiment. The crabs were transported to the University of South Carolina and placed in 12.2 l individual holding tanks held at room temperature (approximately 22°C). Tanks were continually bubbled with air to maintain dissolved O₂ levels. All 6 sides of the holding tanks were transparent to facilitate observation. High-definition video recordings of feeding behavior were made using a GoPro Hero 4 video camera mounted directly underneath the holding tanks for a ventral view of each crab. Each tank was filmed with an individual camera to enhance the view of the video recordings collected.

Crabs were fed a single oyster (mean \pm SD, 85.3 \pm 10.7 mm) overnight with a red lamp used to illuminate the camera's view while minimizing any visual disturbance to the crab (Griffen & Williamson 2008). Each crab's feeding was recorded 3 separate times to observe variation within an individual. Analysis of video recordings proceeded as follows. Total handling time was recorded, in seconds, such that it began when the crab made initial contact with the oyster and ended once the crab no longer actively engaged with oyster shell fragments. The total time was then split into 2 categories: 'time eating' consisted of all seconds that the crab was actively manipulating or feeding on the oyster, while 'time not eating' consisted of all seconds that the crab was not manipulating and/or feeding on the oyster. The number of times each appendage (major claw, minor claw, or walking legs) was used was counted for 'time eating.' Each tally was defined by an appendage being used to independently manipulate shell fragments after the oyster had been opened. After the major claw was used to crack the oyster shell, it was often placed in front of the crab and used as a barrier to prevent shell fragments from sliding away; this was not counted as a manipulation in the tally because the major claw was motionless and did not manipulate oyster fragments. Counts for the front 4 walking legs were combined to compare claw versus walking leg use. We chose not to quantify the relative use of walking legs to manipulate food after crabs had automated 1 or both claws because walking legs were already used far more often than either claw when both were present. The number of times used for each appendage type was transformed using a 2-parameter Box-Cox transformation (Box & Cox 1964) to reduce variance in the appendage use. We analyzed the transformed number of times each ap-

pendage was used with an ANOVA followed by Tukey's HSD test. We analyzed handling time and time eating using mixed-effects linear models with the crab's CW and oyster shell size treated as fixed continuous variables and with crab ID treated as a random factor to control for repeated measurements of the same individuals.

RESULTS

Mortality and acclimation experiment

Crabs that did not experience claw loss had decreasing respiration rates over the course of the experiment, suggesting acclimation to experimental conditions. Respiration rates independent of claw loss decreased 30% between Weeks 1 and 2 ($t = -3.72$, $p = 0.0002$) and 14% between Weeks 2 and 3 ($t = -5.17$, $p < 0.0001$). Conversely, the loss of both major ($t = 5.09$, $p < 0.0001$) and minor ($t = 3.68$, $p = 0.0003$) claws led to increased respiration rates. After correcting for decreases in respiration rates associated with time in the lab (using results from control crabs), major and minor claw loss led to an average respiration rate increase of 80 and 69%, respectively (Fig. 1). Changes in oxygen depletion increased 4 ×

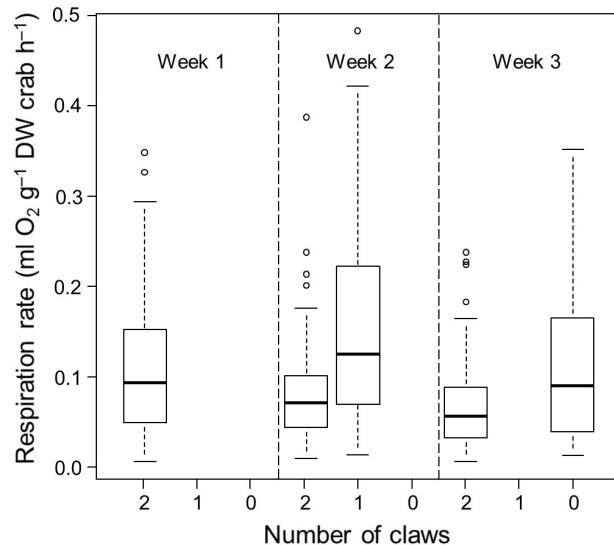


Fig. 1. Mass-specific oxygen depletion by stone crabs (*Menippe* spp.) in the mortality and acclimation experiment. In the first week, all crabs had both claws; experimental crabs lost their major and minor claws in Weeks 2 and 3, respectively, while control crabs retained both claws throughout. The heavy line represents the median while the box gives the upper and lower quartiles. Whiskers encompass 95% of the data, and circles are outliers. DW: dry weight

