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Sublethal behavioral and physiological effects of claw removal on Jonah crabs (*Cancer borealis*)

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ABSTRACT

Jonah crabs (*Cancer borealis)* have been caught as incidental bycatch for over 80 years, but in recent years they have become a targeted fishery, especially in Southern New England where the American lobster (*Homarus americanus)* population has declined, and harvesters have begun seeking alternative fisheries. This shift has prompted the need for more biological data for Jonah crabs so that this expanding fishery can be managed more effectively. For example, in some areas of its range males have both of their claws removed at sea and only the claws are landed; however, little is known about what happens to the crabs that survive this practice. The focus of this study was to evaluate the impacts of claw removal on Jonah crab mating success, feeding ability and locomotion. In mating trials, all males, regardless of claw status, managed to successfully mate with females that molted while they were paired together (clawed $n = 4$, claws removed $n = 8$). When Jonah crab activity was measured in the laboratory, crabs with intact claws were significantly more active than crabs with both claws removed (clawed: 25.0 ± 8.0% of each hour active, 1 claw removed: 18.1 ± 7.3% of each hour active, clawless: 13.6 ± 9.04% of each hour active, mean ± SD). Similarly, based on data from a tag/recapture experiment, crabs with both claws missing moved about half the distance per day as control crabs, between the time they were released and first recaptured (clawed: 117 ± 43.1 m/day, clawless: 50 ± 11.3 m/day, mean ± SE), although the difference was not significant. These changes in locomotion could be the result of the blood loss associated with claw removal. We found that hemocyanin levels dropped significantly after the removal of both claws and remained so for up to two weeks. Finally, crabs with no claws were able to feed, but they had difficulty opening mussel shells, which might influence their diet in their natural habitat. These data suggest that those Jonah crabs that do survive the claw removal process might be impaired, but should be able to forage, mate, and help sustain the population.

1. Introduction

Exposure of crustaceans to nonlethal stressors can lead to changes in their behavior, physiology, and the effectiveness of their immune system (Wilson et al., 2014). For decapod crustaceans, such as lobsters and crabs, such sublethal effects are often caused by limb loss or injury, due to being handled and released during normal fisheries practices, or in some fisheries, intentional limb removal for harvest (Juanes and Smith, 1995; Wilson et al., 2014; Butler et al., 2018). Intentional limb removal is currently a minor part (~1%) of the growing Jonah crab fishery, but the practice could increase because many states allow for claw removal, and thus a stronger understanding of its impacts on the population is necessary in order to effectively manage this resource in the future (ASMFC, 2015; Goldstein and Carloni, 2021).

Jonah crabs (*C. borealis*) have been captured as incidental bycatch in the New England lobster industry for over 80 years (Reardon, 2006). More recently, Jonah crab has become an alternative fishery target and an emerging fishery, particularly in Southern New England where lobster stocks have been declining (ASMFC, 2015, 2019; Mercer et al., 2018; Truesdale et al., 2019). Despite an increase in landings in the United States, from two million pounds of crabs in 1990 to approximately 20 million pounds in 2018, little information is available about

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Jonah crab biology and ecology relative to other commercially harvested crab species and there have been no stock assessments to-date (ASMFC, 2015, 2019). However, in 2015 an Interstate Fisheries Management Plan for Jonah crabs was approved, setting a minimum size limit and prohibiting the harvest of egg-bearing (i.e. ovigerous) females (ASMFC, 2015). Additionally, some states (Maine, New York, New Jersey, Delaware, Maryland and Virginia) allow the harvesting of claws from live Jonah crabs (ASMFC, 2015; see description of the claw removal method in Section 2.2 of the Methods).

The technique of harvesting just claws from crabs before returning them to the sea is also commonly employed with brown crabs, *Cancer pagurus* (Patterson et al., 2009), fiddler crabs, *Uca tangeri* (Oliveira et al., 2000), and stone crabs, *Menippe* spp. (Duermit et al., 2015). In brown crabs, removal of a single claw resulted in a 17.8% mortality rate, which likely underestimates mortality in the fishery as harvesters typically remove both claws (Patterson et al., 2007). In stone crabs, mortality ranged between 28 and 40.8% after removal of a single claw and 47–62.9% when both claws were removed (Davis et al., 1978; Gandy et al., 2016). Similarly, Saher and Qureshi (2012) found up to 22% mortality after single claw removal in fiddler crabs. Finally, removing claws from Jonah crabs results in 70% mortality when both claws are removed (Goldstein and Carloni, 2021).

