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Cover Photograph: A Stone Crab (*Menippe mercenaria*) used in the simulated fisheries study described herein. A coded numeric tag, which was glued to the upper carapace and used to identify the individual through the course of the experiment, is visible. Photograph © Cape Eleuthera Institute.

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Evaluation of Stone Crab (*Menippe mercenaria*) Fisheries Practices Using Simulated Fishery Scenarios in the Laboratory

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Abstract - *Menippe mercenaria* (Stone Crab) fisheries primarily occur along the Gulf of Mexico and Atlantic coasts of the southeastern US. Crabs are generally captured in baited traps during the commercial and recreational claw-only fisheries. Fishing regulations differ by region and country, but often dictate that harvested claws must be legal size, with ovigerous females and crabs with sub-legal sized claws returned to the water. However, despite traps remaining close to the site of capture, repeat captures of claw-harvested crabs are relatively low, suggesting either low survival of crabs following release, learned behavior towards avoiding traps, or a physiological or anatomical impairment preventing trap re-entry. Using a combination of laboratory simulations of the Stone Crab fishery practices including trapping experiments, post-release feeding experiments, and respirometry to measure energetic cost, we examined: (1) the relative role and repeatability of physiological and behavioral traits in the capture process, and how this may change following claw removal and release; (2) the effect of claw removal on the immediate behavior (shelter use, exploration, and feeding) of crabs following release; and (3) the immediate physiological cost associated with the practice of removing claws. Results suggest that claw removal had a negligible effect on trapping behavior. However, crabs with claws removed spent less time feeding and had a higher relative standard metabolic rate (SMR) and relative routine metabolic rate (RMR) compared to crabs with no claws removed. Lastly among the intact crabs, individuals with higher relative SMR and relative RMR took significantly less time to enter the trap, suggesting these individuals were more catchable. Given the results, we suggest Stone Crab fisheries practices may have the potential to cause significant behavioral and physiological changes at both the individual and population level that may transcend to ecosystem and potentially wider evolutionary changes to populations.

Introduction

Menippe mercenaria (Say) (Stone Crab) fisheries primarily occur along the Gulf of Mexico and Atlantic coasts of the southeastern US, and are estimated to be worth \$30.4 million annually in Florida, USA, and \$2.8 million annually in export value from The Bahamas to the USA (Moultrie et al. 2016). Stone Crabs are generally captured in commercial and recreational claw-only fisheries using baited traps.

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Traps are typically fabricated using rectangular polypropylene slotted panels with a funnel-shaped entrance on the top of the trap for crabs to enter. A layer of concrete is often poured in the bottom of the trap to act as a weight and keep the trap on the seafloor. To ensure animals can exit in the event a trap is lost, all traps must be fitted with a degradable wooden panel (14.0 cm x 8.9 cm). Sets of commercial traps often span several kilometers and are left to soak for several days to weeks. Once a trap is hauled to the surface, the fisher removes individual crabs, harvests legal-sized claw(s), and returns the crabs to the water alive, generally close to the site of capture. Repeat captures of claw-harvested crabs are relatively low (Duermit et al. 2017, Wilber 1995), suggesting either low survival of crabs following claw removal, physiological or anatomical impairment preventing trap re-entry, or the potential for learned behavior toward avoiding traps. Fisheries regulations dictate that harvested claws must be legal size, with ovigerous females and crabs with claws smaller than legal size returned to the water unharmed. Legal size limits, number of claws harvested, and seasonality of fisheries can vary by region and country. In Florida, USA, propodus length of harvestable Stone Crabs must be ≥70 mm, whereas in The Bahamas the minimum legal size is ≥102 mm. Best practice recommends that only a single (larger) claw be removed so the crab can adequately feed following release and survive to re-enter the fishery once the harvested claw has regenerated (Bert et al. 2016); nevertheless, both claws are often harvested in many areas (Gandy et al. 2016, Sullivan 1979). Studies suggest that re-entry into the fishery is relatively uncommon given the number of required molts for claws to reach harvestable size (~3–4 years; Savage and Sullivan 1978) and the life span of the Stone Crab (~8 years; Cheung 1973). Analysis of long-term trends in stridulation ridges (used to assess whether a claw has been regenerated or not; Simonson 1985) for claws harvested in commercial fisheries along the coasts of Florida and South Carolina, USA, suggests only 3–13% of total landings are regenerated claws (Duermit et al. 2017, Gandy et al. 2016, Muller et al. 2011, Simonson and Hochberg 1986, Wilber 1995). The Florida Stone Crab fishery has been historically overexploited, with exponential increases in trapping from 15,000 traps in 1962–1963, to 1.6 million traps in 2001–2002 (Muller et al. 2006). In contrast, Stone Crabs are an emerging fishery in The Bahamas, with no current abundance estimates or sustainable harvest limits established, despite an estimated 54,204 kg of claws harvested in 2015 (Moultrie et al. 2016). Although landings and catch-per-unit-effort data suggest the abundance of Stone Crabs in The Bahamas are a fraction of those in continental United States, the claws are typically larger (Bert and Hochberg 1992) and marketed as a premium product, making the fishery selective towards individuals with larger claws.

While Stone Crabs have the natural ability to autotomize (voluntarily drop) their claw(s) when damaged or threatened, existing research on the physiological, ecological, and behavioral implications of claw removal remain limited (although see Duermit et al. 2015, Hancock and Griffen 2017, Wilber 1995 for exceptions). For example, while the autotomy process may provide immediate survival benefits to the individual, there is potential for long-term functional and energetic costs due to a reduction in defense, locomotion, and feeding (Juanes and Smith 1995).