10^{-4} ml O₂ g⁻¹ crab dry weight (DW) h⁻¹ for every 1 ml O₂ l⁻¹ increase in initial O₂ concentration ($t = 3.73$, $p = 0.0002$). Variation in respiration rates was high (SD = 7×10^{-5} ml O₂ g⁻¹ crab DW h⁻¹). Mortality rates following sequential autotomy for first and second claw loss were 6.25 and 13.3 %, respectively. Respiration rates were not significantly influenced by gender ($p = 0.2977$) or crab size ($p = 0.6195$).

Temperature-respiratory experiment

Mass-specific respiration rates increased with water temperature (parameter estimate [PE] = 0.006, $t = 3.48$, $p = 0.0017$, Fig. 2), initial O₂ concentration (PE = 0.028, $t = 6.35$, $p < 0.0001$), and sequential autotomy (PE = 0.022, $t = 4.95$, $p < 0.0001$, Fig. 2). Q_{10} was 1.536. Variation in respiration rates with initial O₂ concentration was high ($R^2 = 0.006$). Mortality due to claw loss increased by a factor of 3.34 for each 10°C increase in water temperature. Mass-specific respiration rates were not significantly influenced by the crab size ($p = 0.5373$) or gender ($p = 0.2532$). Using z-scores, the initial O₂ concentration and water temperature had similar impacts on respiration rates (PE ± SE; 0.033 ± 0.005 for initial O₂ concentration and 0.031 ± 0.010 for water temperature). The consumption of tilapia increased with CW ($t = 2.72$, $p =$

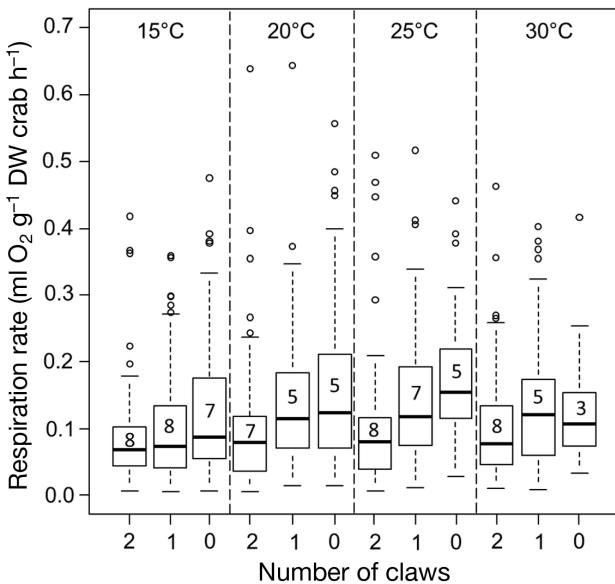


Fig. 2. Mass-specific oxygen depletion by stone crabs (*Menippe* spp.) in the respiratory experiment. The numbers inside the boxes represent the numbers of crabs measured at a certain number of claws and temperature (these numbers decreased throughout the experiment due to crab mortality).

Box plot parameters as in Fig. 1

0.0100) and claw loss ($t = 2.44$, $p = 0.0155$), but not temperature ($p = 0.5971$).

Consumption experiment

Control cages exhibited a decrease in oyster mass ranging between 5.1 ± 2.6 and 199.9 ± 7.8 g. Consumption rates increased with water temperature ($t = 4.23$, $p = 0.0002$, Fig. 3) and crab mass ($t = 3.09$, $p =$

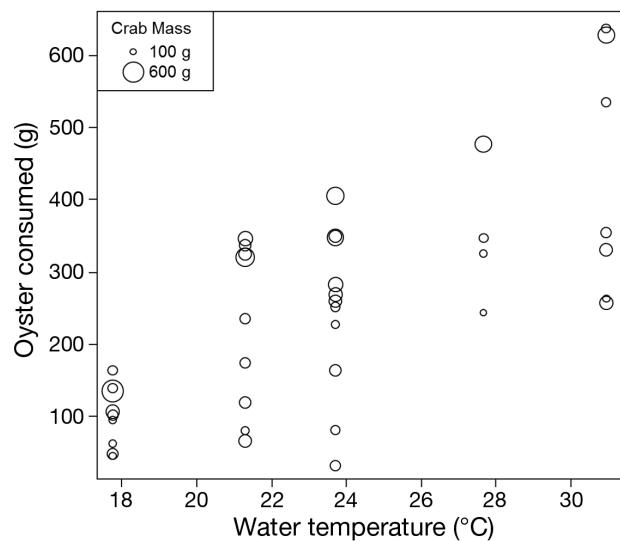


Fig. 3. Consumption rates of stone crabs (*Menippe* spp.) on oysters with the corresponding crab mass. Data points are scaled to the water temperature during the experimental period