Claw removal, or loss, has also been shown to have sublethal effects on crabs, including an impaired ability to mate, decreases in locomotion, and difficulty feeding (reviewed by Juanes and Smith, 1995). For example, in blue crabs (*Callinectes sapidus*), individuals with autotomized limbs showed precopulatory embrace in the absence of competition, but often had difficulty defending potential mates from intruders (Smith, 1992). Likewise, in the green crab (*Carcinus maenas*), medium-sized individuals with one or both claws missing almost never successfully copulated due to competition, while claw loss in large males did not affect their mating success (Sekkelsten, 1988). In stone crabs, declawing led to a decrease in activity and alertness, which might reduce their ability to avoid predation or compete with other individuals for mates and food (Davis et al., 1978). Similarly, in blue crabs, limb loss reduced their ability to defend themselves against predators when escape was not possible, which was also manifested in altered activity patterns, and a possible change in feeding efficiency (Smith, 1995). Feeding may also be further reduced if claw removal impairs their ability to handle prey, particularly bivalves (i.e. opening shells). The loss of a single claw in brown crabs significantly reduced feeding on mussels, which could potentially lead to a shift in diet to softer prey, or even starvation (Patterson et al., 2009). Similarly, if both claws were removed from stone crabs they could not eat hard-shelled prey until their claws regenerated, while if only one claw was removed there was reduced consumption of mussels (Duermit et al., 2015).

To our knowledge, the potential sublethal effects of claw removal on Jonah crabs have not yet been examined. Given the rapid growth of this fishery, proper management will require additional information about both the lethal and sublethal impacts of claw removal. Therefore, to gain a better understanding of the sublethal impacts of claw removal, we carried out a series of experiments to determine if claw removal impacted: 1) the ability of male crabs to mate; 2) locomotor activity in the laboratory and in their natural habitat; and 3) prey manipulation and feeding.

2. Methods

2.1. Animal collections and maintenance

Adult Jonah crabs (*C. borealis*) were purchased from fishers, as well as collected from traps and by SCUBA divers in the vicinity of New Castle, NH in the southern Gulf of Maine. Prior to the start of experiments, crabs were held communally in flow-through, aerated ambient seawater systems at the University of New Hampshire (UNH) Coastal Marine Laboratory (CML) in New Castle and fed weekly with lobster trap bait (herring, *Clupea harengus*) and live blue mussels (*Mytilus edulis*).

2.2. Claw removal

Two methods were used to remove claws from male Jonah crabs (see Goldstein and Carloni, 2021, for additional details). The first method, hereafter referred to as ‘manual removal’, was intended to mimic how claws are typically removed in the fishery. In brief, the body of the crab was grasped with one hand, and one of the claws with the other, and then a twisting motion used to snap off the claw. This was then repeated with the other claw. In the second method, hereafter referred to as ‘mechanical removal’, 25 cm straight pattern tin snips (Wiss model A11, Apex Tool Group, Netherlands) were used to remove both claws between the merus and the coxa. The latter removal technique is designed to more closely reflect autonomy, as the claw break is made at the natural fracture plane between the merus and the coxa. This technique was tested in Goldstein and Carloni (2021) and yielded better survivorship in laboratory-based trials compared with the manual claw removal technique and so we used both techniques in our mark-recapture study in the field.

2.3. Mating trials

These experiments, and all the subsequent laboratory studies, were carried out at the CML over two consecutive summers. In 2018, 26 male Jonah crabs (16 unmanipulated controls and 10 that had both claws removed mechanically) were paired with 26 females that appeared to be premolt, as evident by wear on their chelae and biofouling on their shells. Selection of premolt females was essential as mating occurs directly after the female molts. The males were 132.6 ± 14.9 (mean ± SD, here and unless stated otherwise) mm in carapace width (CW), while the females were 90.7 ± 10.8 mm CW. These pairs were placed in individual 75 L holding containers that received a continuous flow of ambient seawater. Each container was 61 × 38 × 33 cm (length x width x height) and filled with a natural sand and gravel substratum. Clumps of mussels (*M. edulis*) were added prior to the start of each trial to allow crabs to feed ad libitum. In 2019, 16 males (4 controls and 12 mechanically declawed) were paired with 16 premolt females; males were 103.5 ± 20.3 mm CW, while the females were 73.2 ± 11.6 mm CW. In the inshore region of the Gulf of Maine the onset of sexual maturity for males is estimated to be 103 mm CW, whereas the size at 50% maturity for females is still unknown (Perry et al., 2017). In 2019, to be more confident that females were premolt and prepared to mate, we used females that were actively engaged in caging (mate guarding) behavior with males either in the holding tanks or when captured. In each mating trial, females were removed from the male that was holding them, and randomly assigned to a tank containing another male of a similar size, either with or without claws.

