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Assessing the implications of live claw removal on Jonah crab (*Cancer borealis*), an emerging fishery in the Northwest Atlantic

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ABSTRACT

In the Northwest Atlantic fisheries management is adapting to emerging fisheries. The fishery for Jonah crab (*Cancer borealis*) is rapidly expanding resulting in a quadrupling of landings over the past 20 years. In response to this increased fishing effort, management plans have begun adopting a suite of regulatory measures, one of which allows the live removal of claws at-sea. The overall goal of this project was to determine if claw removal has an impact on crab mortality. Results from a series of laboratory trials with individual crabs ($n = 240$) indicate that double-claw removal incurs markedly more mortality (70 %) compared with single-claw removal (51 %). Mortality was significantly correlated with wound size, temperature, and shell condition (GLM, $p < 0.05$), as well as elevated levels of glucose and lactate in the haemolymph of declawed animals. We also conducted a comparative claw removal trial ($n = 40$) using both manual- and mechanically-induced (using a declawing tool) methods and showed that mortality in manually declawed crabs (87 %) was much higher than when claws were removed mechanically (40 %, Wilcoxon pairs test, $p < 0.0001$). Finally, when claws were removed from tagged crabs released in the field ($n = 464$), four times as many control crabs were recaptured than crabs with claws mechanically removed, and none of the crabs whose claws were manually removed were recaptured ($p = 0.0048$). Overall, claw removal results in a significant number of mortalities. However, our findings also provide a foundation for future investigations on the sub-lethal effects of claw removal on Jonah crabs as well as the impacts of claw harvesting to improve fisheries management of this rapidly burgeoning fishery.

1. Introduction

Recent broadscale changes in marine ecosystems have had measurable and consequential impacts on marine fisheries including changes in species abundance, resulting in distributional shifts for many key species (Seldon and Pinsky, 2019; Staudinger et al., 2019). These changes have spurred innovative strategies towards managing existing fisheries as well as adapting to ones that are emerging or expanding (Pinsky and Mantua, 2014). In the Gulf of Maine (GoM) for example, historically important species notably, northern shrimp (*Pandalus borealis*) and Atlantic cod (*Gadus morhua*), have diminished in recent years and, as a result, harvesters have become increasingly reliant on fewer species (e.g. Steneck et al., 2011; Mills et al., 2013). By contrast, American lobster (*Homarus americanus*) landings are at time series highs in the GoM (ASMFC, 2020) although future decreases in abundance are projected (Le Bris et al., 2018; Greenan et al., 2019; Oppenheim et al., 2019). If these predicted declines prove true, this may prompt harvesters in this region to more heavily target alternative species like Jonah crab (*Cancer borealis*) that commingle with lobster in commercially fished traps (ASMFC, 2019). This has certainly been the case in the southern New England (SNE) lobster stock where a cascading suite of adverse factors have contributed to a measurable decline in that lobster stock (Glenn and Pugh, 2006; Shields, 2013; ASMFC, 2020). Consequently, harvesters in SNE have been actively targeting Jonah crab, leading to a steep upsurge in landings (Mercer et al., 2018; ASMFC, 2019; Truesdale et al., 2019a). In fact, since the early 2000s, Jonah crab catch has increased 650 % with 20 million pounds of crab landed in 2018, representing an ex-vessel value exceeding $18 million USD (http://www.asmfc.org/species/jonah-crab). Because of a sharp increase in fishing pressure on Jonah crab over a relatively short time, the long-term health and management of this burgeoning fishery is of substantial concern to many stakeholders (Seafood Watch, 2014; ASMFC, 2014; Truesdale et al.,

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2019a).

Jonah crab was 'red-listed' by Seafood Watch (2014), primarily because this expanding fishery has lacked a comprehensive fisheries management plan. In response to the dearth of biological knowledge and relatively unknown stock status for this species, the first Interstate Fishery Management Plan (FMP) for Jonah crab was adopted by the Atlantic States Marine Fisheries Commission in 2015 (ASMFC, 2015). Among other implementations, the FMP set prohibitions on egg-bearing (ovigerous) crabs, limits to crab bycatch in lobster pots, and the establishment of a minimum size (carapace width of 121 mm) for harvest. However, a more comprehensive management plan is needed for this species to ensure a sustainable and 'climate-ready fishery' (Pinsky and Mantua, 2014; Wilson et al., 2018). This ongoing process will rely heavily on the additional collection and evaluation of key biological metrics that currently remain deficient including growth, size at maturity, movement dynamics, disease indices, and alternative harvest practices. Cheliped (herein, claw) removal (i.e. live claw removal and the release of crabs back to the sea) is one such practice that deserves attention in this context and was the focus of this work.