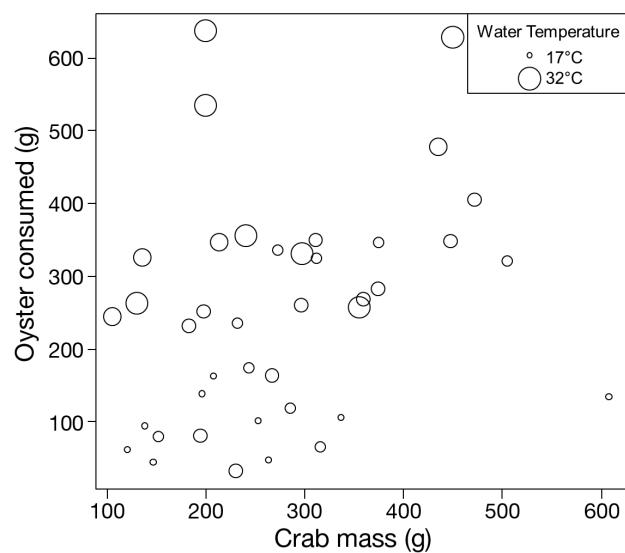


Fig. 4. Consumption rates of stone crabs (*Menippe* spp.) on oysters with the corresponding water temperature. Data points are scaled to the mass of each crab

0.0042, Fig. 4). Mass-specific consumption of oysters increased by 15.8% for every 10°C increase in water temperature ($R^2 = 0.509$). Using z-scores, the water temperature had a nearly 2-fold greater impact on the consumption rate than the mass of the crab ($PE \pm SE = 103 \pm 24.5$ for water temperature and 54.9 ± 17.8 for crab mass). There were no significant changes in consumption rates with gender ($p = 0.4786$) or salinity ($p = 0.9052$).

Ingestion efficiency experiment

Ingestion efficiency increased with the mass of tilapia the crab attempted to eat ($F = 4.12$, $p = 0.0460$, Fig. 5). Efficiency was not significantly different ($t = 1.24$, $p = 0.2315$) between 2-clawed ($E_I = 80.4\%$) and 1-clawed crabs ($E_I = 89.7\%$), nor between 1-clawed and 0-clawed crabs ($E_I = 46.9\%$, $t = -1.77$, $p = 0.0955$). There was no significant change in ingestion efficiency with water temperature ($p = 0.2906$) or crab size ($p = 0.3860$).

Feeding behavior experiment

The front 4 walking legs were used significantly more in food manipulation than minor claws ($p < 0.0001$), and minor claws were used significantly more than major claws ($p < 0.0001$, Fig. 6). The back

4 walking legs were observed stabilizing the crab against the substrate when oysters were handled, but never manipulating food. Total handling time was inversely related to CW ($t = -3.91$, $p = 0.0298$) but did not significantly vary with oyster size ($p = 0.7834$). However, the proportion of the handling time defined as 'time eating' did not increase with oyster size ($p = 0.0575$). Individual variability in handling time was generally low, but was very high for a single crab (Fig. 7).

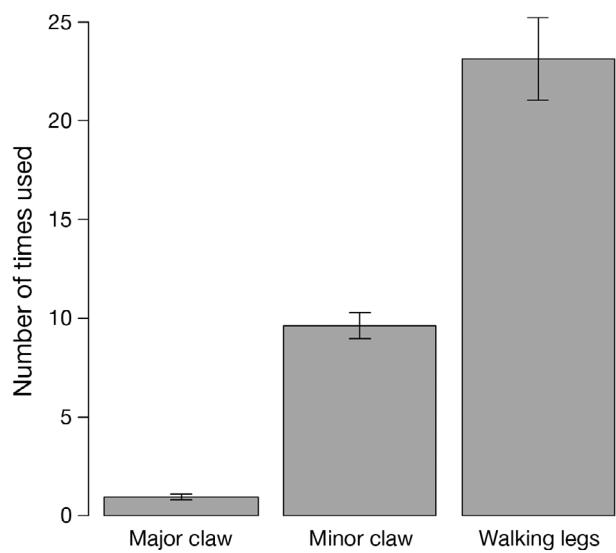


Fig. 6. Number of times each appendage was used by stone crabs (*Menippe* spp.) to manipulate oysters during feeding. Each bar includes all 3 replicates from each of the 5 crabs. Error bars represent \pm SE about the mean