Mating crab pairs were left together in individual tanks until the female molted and the male attempted to mate (or not). In most cases digital time-lapse cameras (Brinno TLC200 Pro, Taipei City, Taiwan) were used to record behaviors before, during, and after mating. When subsequently analyzing the digital videos we assessed the following distinct behaviors: (1) “nesting” behavior, during which the male creates a small depression in the gravel where they would reside with the female during caging; (2) caging pre-copulation, during which the male would position himself over an upright female to guard her (see Elner et al., 1985 for more details); (3) mating and; (4) caging post-copulation that was characterized as the same protective behavior as pre-copulation. Due to the change in premolt determination, pre-copulation behavior was mostly observed in 2018. Finally, to confirm that mating was successful, females were examined visually after any apparent mating activity to confirm that a fresh sperm plug was present in the female spermathecae (Elner et al., 1985).

2.4. Crab activity

2.4.1. Laboratory activity measurements

Fishery-sized male crabs (CW = 122 ± 22 mm; n = 9) obtained from commercial lobster fishers were each fitted with a HOBO Pendant G accelerometer (Onset Computer Corp., Bourne, MA) that was placed in the middle of their dorsal carapace as described in Jury et al. (2018) (Supplemental Fig. 1). The accelerometers were programmed to log triaxial acceleration every 30 s. Individual crabs were then placed in 1 m diameter round tanks in the CML that were continuously perfused with ambient seawater. Data were collected for two days, after which one claw was removed from each animal mechanically, after which, crabs were returned to their respective tanks. Two additional days of data from crabs with only one claw were collected and then the other claw was removed with tin snips and an additional two days of data were obtained from the Jonah crabs with no claws, for a total trial time of 6 days. It should be noted that in a subsequent study, during a six day control period, there was no was no effect of day number on the activity of individual crabs, F(5,30) = 2.009, p = 0.106 (A. Dorrance, unpublished data).

The amount of time each crab was active per day, was calculated from the data downloaded from the accelerometers using the technique described for lobsters in Jury et al. (2018). First, the absolute value of the difference in acceleration between consecutive data points was used to calculate the change in acceleration between measurements. We then calibrated these acceleration data by comparing it with time-lapse videos of crabs in the experimental tanks. This made it possible to determine the minimum acceleration value (threshold) that indicated a crab was active, vs sedentary. If the absolute value of change in acceleration was above that threshold, then the crab was considered to have been active for that minute. These data were then used to calculate the number of minutes each animal was active per hour for the two days that each treatment lasted. The effects of claw removal were then determined with a repeated measures ANOVA followed by a Tukey test using R 4.0.2 (R Core Team, 2019) and R Studio 1.1.463 (R Studio Team, 2020).

2.4.2. Tag recapture study

Crabs (n = 233) were obtained from local commercial fishermen approximately one week prior to the release date in mid-July and held at the CML in flow-through, ambient seawater tanks. A few days prior to their release, crabs were fitted with individually numbered identification tags (Floy Tag & Mfg., Seattle, WA) that were affixed to the dorsal carapace by means of an elastic band stretched between the grooves on opposite sides of the carapace and secured with two zip ties to apply tension to the band (Supplemental Fig. 2). To confirm tags would be retained, a separate set of 40 crabs (size range = 88–156 mm CW) were held for two months in a 2 m diameter 600 L flow-through tank at the CML. All tags were retained for this time period, including those from seven mortalities.