Although the taking of whole crabs is the current harvest practice in most areas of the Jonah crab fishery, claw-only harvesting is routinely practiced in other areas (e.g. mid-Atlantic states; Seafood Watch, 2014), where harvesters remove both claws from a single Jonah crab (ASMFC, 2015; 2019) and then release it at sea. Although at present, this harvest practice comprises only a small proportion of the overall commercial fishery effort (~ 1 %; ASMFC, 2015), given the potential expansion and growth of this fishery to other areas, it is plausible that a claw-based fishery could become more widespread. In a preliminary study, we noted that manual declawing left large wounds in Jonah crabs, and they tended to show elevated mortality levels (Duermit et al., 2015; Goldstein and Carloni, unpub. data). Therefore, a primary goal of this study was to determine the proportion of Jonah crabs that survive the removal of one or both claws, using the techniques currently practiced by harvesters. A secondary goal was to attempt to develop an alternative method for removing claws that left a smaller wound, leading to lower mortality, similar to observed natural breaks in crabs that are found *in-situ* (Goldstein and Carloni, unpub data).

Historically, other crab fisheries utilize claw removal prior to releasing animals back to the sea with the assumption that declawed crabs will survive and continue their cycle of molting and regenerating new claws to again be harvested. This practice includes the highly valued stone crab (*Menippe mercenaria;* Duermit et al., 2015; Gandy et al., 2016; Kronstadt et al., 2018; Orrell et al., 2019), northeast Atlantic deep-water red crab (*Chaceon affinis*; Robinson, 2008), European brown or edible crab (*Cancer pagurus*; Fahy et al., 2004), and fiddler crab (*Uca tangeri*; Oliveira et al., 2006). Many of these fisheries have been afforded decades to test and evaluate the effects of claw removal (e.g. Davis et al., 1978). Although in some of these regulated crab fisheries (e.g. stone crab) claw removal mortality can be high (> 50 %; Davis et al., 1978; Gandy et al., 2016), the full breadth of claw removal for Jonah crab has yet to be explored in detail. Therefore, a third goal of this study was to investigate other implications of claw removal on the stress response in Jonah crabs. Claw removal results in markedly dramatic physiological stress responses in many crustacean species with subsequent changes in haemolymph (blood) chemistry (Patterson et al., 2007). Furthermore, declawing typically results in prominent wounds that may increase levels of overall mortality and susceptibility to disease or necrotic infection (see Patterson et al., 2007, 2009).

The overall aim of this study was to begin to develop baseline data that examines the implications of claw removal in the expanding Jonah crab fishery. A series of trials sought to assess crab mortality resulting from removing claws during simulated fishing practices both in the laboratory and in the field. We also tested a mechanical method (claw removal tool) for claw removal in an effort to reduce mortality associated with this practice.

2. Materials & methods

2.1. Animal collection and holding

Jonah crabs ($n = 839$ total, Table 1) were collected from the southern Gulf of Maine (coastal New Hampshire) using baited lobster traps fished at depths ranging from 10 to 40 m as well as opportunistically by SCUBA divers who collected crabs in similar locations. Crabs were kept alive onboard commercial lobster boats or research vessels in live-wells with aerated, running, flow-through ambient seawater and transported directly to the University of New Hampshire Coastal Marine Laboratory (CML) in New Castle, NH. Crabs were initially held communally (n = 50/tank) in large (round 1.8 m-diameter, 800 L) fiberglass tanks that were supplied with ambient, flow-through (flow rate = 35−40 L/min), aerated seawater. Holding tanks were furnished with shelters and crushed shell substrate and all crabs were fed regularly (3x/week) fresh and frozen squid, fish, and whole mussel to satiation. It is important to note that all crabs used in our trials were males given that they comprise the target for commercial harvesting markets (ASMFC, 2019; Truesdale et al., 2019b).

2.2. Crab processing, claw removal, and fluid loss

We set out to test the hypothesis that crabs with 2-claws removed would result in markedly decreased survivorship (higher mortality) compared with 1-claw removal or no claws removed (control). Our experimental design included using a large, flow-through seawater tray (dimensions: 2.3 m L x 1.1 m W x 20 cm D), containing a series of individual baskets (dimensions: 30 cm L x24 cm W x 20 cm D) where we could hold and isolate each crab with its own water source through an ambient seawater manifold (flow rate = 2 L/min), allowing each crab to be tested and later evaluated independently. For each study trial we monitored and assessed crab survivorship over a 27-day post-claw removal period.