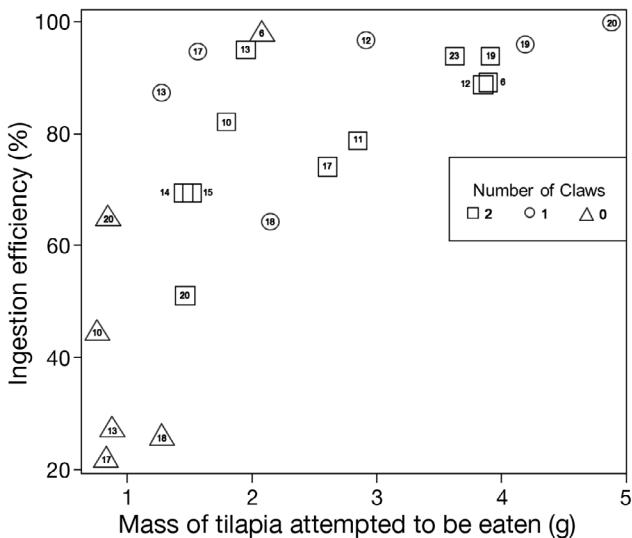


Fig. 5. Ingestion efficiencies of stone crabs (*Menippe* spp.) with the corresponding mass of tilapia that each crab attempted to eat. The number within each data point represents the crab ID while the point shape represents the number of claws present for each measurement period

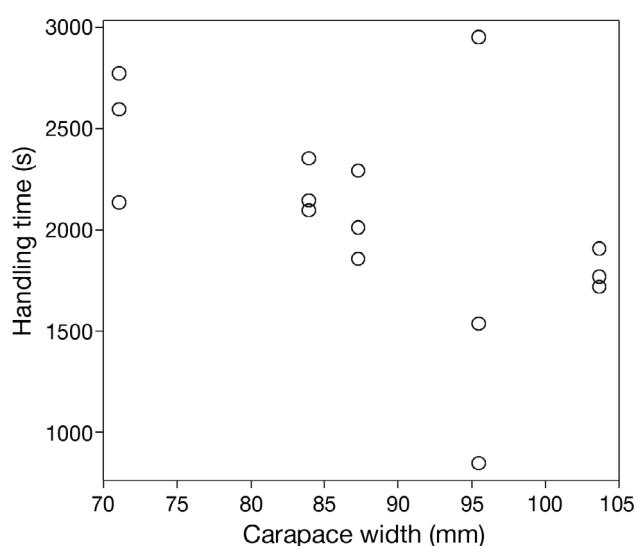


Fig. 7. Handling time of stone crabs (*Menippe* spp.) on single oysters (85.3 ± 10.7 mm shell length) with the corresponding crab carapace width

DISCUSSION

The various components of this study yielded several interesting findings. First, as expected, we found that mass-specific respiration rates increased with water temperature, dissolved O₂, and claw loss. By showing that respiration rates are depressed under low O₂ conditions, our results support previous work by Albert & Ellington (1985), who found low O₂ levels to negatively influence stone crab health and survival. Increased mass-specific respiration rates following claw loss may have come from the energetic cost of regenerating a claw or may be an artifact of removing a large portion of the body that has a relatively low energetic maintenance cost. It is important to note that respiration rates here reflect the combined respiration of crabs and the bacterial community. Independent measurements of oxygen loss in the absence of crabs suggests that up to 47% of the respiration reported here may be attributable to bacteria. Second, in the consumption experiment we found that crabs again behaved as expected and consumed more oysters as the crabs' size and the water temperature increased. Third, as a part of the temperature-respiratory experiment we found that crabs consumed more fish flesh after claw loss, similar to *Cancer pagurus* (Patterson et al. 2009). This finding suggests that if easily consumed food (i.e. non-hard-shelled prey) is readily available, stone crabs will meet the increased energetic demands of claw regeneration by increasing food consumption. Fourth, although the ingestion efficiency of clawless crabs was numerically lower than that of the 2- or 1-clawed crabs, it was not significantly lower at $\alpha=0.05$, possibly due to low power resulting from small sample sizes. It appears that use of walking legs may be the primary reason that ingestion efficiency did not change with the loss of a single claw. Stone crabs used their walking legs in food manipulation far more than expected, perhaps due to the relatively large and cumbersome claws of this genus.