Immediately before the tagged crabs were released from a research vessel at Foss Ledge (NH) (position 43° 00.1843′ N, 70° 43.434′ W, ~ 15 m depth), they were randomly assigned to one of three groups and treated as follows: 1) manual claw removal (n = 77, CW = 140.2 ± 6.54 mm); 2) mechanical claw removal using tin snips (n = 79, CW = 140.0 ± 7.39 mm) or; 3) control (no claw removal, n = 77, CW = 138.3 ± 6.91 mm). Total distance traveled by each recaptured crab was calculated by taking the distance between the release site and the location where the crab was first reported captured and then entering the coordinates into the online Great Circle Calculator tool (http://edwilliams.org/gccalc.htm, km, Earth model WGS84/NAD83/GRS80). The distance traveled per day was then determined by taking the total distance traveled and dividing it by the number of days that had elapsed between release and recapture. Only animals that were at large for less than a year at the time of their first recapture were used in the analysis. The distance traveled per day was compared between control and declawed crabs using a t-test. As the data initially failed the assumption of normal distribution with the Shariro-Wilks normality test, data were square-root transformed to meet the assumption of normality.

2.5. Hemocyanin levels after claw removal

Jonah crabs (n = 10) obtained from commercial lobster fishermen (range: 124–158 mm CW) were held individually in 1 m diameter wire mesh rings that were arranged within a 2 m diameter tank that was continuously perfused with ambient seawater. On the day they were placed in the tank (one week prior to claw removal) a sample of hemolymph (~ 0.5 mL) was drawn from the sinus between the 3rd and 4th walking legs using a 1 mL syringe and 22-gauge needle, and then the hemocyanin concentration was determined using the spectrophotometric methods described in Coates et al. (2012). Additional hemolymph samples were taken immediately before claw removal, one week after they had both claws removed using tin snips, and then again two weeks after both claws were removed. A repeated measures ANOVA was run followed by Tukey's HSD test to assess changes in hemocyanin levels between time points, using claw status as the factor of interest and blocking by individual crab.

2.6. Feeding studies

2.6.1. Mussel manipulation trials

This experiment was designed to test the ability of Jonah crabs to actively open mussels with the impairment of a missing claw. In each trial, individual Jonah crabs that had not been fed for 1 week were placed in a 6 L aquarium with flow through seawater that contained a single mussel (sized similarly for all trials) attached by byssal threads to a small (10 × 10 cm^2) ceramic tile. A total of 16 crabs were used for this experiment; 8 controls (CW = 112 ± 0.8 mm) and 8 with 1-claw removed (CW = 115 ± 0.5 mm). Each trial was recorded with a digital time-lapse video camera (Brinno TLC200 Pro; Taipei City, Taiwan) for up to a maximum of 16 h (960 min). The resulting digital videos were then analyzed to determine the total amount of time for each crab to open a mussel (i.e. the total number of minutes each crab spent handling a mussel before successfully opening it). A series of t-tests were then used to compare the average handling time between crabs with both claws intact (controls) and crabs that had one claw mechanically removed. A Fisher's exact test was used to evaluate if there was a difference in feeding success rate between 2-clawed and 1-clawed crabs.

2.6.2. Food preference (Live (in-shell) Versus Shucked Mussel)

A complementary study was conducted to evaluate whether crabs with 1 claw, 2 claws, or no claws manually removed had a preference between live (in-shell) and shucked mussels. Jonah crabs (CW = 139 ± 6.88 mm) were obtained from local fishermen and retained in a flow through tank for 3 days and then subjected to one of three treatments: 1) both claws removed manually (n = 100); 2) one claw removed manually (n = 100); or 3) no claws removed (n = 40). Crabs were then offered both a shucked mussel with the shell removed and a live (in-shell) mussel. Food items were left in the individual holding containers with the crabs for 48 h and each food item was evaluated as to whether it had been consumed or not. Partially eaten food items were noted, but not included as "eaten" in the final analysis. The initial feeding trial was conducted immediately following the declawing procedure, while a second repeat feeding trial was conducted two weeks later in a similar manner. A chi-square test of independence was used to evaluate if there was a change in food preference after claw removal.

3. Results

3.1. Mating

In all cases where a female crab molted in an experimental tank (n = 12), mating occurred successfully regardless of claw removal status

Table 1
The mating success of male Jonah crabs with, and without claws, with females that molted in 2018 and 2019.

Male Claw Status	Mating Success 2018	Mating Success 2019
Control	2/2	2/2
Two Claws Removed	2/2	6/6

(Table 1). There were also no noticeable differences in courtship behavior (nesting, copulation, or caging) between controls and declawed male Jonah crabs. Caging and copulation always occurred if the female molted, and nesting occasionally occurred before molting, but none of these behaviors appeared to be dependent on the presence of claws. Therefore, at least in the absence of clawed competitors, declawed male Jonah crabs are capable of mating with female Jonah crabs.