Ecosystem-wide effects are also plausible, as individual crabs shift from the role of active carnivore, primarily consuming hard-bodied molluscs, to passive detritivore, primarily feeding on carrion, especially when both claws are harvested (Duermit et al. 2015).

Despite the potential for long-term functional and energetic costs to the crab and ecosystem, claw-only fisheries are often regarded as sustainable because they are believed to exploit the natural ability of the species to autotomize and regenerate their claw(s). In addition, the use of traps ensures minimal by-catch compared to other commercial fisheries practices such as long-lines, gillnets, and trawls. Nevertheless, evidence suggests that Stone Crab fisheries may not be sustainable. The mortality of de-clawed crabs following release (especially in cases where 2 claws are removed) has been shown to be 1–57% in the laboratory (Davis et al. 1978, Duermit et al. 2015) and 23–51% in the wild (Davis et al. 1978, Gandy et al. 2016). The large variation in survival is due to the myriad of factors that influence survival after claw loss, including, but not limited to, the number of claws removed (Davis et al. 1978, Duermit et al. 2015), harvester experience (Duermit et al. 2017), water temperature (Gandy et al. 2016), wound size (Duermit et al. 2015), and break location (Gandy et al. 2016, Simonson and Hochberg 1996). If claw removal is done correctly, the break should occur at the basi-ischium, located at the base of the merus, and allow for the formation of a hypodermal diaphragm that immediately stops bleeding (Savage and Sullivan 1978). While the factors affecting the survival of the Stone Crab following claw removal have been relatively well studied, there remains a paucity of studies investigating the immediate behavioral and physiological impairment of the crab following claw removal and release. Furthermore, discussion of the potential larger ecosystem-wide and evolutionary consequences associated with Stone Crab fisheries practices also remain largely ignored.

Standard metabolic rate (SMR; the baseline level of energy intake needed to sustain life, analogous to basal metabolic rate in endotherms) and, to a lesser extent, the routine metabolic rate (RMR; the average rate of metabolism when the animal is undergoing normal behaviors) have been linked to a variety of traits and behaviors (e.g. activity, boldness, risk-taking) important in the capture process in commercial and recreational finfish fisheries (Diaz Pauli and Sih 2017, Hollins et al. 2018, Killen et al. 2015,Thambithurai et al. 2018). To our knowledge, however, no studies have attempted to evaluate the physiological and behavioral implications of Stone Crab fisheries practices in this context.

To examine the immediate physiological and behavioral effects of Stone Crab fisheries practices and discuss the potential for wider ecosystem and evolutionary implications of the fishery, we collected Stone Crabs from the waters surrounding Eleuthera, The Bahamas, where an emerging fishery has occurred since 2013, with significant increases in harvest predicted for the future. Given the commercial fishery in Eleuthera is relatively new, it provides a unique opportunity to study a relatively unexploited population of Stone Crabs and provide baseline data to potentially track evolutionary changes that may occur over time with increasing fishing pressure. We examined: (1) the relative role and repeatability of physiological and behavioral traits in the capture process and how this may change following claw removal and release; (2) the effect of claw removal on the immediate behavior (shelter use, exploration, and feeding) of crabs following release; and (3) the immediate physiological cost associated with the claw removal practice.

Methods

Animal collection and housing

We used baited traps to collect Stone Crabs (mean mass = 357.2 ± SD 66.4 g; mean carapace width = 99.7 ± SD 7.4 mm; right propodus length mean = 86.8 ± SD 12.5 mm; left propodus length mean = 77.3 ± SD 9.8 mm) with both claws intact from the waters surrounding Eleuthera, The Bahamas. Following capture, we covered crabs with seawater-moistened newspaper for transport in several large coolers to the aquatics holding facility at the Cape Eleuthera Institute (Eleuthera, The Bahamas). Crabs were weighed, measured, sexed, and tagged with a small (< 5 mm) uniquely coded numeric tag, glued to the upper carapace surface so that individuals could be identified throughout the study. We held crabs in 2 circular tanks (3.7 m diameter, 1 m filled height), supplied with flow-through seawater pumped directly from the ocean at ambient salinity (mean = 37.0 ± SD 2.3 ppt) and temperature (mean = 27.4 ± SD 2.7 °C). The holding tanks contained an abundance of PVC piping of various sizes to provide adequate shelter and enrichment, and to limit agonistic behavior, as well as a large air stone to ensure adequate oxygenation of the water. Crabs were acclimated to the laboratory for ~3 weeks prior to experimentation, during which time we fed them fish carcasses ad libitum once per day. We released all crabs several months later upon completion of the study. All work was carried out under The Bahamas Department of Marine Resources permit number MAMR/FIS/17.