Just prior to declawing, each crab was processed to obtain the following metrics: 1) carapace width (CW) to the nearest 1 mm using standard dial calipers; 2) crab weight to the nearest 0.1 g using a digital balance (Ohaus 600 g digital scale, model SPJ601); and 3) shell

Table 1
Summary of crab sample sizes used for each of the experiments, referred to by section number (see Methods for more details). * Represents a compilation of four separate trials (n = 10/ea. control; n = 25/ea. claw removal).

Treatment	*N (total)*
2.2. Claw Removal*	
control	40
1 claw	100
2 claw	100
Totals	***240***
2.4. Manual vs. Mechanical Claw Removal	
control	10
2 claws (manual)	15
2 claws (mechanical)	15
Totals	***40***
2.5. Haemolymph Stress Response	
control	15
1 claw	22
2 claw	22
Totals	***59***
2.6. Fisheries Simulation Study	
control	153
2-claw (manual)	152
2 claw (mechanical)	159
Totals	***464***

condition (old, medium, or new shell) based on general (and similar) criteria and descriptions from Stevens and Guida (2016) for red deep sea crab (*Chaceon quinquedens*). Claw removal closely followed routine harvesting practices commonly used by commercial harvesters in our area (see video, S1). In all, a total of four separate trials were carried out ($n_{\text{total}} = 100$ crabs/treatment, one and two claw, and $n_{total} = 40$ for controls, Table 1) over the course of approximately one year to incorporate the potential impact of seasonal seawater temperatures. Crabs were chosen haphazardly and subjected to one of three treatments (one, two, or no claws removed). We decided upon a smaller sample size for control crabs due to the comparatively higher survival rates observed in prior pilot studies at the same laboratory facility (Carloni and Goldstein, unpub data).

Additionally, we collected three other related metrics: 1) claw weight as a proportion of the total weight for each crab; these weights were obtained from claws immediately after they were removed; 2) wound widths of claws removed using fine-scale calipers to measure the maximum gap at the base of the claw; and 3) fluid (i.e. haemolymph) loss which was collected by obtaining an initial weight of each crab, then removing claws, letting the crab exude fluid for 45 s, then re-weighing the crab (post-claw removal) and its removed claws to calculate a difference in weight before and after declawing. Control crabs were handled and kept out of the water the same amount of time (60 s) as the other two treatments for consistency.

2.3. Environmental monitoring

Seawater temperatures were recorded concurrently during all trials using HOBO temperature pendant loggers (model UA-002−64, Onset Computer Corp., Bourne, MA) logging at 30-min intervals and placed in the reservoir of the incoming seawater input. We calculated average temperatures (± sem) over the course of each 27-day trial to later examine the relationship between temperature and mortality.

2.4. Manual vs. mechanical claw removal

To test the hypothesis that there are survivorship differences between claw removal methods, we applied two contrasting techniques to assess the efficacy of using a tool to reduce wound size and mortality rates in declawed crabs. A separate group of crabs ($n = 40$) were assigned to one of the following three treatments: 1) no claws removed (control, $n = 10$); 2) two claws removed by hand (manual, $n = 15$); and 3) two claws removed with a tool (mechanical, $n = 15$) which entailed using pair of 25 cm tin straight pattern snips (Wiss model A11, Apex Tool Group, Netherlands) to sever the claw between the merus and the coxa (Fig. 1, Table 1). Crabs from both treatments were handled similarly. All crabs were kept in running, well-oxygenated seawater trays and held in similar conditions to the other trials.

2.5. Haemolymph stress response

Physiological stress response in declawed crabs was evaluated using two key assays, glucose and lactate. A subset of crabs ($n = 22$ each for 1- and 2-claw removal; $n = 15$ controls, not declawed ($n = 59_{total}$, Table 1) from a separate claw removal trial were selected and evaluated for stress response (i.e., changes in these two haemolymph constituents) and evaluated over three successive time periods: 1) time-0 or the initial handing time; 2) time-1 (10 min.) just after claw removal; and 3) time-2 (∼ 24 h later); crabs were held individually within baskets in a flow-through seawater tray as previously described. At each time interval each crab was removed and placed into an acrylic seawater perfusion chamber and a small haemolymph sample (∼ 0.5 mL) was taken from the sinus at the base of the last walking leg using a 3 mL syringe and a 22-gauge needle (Becton-Dickinson and Co., Franklin Lakes, NJ); control crabs were handled in a similar manner as our declawed crab group. Haemolymph samples were deposited into labeled 2.0 mL scintillation tubes, immediately snap-frozen using a slurry bath of 90 % ethanol, 10 % acetone and dry-ice, and then stored ∼ 1 h. later in an ultracold (- 80 C) freezer.