3.2. Locomotion

3.2.1. Activity in the laboratory

Jonah crab locomotor activity decreased following claw removal (ANOVA, F (2,16) = 6.47, $p = 0.009$). Jonah crabs with both claws intact (controls) were active for 25 ± 8.0% of each hour during the two-day control period. Then, after one claw was removed, they tended to be less active (18 ± 7.3% of each hour), but not significantly so per post-hoc Tukey's HSD test. However, after both claws were removed, there was a significant reduction of locomotion compared to controls (Fig. 1, active 13.6 ± 9.0% of each hr).

3.2.2. Tag-recapture study

Of the 233 crabs that were tagged and released, 12 were recaptured (5.4%) and reported with sufficient detail to allow further analyses. Of the 12 recaptures, eight (67%) were control crabs (both claws still present) and four (33%) were declawed. All four of the declawed crabs that were recaptured had their claws removed using the mechanical (tin snip) method. The 12 recaptured crabs were at large for about two months (control = 65.9 ± 30.2 days, declawed crabs = 64.0 ± 23.7 days; range for all 12 was from 7 to 209 days). Crabs without claws moved 50.9 ± 11.3 (SE) m/day, while control crabs moved more than twice as far (117.4 ± 43.1 (SE) m/day), but this difference was not significant (unpaired t-test, $t = 1.337$, df = 9.137, $p = 0.213$, Fig. 2).

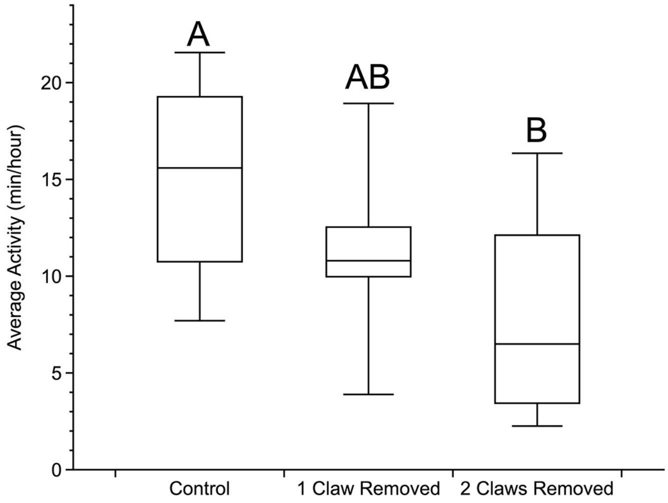

Fig. 1. Locomotor activity (average minutes active/h) for Jonah crabs that had 1, 2 or no claws removed. While controls (crabs during the two days before any claws were removed) did not differ from those with 1 claw removed, crabs with 2 claws removed moved significantly less that controls. Whiskers indicate minimum and maximum values and letters indicate homogenous subsets per Tukey HSD post-hoc test.

3.3. Hemocyanin levels following claw removal

There was a significant effect of time on hemocyanin levels (ANOVA, F (3,27) = 27.05, $p < 0.001$). Post-hoc analysis with Tukey's HSD test revealed that baseline hemocyanin levels did not change during the one-week control period in the laboratory prior to claw removal (initial concentration 36.5 ± 16.1; subsequently 36.7 ± 15.0). However, the hemocyanin concentration in the hemolymph was significantly lower than baseline one week after removing both claws and two weeks after claw removal (1 week after removal 24.3 ± 9.7; 2 weeks after removal 24.2 ± 9.; Fig. 3).

3.4. Feeding

3.4.1. Mussel manipulation trials

Four control crabs (67%) and three of the 1-clawed crabs (43%) successfully opened a mussel and this difference in success rate was not significant (Fisher's exact test, $p = 0.310$). Successful control crabs spent 236.3 ± 260.1 min (range = 15–550 min) handling a mussel before opening it while 1-clawed crabs took almost three times as much time (615.0 ± 262.5 min (range = 350–875 min)) to open a mussel; however, this difference in handling time was not significant (unpaired t-test, $t = 1.8997$, df = 5, $p = 0.116$).