Trapping experiments

Crabs were chosen haphazardly from the holding tanks, fitted with a large colored plastic tag (which was glued to the carapace and facilitated visual tracking of individuals), and introduced to an outdoor, shaded experimental arena (2150 L circular tank; 3.7 m diameter, 1 m filled height) which contained in the middle a single standard Stone Crab trap (41 cm x 41 cm x 30 cm) baited with tilapia. We initially performed the experiment using animals with both claws intact to obtain baseline measurements for (a) time of first contact with the trap, (b) time elapsed between first trap contact and time to reach the top of the trap, (c) cumulative time from the start of the trial to trap entry, and (d) capture efficiency. We repeated the experiment 14 days later using crabs with either no claws removed, 1 claw removed, or 2 claws removed to determine the repeatability of individual responses to trapping and the effect of claw removal on trapping and repeat capture. Five crabs were placed into the tank and allowed to settle in separate opaque PVC tubes (situated against the wall of the tank) for 2 hours prior to the start of each trial. For each trial, we introduced the crabs to the experimental tanks at ~16:00 hours, removed the PVC tubes at 18:00 hours, and observed the trial subjects for a total period of 36 hours under ambient photo-thermal conditions. Five crabs were used per trial to simulate conditions experienced naturally in the wild. Therefore, we cannot rule out possible social effects associated with behaviors of interest (Thambithurai et al. 2018). To monitor crab behaviors during the trials, we used an overhead camera (GoPro Hero5, Woodman Labs, Inc., CA, USA) mounted directly above the tank to take photographs every 30 s. Because the Stone Crab is primarily nocturnal (Powell and Gunter 1968), we mounted a red-light above the tank to allow for observations during periods of darkness (Cronin 1986). Once the trial was complete, we returned all crabs to their holding tank; drained, cleaned, and re-filled the experimental arena; and removed, cleaned, and re-baited the trap prior to the start of the next trial. For each crab, we calculated the time of first contact with the trap, time elapsed between trap contact and time to reach the top of the trap (climbing time), cumulative time from the start of the experiment to trap entry (time of capture), and capture efficiency (y/n).

Metabolic rate measurements (SMR and RMR)

We measured oxygen consumption using intermittent flow respirometry (Steffensen 1989). Intact crabs of both sexes, were chosen haphazardly from their holding tanks, weighed, and placed into 1 of 8 separate plastic respirometry chambers (23 cm x 19 cm X 22 cm; 9614 ml) that were submerged in a water bath and maintained at a constant temperature (29.37 ± SD 1.0 °C). We placed an opaque plastic divider between each chamber to prevent visual contact between individual crabs. An air-stone in the header tank of the respirometer apparatus ensured inflow water was fully air saturated. We measured water oxygen concentration using fiber-optic oxygen probes (Witrox 1, Loligo Systems) calibrated using oxygen-free and air-saturated water. Measurements occurred every second for 30 min during the closed phase, which allowed for the rate of oxygen depletion (due to crab respiration) to be determined. During this time, a pump re-circulated water within the chamber at a rate of 5 L/min, thereby ensuring gradients did not form in the chamber. The 30-min closed period allowed a measurable drop in oxygen levels without subjecting the crab to a hypoxic regime. We programmed flush pumps (Eheim 300 universal, Deizisau, Germany) to switch on following the closed period for 10 minutes and deliver oxygenated water through each respirometer, allowing oxygen saturation levels to be restored before the start of the next measurement cycle. This procedure was repeated for a total period of 24 h. Next, we removed individual crabs from respirometry chambers and subject them to 1 of 3 treatments (no claws removed, 1 claw removed or 2 claws removed) before being re-weighed and returned to the respirometer for an additional 24 h. We processed the data using AutoResp software, which calculated oxygen consumption as mg O_2 kg^{-1} h^{-1} (Version 1.4, Loligo, Viborg, Denmark).

Dissolved oxygen values were corrected for background oxygen consumption, which we calculated by measuring the oxygen concentration for at least 3 cycles in the absence of the crab at the beginning and end (i.e., after the 48 h) of each measurement trial. Whole-animal SMR (mg O_2 h^{-1}) was estimated for phase 1 (first

24 h before claw removal) and phase 2 (second 24 h after claw removal) as an average of the lowest 10^{th} percentile of measurements taken throughout each measurement period. RMR was estimated for phase 1 (first 24 h) and phase 2 (second 24 h) separately as an average of all measurements taken for each 24-h period, excluding the first 5 hours, when oxygen consumption of crabs was likely elevated due to handling stress.

Claw removal and mortality

Claw removal followed common procedures used in commercial and recreational Stone Crab fisheries. With the cheliped fully extended, a firm downward motion was used to remove the claw cleanly along the autotomy plane at the basi-ischium, located between the coxa at the base of the leg and merus. All claw removal procedures were carried out by the same researcher to remove bias associated with technique. Although common Stone Crab claw removal practices were followed, it should be noted that excessive time was taken to ensure clean breaks and maximize survival of crabs (a) to limit the amount of crabs needed for the study and (b) because the aim of the study was not necessarily to evaluate mortality per se (which has been relatively well studied) but to evaluate behavior of surviving crabs following claw removal and release. Therefore, the level of mortality presented in our study may not necessarily be reflective of those encountered during normal fisheries operations.

Post-release feeding experiment

Following respirometry measurements and 48 hours after claw removal, we subjected crabs of both sexes with no claws removed, 1 claw removed, or 2 claws removed to a post-release feeding experiment to assess the potential effects of claw removal on feeding, foraging, and sheltering behavior. Trials were conducted in the same circular arena and followed the same experimental procedures (camera mount, settling time, etc.) as the trapping experiment. However, for the feeding experiment we partitioned the arena into 8 individual cone-shaped sections that fanned outward from the middle of the tank. The partitions were opaque and prevented visual and behavioral interactions among crabs; however, we cannot rule out possible circulation of chemical cues among individual arenas. We placed settling tubes in the narrow end of each arena prior to the start of the trial. Each arena contained a small shelter at the narrow end with a piece of tilapia fixed to a weight at the other. Tilapia was used, instead of the preferred prey (hard-bodied molluscs; Hancock and Griffen 2017) to reduce the impact of feed handling (associated with opening the prey) on feeding behavior (Hogan and Griffen 2014). Once the trial was complete, we returned all crabs to their holding tank and drained, cleaned, and refilled the arenas prior to the start of the next trial. We determined the amount of time each individual spent in shelter, exploring (time spent outside shelter but not feeding), and feeding (time spent directly with the bait) by multiplying the number of photographs for each behavior by the duration interval of the photograph (30 s).