We found that the rates of food consumption and oxygen utilization varied differently with changes in temperature, and this finding has implications for the climate-induced range expansion of this genus. Specifically, the imbalance in energy expenditure (respiration) and intake (oyster consumption) with water temperature shown in this study suggests a potential temperature threshold for stone crabs determined by energetics. A rough estimate of this threshold can be derived using respiration and consumption results over the range of temperatures presented here. To do this, we made some unit conver-

sions to put energy expenditure and intake into comparable units. For energy expenditure, we first converted the respiration rates from the temperature-respiratory experiment (ml O₂ g⁻¹ crab h⁻¹) to mg O₂ g⁻¹ crab wk⁻¹. Consistent with our observations while capturing experimental animals, we next assumed that stone crabs are only active at night, which we defined as 8 h d⁻¹. We therefore estimated total metabolic expenditure by assuming that active respiration by stone crabs is 3× higher than passive respiration, consistent with relative active and passive rates of other crab species (Wallace 1972). We then converted the total (i.e. active + passive) respiration rates from mg O₂ g⁻¹ crab wk⁻¹ to calories g⁻¹ crab wk⁻¹ using the proportion of fat, protein, and carbohydrates in the crabs' primary diet, the eastern oyster *Crassostrea virginica* (16.9% fat, 56.3% protein, and 26.8% carbohydrates; USDA 2016), and using conversion rates of 3.28, 3.25, and 3.53 cal mg⁻¹ O₂ consumed for fat, protein, and carbohydrates metabolized, respectively (Elliott & Davison 1975). Finally, we converted energetic equivalents in cal g⁻¹ crab wk⁻¹ to joules g⁻¹ crab wk⁻¹.

For the consumption half of the calculations, we first applied the ingestion efficiency of 2-clawed crabs ($E_I = 80.4\%$) to the difference in oyster mass in between the beginning and end of the consumption rate experiment to determine the mass of oysters (g oyster week⁻¹) that was actually ingested. We then standardized oyster consumption rates across crab size into units of g oyster g⁻¹ crab wk⁻¹. Our consumption experiment enclosed crabs in cages where they had access to excess food, refuge via a false burrow, and no predation risk. The ~80% of body mass consumed by these crabs weekly therefore represents maximum possible consumption rates under ideal conditions. We then converted the mass of oyster consumed into the energy intake using 0.51 kcal g⁻¹ oyster (USDA 2016), assuming that assimilation efficiency was 100% and consistent across temperatures (Giguere 1981). Finally, we converted kcal g⁻¹ crab wk⁻¹ to joules g⁻¹ crab wk⁻¹. Although the calculations described above contain many assumptions, they provide the following general estimates for relative changes in energy expenditure and intake with temperature variation. For every 10°C decrease in ambient temperature, the energy intake is reduced by roughly 550 joules g⁻¹ crab wk⁻¹ while the energy expenditure only reduces by 70 joules g⁻¹ crab wk⁻¹. This suggests that at low temperatures, energy expenditure will outpace energy intake, creating a potential temperature threshold for stone crabs.

While the above calculations provide a mechanistic basis for the lower temperature threshold of stone crabs, they do not identify a specific temperature of a tipping point between the rate of energy expenditure and energy intake. In preliminary experiments, we observed reduced feeding in waters below 15°C, and inhibited claw use has been demonstrated in stone crabs in waters below 8°C (Brown et al. 1992). At the northern edge of the stone crabs' range, summertime temperatures are sufficiently warm such that energy intake exceeds energy expenditure, while the reverse is likely true at wintertime temperatures. The specific northern extent of stone crabs may therefore be determined by degree days (i.e. the cumulative average of daily temperatures; Kurata 1961). Stone crabs are expanding their range northward (Rindone & Eggleston 2011); however, the rate at which this will occur with further warming likely depends on the balance of energy intake and expenditure at different temperatures. Further research is required to determine the degree days that provide the precise tipping point in the energetics of this genus.