3.4.2. Food preference (Live (in-shell) Versus Shucked Mussel)

During the initial feeding trial, 63% of control crabs fed on both the live (in-shell) and shucked bivalves, and 87% of them ate at least one of the food items (Fig. 4). In contrast, 55% of crabs with one claw removed and 32% of crabs with two claws removed ate at least one food item. During the second feeding trial, two weeks later, 96% of control crabs fed on both the live and shucked food and 96% of them ate at least one of the food items (Fig. 4). In contrast, 74% of crabs with one claw removed and only 47% of crabs with two claws removed ate at least one food item. A chi-square test of independence showed that there was a significant difference between the observed and expected food preferences of Jonah crabs with varying claw status (week 1 χ^2 (6, $n = 133$) = 43.68, $p < 0.001$; week 2 χ^2 (6, $n = 77$) = 31.87, $p < 0.001$). In both weeks control crabs (both claws present) consumed both shucked and live food

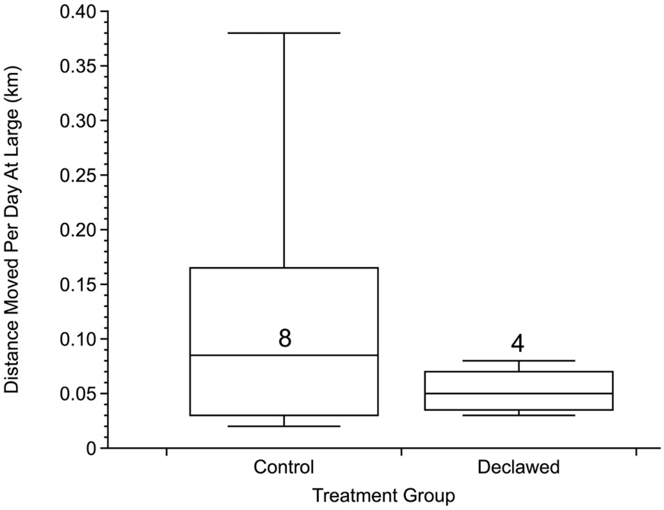

Fig. 2. Average distance traveled per day by Jonah crabs, from the day they were released to the day of their first recapture. Control crabs had no claws removed and the experimental crabs had both claws mechanically removed. While control crabs tended to move further, this difference was not statistically significant. Whiskers indicate maximum and minimum values and numbers represent crabs in each group.

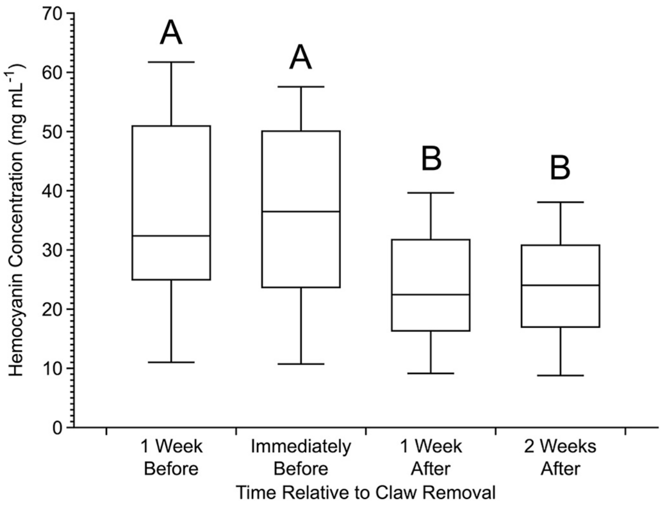

Fig. 3. Changes in hemocyanin levels following claw removal. The concentration of hemocyanin in the hemolymph of Jonah crabs (n = 10) was significantly lower one week after both claws were removed and continued to be low two weeks later. Whiskers indicate minimum and maximum values. Letters indicate homogenous subsets as determined by Tukey's HSD post-hoc test.

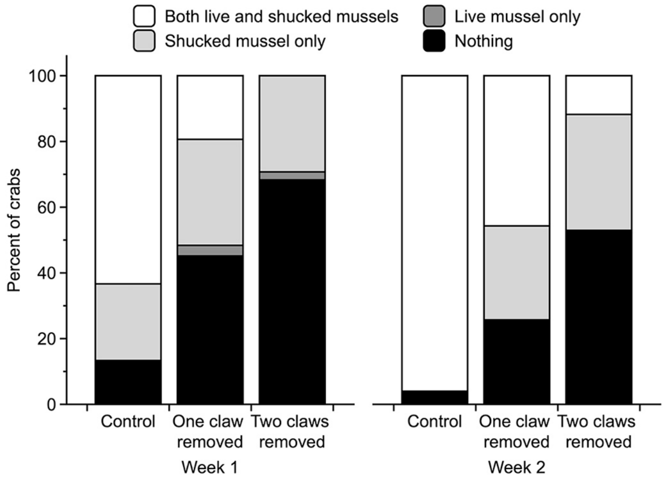

Fig. 4. Percent of Jonah crabs subjected to one of three treatments that consumed a particular type of food during the initial feeding trial, and then two weeks after their respective treatments.

and rarely consumed no food items, while crabs with no claws were less likely to eat both food options and more likely to consume nothing (Fig. 4).