Calculations and statistical analyses

Data for the effect of claw removal, SMR, and RMR on time of first trap contact, time of climbing around the trap, and time to capture were analyzed individually using a general linear mixed effect model in the package nlme in R. To control for the use of multiple crabs in a single trial and potential effects of behavioral interactions (e.g., agonistic behaviors among crabs) influencing contact time, climbing around the trap time, and trapping time, we used trial number as a random effect. We pooled data for the effect of claw removal on capture efficiency among all trapping trials completed throughout the study and used a general linear model with a binomial distribution for analyses. We used an ANOVA to separately analyze data for the effect of claw removal on time spent in shelter, time spent exploring, and time spent feeding, and a general linear model that included mass as a covariate to analyze data for the effect of claw removal on SMR and RMR. All models for SMR and RMR were used with mass as a covariate because of the strong but somewhat predictable influence of mass on metabolic rate measures. To test whether the results of time spent in shelter, time spent exploring, and time spent feeding were a result of low statistical power, we pooled data for individuals with 1 and 2 claws removed to create a claw-removal group. We used a *t*-test to further analyze differences between the control and claw-removal groups for time spent in shelter, time spent exploring, and time spent feeding. To test the repeatability of SMR, RMR, time of first trap contact, time spent climbing around the trap, and time to capture, before and after claw removal, we used a Pearson product-moment correlation.

Visual inspection of residual plots for all models did not reveal any obvious deviation from normality. Where appropriate, we compared the models using AIC criterion before and after removal of the interaction term if not significant at $P <$ 0.05. All statistical analyses were performed in R 3.2.2 (R Core Team 2016). Lastly, we calculated mortality by dividing the number of surviving crabs over the entire experiment and dividing it by the total number of crabs for each treatment and multiplying by 100.

Results

Trapping experiment

After statistically controlling for potential differences in behavioral interactions among trials (non-independence of measures), there was no significant difference in time of first contact with the trap ($F_{2, 19} = 0.09$, $P = 0.91$; Fig. 1A), time climbing around the trap ($F_{2, 19} = 1.12$, $P = 0.35$; Fig. 1B), time to capture ($F_{2, 19} = 1.14$, $P =$ 0.34; Fig. 1C), and capture efficiency ($Z_{44, 45} = 1.37$, $P = 0.17$) among crabs with 0, 1, and 2 claws. Even after pooling crabs with 0 and 1 claws (to create a claw-removal group) there was no significant effect of claw removal on time of first contact with the trap ($F_{1, 20} = 0.19$, $P = 0.67$), time climbing around the trap ($F_{1, 20} = 1.57$, $P =$ 0.23), time to capture ($F_{1, 20} = 1.19$, $P = 0.18$), and capture efficiency ($Z_{44, 45} = -0.49$, $P = 0.62$).

Post-release feeding experiment

There was no significant difference in time spent in shelter ($F_{2, 19}$ = 1.11, P = 0.35; Fig. 2A), exploring ($F_{2, 19}$ = 0.94, P = 0.41; Fig. 2B), and feeding ($F_{2, 19}$ = 2.53, P = 0.11; Fig. 2C) among crabs with 0, 1, and 2 claws. However, when crabs with 0 and 1 claws were combined, there was a significant effect associated with claw removal. Crabs with 0 and 1 claws spent significantly less time feeding compared to crabs with 2 claws ($t_{2, 19}$ = -2.21, P = 0.04; Fig. 2C). Pooling of data for crabs with 1 or both claws removed still revealed no significant difference in time spent in shelter (t_{20} = 1.31, P = 0.21) and exploring (t_{20} = -0.95, P = 0.35) when compared to intact crabs.