Our results also have implications for the stone crab fishery. The claw-only stone crab fishery lessens the impact on populations because harvested individuals are not necessarily killed (Costello et al. 1979). However, our results suggest that stone crabs may struggle to cope with the combined effects of increasing water temperatures and fishery-style claw loss, especially in areas that are O₂ depleted. Although we did not experimentally manipulate O₂ levels, we found that low dissolved O₂ and increased temperature were of similar importance in influencing respiration. This suggests that dissolved O₂ concentrations may potentially influence the stone crab fishery, yet regulations for this stock do not incorporate consideration of dissolved O₂. Low O₂ levels could be especially problematic in some regions on the Florida coast. Although the stone crab population in Florida has a different genetic makeup than the population sampled in South Carolina (Bert 1986, Williams & Felder 1986, Bert & Harrison 1988, Rindone & Eggleston 2011, Gandy et al. 2016), low dissolved O₂ could negatively influence stone crabs in Florida in similar ways. For instance, there is concern in Florida over pollution from Lake Okeechobee draining into the Caloosahatchee River Estuary (Anton & Pittman 2016, Garcia 2016, Reid et al. 2016). Agricultural production and urban development in the watershed load nitrogen and phosphorus into the estuary, contributing to an increasing frequency of eutrophication (Knight & Steele 2005). Although Florida's commercial fishery is largely based off-

shore, stone crab larvae and juveniles often live in nearshore waters (Bert 1985, Bert et al. 1986, Brown et al. 1992) including this estuary. Between the 2003–04 and 2009–10 fishing seasons, the region which contains the Caloosahatchee River Estuary pulled the highest number of traps by at least 1.2 million each fishing season, while only yielding the highest landings in 1 of those 7 seasons (Muller et al. 2011). Since low dissolved oxygen in estuaries has corresponded to declines in production of other offshore fisheries (Hughes et al. 2015), it is possible the same is happening in Florida with stone crabs. If the negative influence of low O₂ applies to the stone crabs in Florida and South Carolina in similar ways, then eutrophication and O₂ depletion in the Caloosahatchee River Estuary could potentially be a contributing factor to the decreased catch per unit effort offshore in the Southwest region.

Eutrophication and O₂ depletion are issues that extend to environmental systems beyond southern Florida and the stone crabs. In the USA, the number and intensity of hypoxic and anoxic waters, harmful algal blooms, and eutrophic areas have increased in coastal waters since the early 1990s (Scavia & Bricker 2006). Globally the trend is the same; the first comprehensive list of hypoxic zones identified 45 areas worldwide (Diaz & Rosenberg 1995), while 13 yr later, the list grew to 169 hypoxic areas with an additional 233 areas of concern for eutrophication (Selman et al. 2008). Underreporting in certain parts of the world causes these numbers to be conservative; in general, therefore, coastal waters are experiencing lower levels of dissolved O₂. However, hypoxia tends to be ignored until higher-level organisms, often commercially important organisms, are affected (Diaz & Rosenberg 2008). Loss of commercial stocks in the Chesapeake Bay, Gulf of Mexico, and Baltic Sea are estimated to be as high as 6, 17, and 106 kt of carbon yr⁻¹, respectively, due to severe seasonal hypoxia (Möller et al. 1985, Diaz & Schaffner 1990, Rabalais & Turner 2001, Diaz & Rosenberg 2008). Hypoxia and the issues associated with low-O₂ waters affect most organisms within each system, not just those that are of commercial importance. The results presented here suggest that hypoxia could potentially be detrimental to stone crab energetics and thus to the stone crab fishery.

In summary, we have shown that stone crab respiration increases with dissolved O₂, water temperature, and claw loss. Food consumption rates also increase with water temperature and crab size, and crabs will increase consumption following claw loss if easily consumable (i.e. soft) animal tissue is readily

available. This increased food consumption is attributable to the unexpectedly high use of walking legs to manipulate food during feeding. Our findings suggest that the relative rates of change of respiration and food consumption with changes in temperature likely set the thermal range limit for this genus, providing a mechanistic basis for understanding its range expansion. Further, the strong influence of dissolved O₂ on respiration rates suggests that low oxygen levels may hamper physiological performance for this genus in some regions, especially following the physiologically stressful removal of claws.

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