4. Discussion

It has been demonstrated that claw removal in Jonah crab results in variable mortality rates of 40–87%, depending both on how many claws are removed and whether claws are removed manually or with a tool (Goldstein and Carloni, 2021). The overall goal of this series of studies was to determine if claw removal impaired the behavior and physiology of the Jonah crabs that survived this process. We found that, while claw removal reduced crab mobility and their ability to prey on bivalves, it did not impair their ability to mate. Therefore, if mortality can be reduced, perhaps by developing a better technique for removing claws, management may view a percentage of the returning crabs as contributing to the population.

4.1. Mating

Jonah crabs successfully mated in all the trials in which the female molted, 8 with clawless males and 4 with clawed males. This contrasts with data from fiddler crabs (*Uca tangeri*), that rely on their large claws to attract females to their burrows. In fact, upon claw removal male fiddler crabs were often treated as if they were females by other male or female crabs (Oliveira et al., 2000). On the other hand, both blue crabs and stone crabs (like Jonah crabs) retained the ability to mate after chelae loss or damage (Smith, 1992; Wilber, 1995). In blue crabs (*Callinectes sapidus*), claw loss did, however, make it more difficult for clawless crabs to compete with normal males, thereby reducing mating opportunities for handicapped males (Smith, 1992). Similarly, in stone crabs (*M. mercenaria*), those with regenerating limbs were not observed in natural mating pairs as often as expected (Wilber, 1995). These studies suggest that, while clawless Jonah crabs are functionally capable of mating in the absence of competition, their ability to compete for females with normal clawed males needs to be assessed.

There were also no notable differences in behavior of clawless Jonah crabs, and their potential mates, immediately before, during, or after copulation. All successful pairs were observed caging (mate guarding) both pre- and post-copulation, which serves to protect the female from other males or predators. During copulation clawed and clawless individuals were both capable of flipping their partners over, holding them while engaging in mating for approximately 2 h, and depositing sperm; as evident by the presence of a fresh sperm plug in the female's spermathecae. In green crabs (*C. maenas*), competition for mates is highly size dependent and contingent on successful pre-copulatory mate guarding; thus, the impact of claw removal on green crabs is also size dependent. While very few medium sized clawless green crab males were able to successfully guard females or copulate with them, being clawless did not appear to impact mating in larger individuals (Sekkelsten, 1988). Possessing intact claws also appears to aid the ability of male crabs to guard a female and prevent other males from stealing their mate, even if the clawed male is smaller (Abello et al., 1994). Given the large size of fishery-legal Jonah crabs (> 121 mm CW) there may not be an effect of claw removal on initially acquiring and defending a mate, but it may make acquiring a defended mate more difficult. Additionally, it should be noted that when we held male and female crabs communally in 2019, clawless male crabs were occasionally seen caging with females before they were separated for the mating trials (A. Dorrance, personal observation). This suggests that, in some situations, clawless male Jonah crabs may not be at a competitive disadvantage to clawed counterparts for mate selection. However, we also ran a series of mate choice trials (n = 5) during which a female had a choice to mate with either an intact two-clawed male, or a crab with both claws removed, and in all 5 trials, the male with claws was the one to successfully mate with the female (B. Gutzler, unpub data), even when the declawed male (n = 1) was larger and was the first to establish caging. This informal suite of trials leads us to suggest that even though declawed males can successfully mate without their claws, they may likely fail to mate in the wild if the density of males is high and there is competition for females. In summary, while the ability to mate does not appear to be reduced by claw removal if the crab survives the initial trauma, mate selection and mate guarding should be investigated to more thoroughly understand the impacts of claw removal on mating and mate competition in their natural habitat.