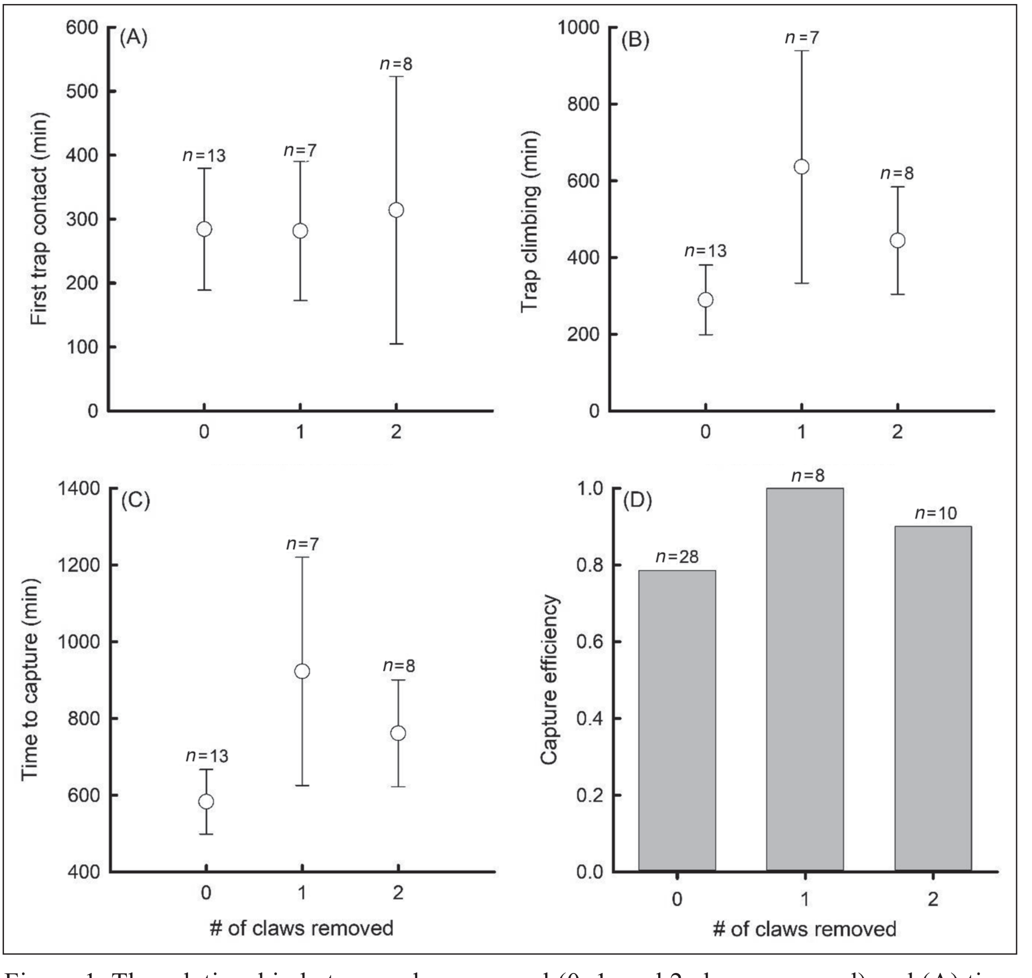

Figure 1. The relationship between claw removal (0, 1, and 2 claws removed) and (A) time of first trap contact (n = 20 male, n = 8 female), (B) climbing around the trap time (elapsed time between first trap contact and top of the trap; n = 20 male, n = 8 female), (C) time to capture (n = 20 male, n = 8 female), and (D) capture efficiency (n = 32 male, n = 14 female) for Stone Crabs subjected to a laboratory trapping experiment which consisted of a baited trap located in the middle of a large circular arena (3.7 m diameter, 1 m filled height). n = sample size for treatments. Error bars represent the standard error of mean.

Energetic cost

After controlling for the effect of body mass on whole body SMR and whole body RMR, there was a significant effect of claw removal (Fig. 3A, B). Crabs with 1 or both claws removed had a significantly higher relative SMR and relative RMR than intact crabs (1 claw removed—SMR: $t_{3, 46} = 3.10$, $P < 0.001$; RMR: $t_{3, 45} = 3.66$, $P < 0.001$; 2 claws removed—SMR: $t_{3, 46} = 3.101$, $P < 0.01$; RMR: $t_{3, 45} = 4.19$, $P < 0.001$).

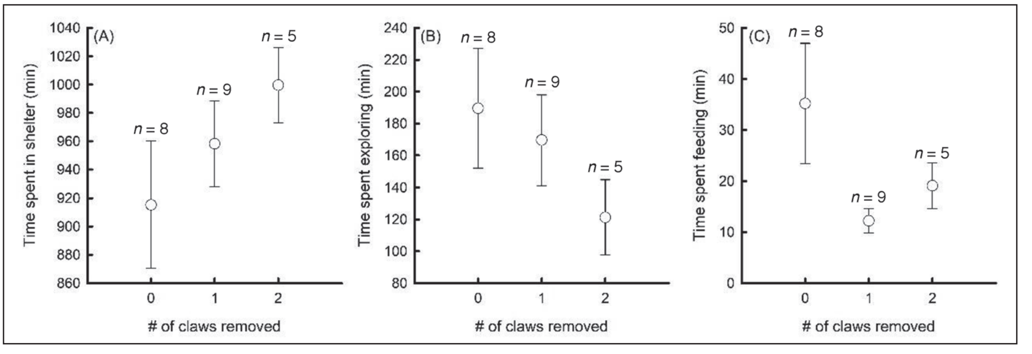

Figure 2. The relationship between claw removal (0, 1, and 2 claws removed) and (A) time spent in shelter, (B) time spent exploring, and (C) time spent feeding for Stone Crabs (n = 16 male, n = 6 female) subjected to a post-release feeding experiment following claw removal and release. n = sample size for treatments. Error bars represent the standard error of mean.

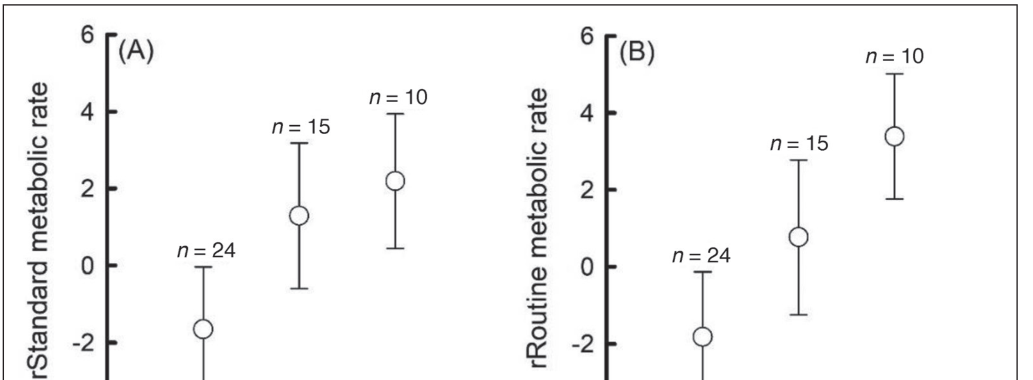

Figure 3. The relationship between claw removal (0, 1, and 2 claws removed) and (A) standard metabolic rate (the baseline level of energy intake needed to sustain life), residual corrected for body mass (rSMR; mg O_2/h), and (B) routine metabolic rate (the average rate of metabolism when the animal is undergoing normal behaviors), residual corrected for body mass (rRMR; mg O_2/h), for Stone Crabs (n = 34 male, n = 15 female). Residuals for SMR and RMR were calculated from the regression equation of the whole oxygen consumption values (mg O_2/hr) against body mass (g) for all crabs. n = sample size for treatments. Error bars represent the standard error of mean.