4.2. Activity and hemocyanin levels

After claw removal, male Jonah crabs were less active than control crabs, both in the field and in the laboratory (Figs. 1, 2). While the data from the tag-recapture study are limited, they are consistent with preliminary findings from an ongoing telemetry study of control versus declawed Jonah crabs in NH coastal waters (the authors, unpub. data). Similarly, stone crabs that had just undergone claw removal traveled a shorter distance than those with a pre-existing missing claw or controls

(Duermit et al., 2017). It has been proposed that this reduction in activity may be a strategy to avoid predation at the cost of fewer foraging opportunities (Juanes and Smith, 1995; Smith, 1995; Duermit et al., 2017). However, given the amount of hemocyanin lost and the time it takes to replenish it, crabs may also be moving less because they have a physiological constraint in their ability to transport oxygen and therefore a decreased aerobic scope (Wang and McGaw, 2014). For example, when 30% of the hemolymph in horseshoe crabs (*Limulus polyphemus*) is removed they become less active than control crabs for at least two weeks (Anderson et al., 2013; Owings et al., 2020). Overall, reduced activity may improve recovery and survival, but ultimately it could also slow regrowth of the missing claws if crabs forage less, and perhaps reduce their probability of obtaining a mate.

4.3. Feeding

Claw removal, especially both claws, reduced prey consumption and altered prey choice in Jonah crabs, which is similar to results reported from other crab species (blue crabs, brown crabs, and stone crabs) (Smith and Hines, 1991; Patterson et al., 2009; Hogan and Griffen, 2014). When one claw was removed, overall prey consumption decreased (Fig. 4). Somewhat surprisingly, when both claws were removed, crabs were still capable of preying on mussels, although they appeared to choose smaller mussels compared to their fully clawed counterparts (A. Dorrance, personal observation). However, the method used for opening mussels in our manipuation trials was different compared to uninjured control crabs. Crabs without claws occasionally used their first pair of periopods to pry open smaller mussels, as has been observed in stone crabs (Savage and Sullivan, 1978), while those possessing both of their claws were able to crush mussels of all sizes (A. Dorrance, personal observation). Stone crabs with no claws also ate soft prey with their walking legs and mouthparts, but they did not consume any hard-shelled prey (Duermit et al., 2015). Overall, the combination of a trend toward increased effort required, decreased feeding motivation, and a reduction in the size of prey chosen could lead to reduced energy intake for declawed crabs.

To compensate for decreased net energy gain from eating mussels, Jonah crabs may supplement their diet with alternative prey. Jonah crabs (regardless of claw status) were observed scraping the outside of mussels with their walking legs, then bringing their legs to their mouths and moving their maxillipeds, and this scraping behavior was observed more often with clawless crabs (A. Dorrance, pers. obs.). This behavior suggests that these crabs may be feeding on epibionts (e.g. polychaetes, algae) on the shells of mussels. While mussels are a primary component of their diets, Jonah crabs are also known to eat polychaetes as well as sea urchins, crabs, and fish remains (Ojeda and Dearborn, 1991). In this study declawed crabs were less likely to consume food, but if they did, they shifted their diet toward more soft-bodied (shucked mussels) prey items (Fig. 4). A similar change has been observed in both stone crabs and brown crabs; where they preferred fish when their claws were missing (Patterson et al., 2009; Duermit et al., 2015). On the other hand, Hogan and Griffen (2014) observed a decrease in consumption of bivalves after claw removal in stone crabs, and no increase in the consumption of soft prey. Taken together, these data suggest that, while crabs without claws are still capable of foraging for food, their overall feeding efficiency might be compromised and over the long-term this could impact growth, molting, and reproduction through reduced, or compromised, energy allocation (Hogan and Griffen, 2014). Field studies of the nutritional condition of Jonah crabs with or without lost claws could provide further information about how claw loss may impact crab diets and health.

4.4. Impacts on the fishery

Although claw removal is currently a small part of the Jonah crab fishery, it is imperative that we are proactive and gain a better understanding of both claw removal mortality (Goldstein and Carloni, 2021) and the long-term impacts on those crabs that survive (results from this study), so that we can provide scientists and management the appropriate tools to properly manage the fishery. While this study indicates that males without claws are capable of mating, due to the changes in their feeding abilities and decreased movement, Jonah crabs may not be as successful in finding and competing for mates as males with both claws. Effective management of the fishery, therefore, should take this into consideration and appreciate that just because declawed males survive the declawing process, these animals may not contribute to the overall reproductive pool of the population as much as intact, healthy, crabs.

Author contributions

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Declaration of Competing Interest

The authors declare that they have no competing interests.

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Appendix A. Supplementary data

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