Metabolic rate (SMR and RMR) and trapping

After statistically controlling for potential differences in behavioral interactions among trials (non-independence) and the effect of mass on whole SMR and whole RMR, there was a significant effect of relative SMR and relative RMR on time to capture. Among the crabs with intact claws, individuals with a higher relative SMR and relative RMR took significantly less time to enter the trap (SMR: $t_5 = -2.89$, $P = 0.03$ [Fig. 4A]; RMR: $t_5 = -4.16$, $P < 0.01$ [Fig. 4B]). However, there was no significant effect of relative SMR and relative RMR on time of first trap contact (SMR: $t_5 = -0.28$, $P = 0.79$; RMR: $t_5 = -0.56$, $P = 0.60$) and climbing around the trap time (SMR: $t_5 = -0.31$, $P = 0.77$; RMR: $t_5 = 0.05$, $P = 0.96$).

Repeatability

Time of trap contact, relative SMR, and relative RMR were found to be repeatable among intact crabs (time of trap contract: $t_7 = 3.99$, $P < 0.01$, $r = 0.83$ [Fig. 5A]; SMR: $t_7 = 12.31$, $P < 0.01$, $r = 0.98$ [Fig. 5D]; RMR; $t_7 = 9.75$, $P < 0.01$, $r = 0.97$ [Fig. 5E]); of these 3 metrics, relative SMR and relative RMR were the only traits remaining repeatable following claw removal (SMR: $t_{14} = 5.51$, $P < 0.01$, $r = 0.83$ [Fig. 5D]; RMR; $t_{14} = 5.57$, $P < 0.01$, $r = 0.83$ [Fig. 5E]), indicating that individuals with a higher relative SMR and relative RMR prior to claw removal also had a higher relative SMR and relative RMR after claw removal. Interestingly, climbing around the trap time was not repeatable among intact crabs, but among the claw-removal group, crabs that spent less time climbing around the trap when claws were intact also spent less time climbing around the trap when claws were removed ($t_6 = 2.71$, $P = 0.04$, $r = 0.74$).

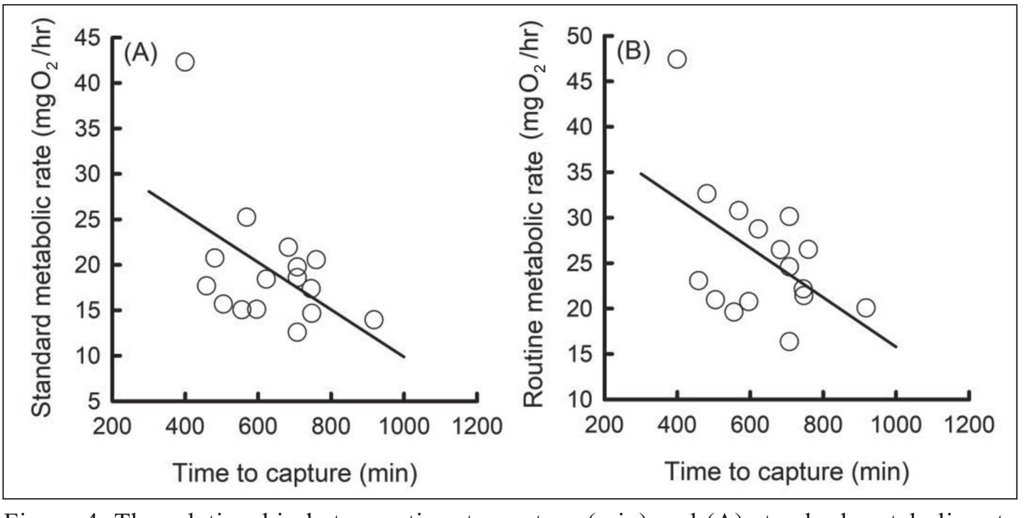

Figure 4. The relationship between time to capture (min) and (A) standard metabolic rate (the baseline level of energy intake needed to sustain life; mg O_2/hr), and (B) routine metabolic rate (the average rate of metabolism when the animal is undergoing normal behaviors; mg O_2/hr) for Stone Crabs (n = 11 male, n = 5 female) subjected to a laboratory trapping experiment which consisted of a baited trap located in the middle of a large circular arena (3.7 m diameter, 1 m filled height).

Survival

The survival rate of crabs with no claws removed and 1 claw removed were the same at 75.0%, whereas the survival rate of crabs with 2 claws removed was 68.7%. Therefore, the removal of both claws resulted in a 6.3% decrease in survival compared to crabs with either no claws removed or 1 claw removed.

Discussion

There was no effect of claw removal on time of first contact with the trap, indicating a similar response to the bait plume and trap by intact crabs and those with claws removed. There was a trend for crabs with 1 or both claws removed to spend more time climbing around the trap and taking longer before capture, but this trend was not statistically significant which may be a result of the low sample size used for this portion of the study. Nevertheless, the results suggest that intact and crabs with 1 or both claws removed respond and mobilize towards a bait plume and trap similarly and that crabs with 1 or both claws removed are able to re-enter traps

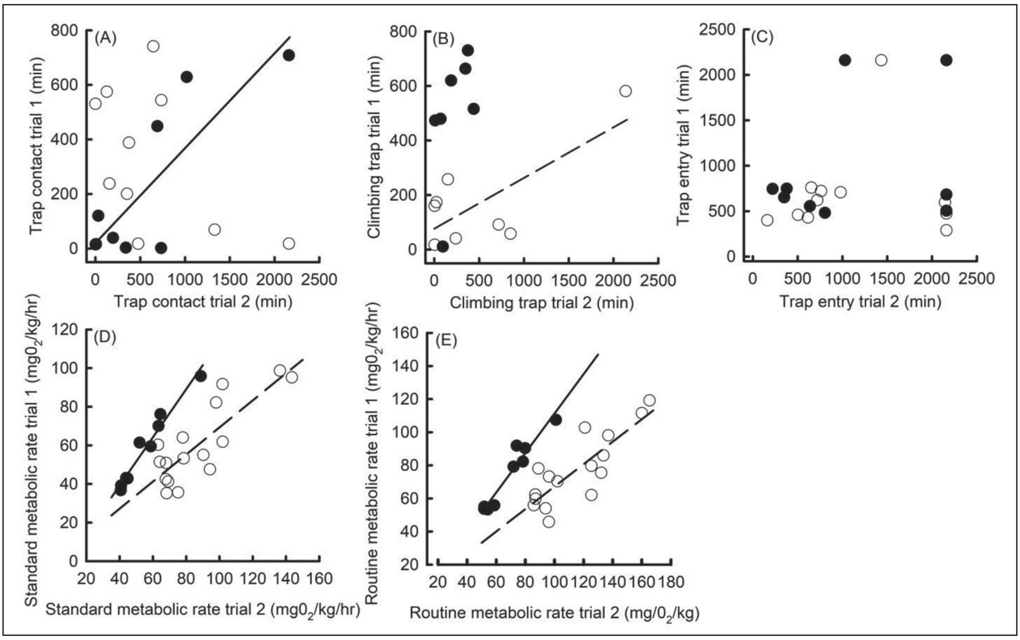

Figure 5. Repeatability of various behavioral and physiological metrics before (dark circles; solid line) and after (open circles; dashed line) claw removal: (A) time of first contact with trap (min), (B) climbing around the trap time (time elapsed between first contact with trap and time to top of trap, (C) time to capture (min), (D) standard metabolic rate (the baseline level of energy intake needed to sustain life; mg O_2/kg/hr), and (E) routine metabolic rate (the average rate of metabolism when the animal is undergoing normal behaviors; mg O_2/kg/hr) for Stone Crabs subjected to a laboratory trapping experiment and metabolic rate measures using intermittent-flow respirometry. Crabs with 1 and 2 claws removed were pooled to create the claw-removal group. Only significant correlations are represented with a trend line. Sample sizes were 7 male and 2 female for intact crabs and were 7 male and 2 female (for de-clawed crabs in A, B, C) and 11 male and 5 female (for de-clawed crabs in D, E).

following claw removal and release. Therefore, if the results of our trapping experiment are reflective of those in the wild and claw-harvested crabs are returned to the water near the site of capture, re-capture rates in the fishery would be expected to be high, especially given the spatial overlap of successive trap deployments by fishers. Current estimates of re-capture rates of Stone Crabs in the wild are generally low (Ehrhardt et al. 1990, Savage et al. 1978). For example, Ehrhardt et al. (1990) reported recapture rates of 1.2% for de-clawed crabs and 10.5% for intact crabs. By ruling out the potential for physiological and anatomical impairments and behavioral learning to limit trap re-entry, the results of our study suggest low survival of crabs (directly as a result of the harvest process or indirectly through increased susceptibility to predation) following release may be the cause of the low re-capture rates observed for the fishery. A potential caveat of the trapping experiment, besides the relatively low sample size, may be the use of multiple crabs in a single trial. As the number of crabs approaching the trap increases, so does the likelihood for intra-specific competition and acts of aggression and territoriality that could influence the capture process and may explain the lack of repeatability of behaviors before and after claw removal. Although our study cannot rule out possible social effects on catchability behaviors (Thambithurai et al. 2018), we were able to statistically control for their influences among trials. It is not uncommon in the wild for multiple crabs to approach and enter a single trap. For example, Collins et al. (2002) observed >50 *Paralomis formosa* Henderson (Globose King Crab) within a 4.9-m^2 field of view of a baited underwater video camera within hours of deployment. Therefore, we argue that the results presented here may be more reflective of the actual trapping process.

The mortality of de-clawed crabs following release has been reported as 1–57% in the laboratory (Davis et al. 1978, Duermit et al. 2015) and 23–51% in the wild (Davis et al. 1978). The large variation in survival is due to the myriad of factors that influence survival after claw removal and release, e.g., harvester experience (Duermit et al. 2017), water temperature (Gandy et al. 2016), wound size (Duermit et al. 2015, 2017), and break location (Gandy et al. 2016). Survival rates for crabs in our study was 75.0% and did not differ between intact crabs and those with only a single claw removed. While that lack of difference in survival suggests that much of the mortality in our study is likely reflective of holding crabs in captivity for extended periods, we did observe a 6.3% decrease in survival for crabs with both claws removed, a finding consistent with the positive correlation between number of claws removed and mortality found in previous studies (Davis et al. 1978, Duermit et al. 2015, Gandy et al. 2016). The overall higher survival rates of de-clawed crabs in our study compared to other studies is likely due to the increased time taken to ensure clean breaks and because crabs were held in the absence of predators following claw removal. These results may provide support for the importance of technique in the harvest process and the notion of mandatory legislation preventing the harvest of both claws from a single crab for Stone Crab fisheries. While harvester-induced mortality as a result of claw removal has been relatively well studied, a further understanding of less conventional causes of mortality following release (through greater vulnerability to predation or loss of limbs during removal from traps) remains an unexplored but worthwhile area of study.

Stone Crabs with 1 or both claws removed spent significantly less time feeding following release than intact crabs and had higher relative SMR and relative RMR but lower whole SMR and whole RMR as a result of the significant reduction in body mass following claw removal. Because hard-shelled bivalves are the preferred food source of Stone Crab (Gunter 1955, Menzel and Nichy 1958) and were previously used in feeding experiments to evaluate the effect of claw removal on feeding, it is not surprising that these studies reported a reduction in feeding (Duermit et al. 2015). However, it was not reported whether the reduced feeding was a result of the inability for de-clawed crabs to access the prey, or a lack of feeding motivation following claw removal. In our study, when crabs were given soft-bodied prey, the reduced feeding time appeared to be linked to decreased activity or feeding motivation. Although not statistically significant, there was a positive trend between time in shelter and claw removal and a negative trend between time spent exploring and claw removal, suggesting reduced feeding may be a result of increased shelter use and lack of exploration. This reduction in activity may be a response to a perceived vulnerability to predation risk following claw removal, although further study is required to confirm this hypothesis. A potential caveat of our post-release feeding experiment, besides the relatively low sample size, may be the possibility of chemical cues circulating in neighboring crab arenas due to the sharing of common water. Therefore, one possibility is chemical cues may have elicited an anti-predatory response in the crabs and caused crabs to become more timid and spend less time feeding and exploring after claw removal. Whatever the case, the observed lack of feeding following claw removal seems counterintuitive at first glance, given the observed increase in energetic cost (relative SMR and RMR) as a result of claw removal.

Claw removal resulted in a dramatic reduction of 25–60% in total body mass. Therefore, given that tissues are energetically costly to maintain, it is plausible that the reduction in body mass may result in a significant decrease in the amount of energy required for general maintenance and movement of this large heavy claw, despite the additional longer-term cost associated with claw regeneration. While relative SMR and RMR increased as a result of regenerative load (Skinner 1985) and the beginnings of cheliped re-growth (Llodra 2002), the overall reduction in whole SMR and whole RMR may allow the crab, at least over the short duration of our study, to spend less time feeding because of a reduction in overall energy requirement for maintenance and routine activities. Estimating the physiological cost of claw removal is difficult because of the strong influence of mass on the calculation and technique used to estimate metabolic rate. For example, a decrease in body mass results in less surface area and less water displacement and therefore an increase in water volume in the respirometer and lower calculated metabolic rate by default. Furthermore, corrections for differences in body mass assume equal tissue costs among individuals, which may not be a valid assumption given that oxygen consumption (used as a proximate for metabolic rate) of a large individual with 2 claws removed is likely different than a small individual with intact claws, eventhough they are now of equal overall body mass. It has been shown in *Calinectes sapidus* Rathbun (Blue Crab) that claw autotomy is associated with an increase in regional blood flow and metabolic rate; however, such changes are transient, and pre-autotomized levels are regained within 2–3h (McGaw 2006). While our study looked at the immediate effects of claw removal on feeding behavior, further studies are needed to investigate if the reduction in feeding motivation and energetic cost observed here remains over extended time periods.

Consistent with previous studies using fish, we also found links between SMR and capture vulnerability (Hollins et al. 2018, Killen et al. 2015). Among intact crabs, relative SMR and relative RMR were both found to be traits that were repeatable over the short term and important in the capture process. Individual crabs with a higher relative SMR and relative RMR took significantly less time to enter the trap, even after statistically controlling for potential behavioral effects of using multiple crabs in a single trial. Because SMR and RMR have been shown to be heritable, vary considerably among individuals (up to three-fold), and have broad ecological relevance (Metcalfe et al. 2016), the results of this study suggests Stone Crab fisheries may also be susceptible to significant evolutionary changes in individual physiology and behavior, as seen for many fish species (Diaz Pauli and Sih 2017, Hollins et al. 2018, Killen et al. 2015, Thambithurai et al. 2018). For example, heavily exploited fish stocks have shown significant trends in age and size of reproduction, with individuals on average becoming smaller in size and maturing earlier with increases in harvest pressure (Ernande et al. 2004, Heino 1998). Furthermore, because the Stone Crab fishery in The Bahamas is selective for individuals with the largest of claws only, which may or may not equate to the largest individuals, evolutionary selection towards populations with younger mean ages and/or smaller individuals with lower metabolic rates and smaller claws remain a likely scenario with future increases in exploitation rate, although further study is needed to understand the accompanying traits that may be under selection when subject to harvest pressure on individuals with the largest of claws.

In conclusion, the results of the study provide further clarification of the potential effects of Stone Crab fisheries practices and highlights the many avenues of the process which are likely to cause significant behavioral and physiological changes at both the individual and population level that may transcend to ecosystem and potentially wider evolutionary changes to populations.

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