Samples were analyzed for total glucose and lactate levels using standard colorimetric biochemical kits for each parameter and all samples were run in triplicate on a digital microplate reader (Chromate model 4300, Ray Biotech Life, Peachtree Corners, GA). Total lactate levels were evaluated using an L-lactate assay kit (Eton Bioscience, San Diego, CA) in a coupled NADH-coupled enzyme reaction at an absorbance of 490 nm while the quantitative determination of D-glucose was obtained using an assay kit (Fujifilm-Wako Diagnostics, Mountain View, CA) at an absorbance of 505 nm. Both assays used standards to correct for absorbance and samples (in triplicate).

2.6. Fisheries simulation study

We designed and carried out a tag-recapture study to test the hypothesis that the survival or recapture of declawed crabs may be compromised by the removal of claws in a series of simulated fishery exercises. We purchased freshly caught harvest-size crabs (all males, size range = 122–163 mm CW, $n = 480_{total}$, Table 1) from a local commercial wholesaler in the area and held these animals temporarily in the UNH

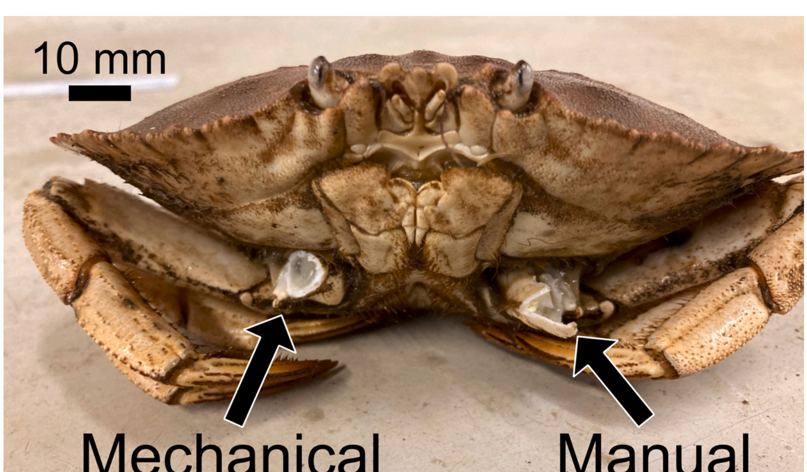

Fig. 1. Comparison of Jonah crab (CW = 130 mm) declawing techniques.; Left claw: mechanical (i.e., clean or natural) break of cheliped, using a snips tool, where the coxa is commonly found intact; wound diameter = 6.3 mm. Right claw: manual cheliped removal often resulting in the displacement of the base of the claw (coxa) and associated with larger wound sizes (wound size = 12.7 mm) and haemolymph loss. (see Supplemental video S1 as well).

CML in conditions as previously described. A day prior to their release, we affixed a poly-based harness across the dorsal carapace of each crab (Spaghetti FT-4, Floy Tag Inc., Seattle, WA) connected with an oval tag imprinted with a unique identifying number and contact information to report recaptures for each crab. To confirm sufficient tag retention, we tagged an additional 20 crabs ($CW_{avg} = 135 \pm 1.3$ mm) and set them in a large 600 L round aquarium tank at ambient conditions for a total of four weeks after which, no tag loss was observed. On the day of release, tagged crabs were transported by research vessel and held on deck in high-flow, ambient seawater tanks.

Experimental crabs were subjected to one of three treatments: 1) two claws manually removed ($n = 152$); 2) two claws mechanically removed ($n = 159$); or 3) no claws removed (control, $n = 153$). We also recorded all the typical biological data for each crab (CW, shell condition), as well as their release location. We were able to process, tag, and release a total of 464 crabs over two release events (233 crabs on July 13, 2018 and 231 crabs on August 10, 2018, Table 1) approximately 0.2 km from shore at a depth of 15 m along the seacoast of NH. The remaining 16 crabs resulted in mortalities prior to release and these animals were excluded. Both manual and mechanical claw removal followed the same practices as described in the lab trials. Reporting for crab recaptures were incentivized by entering the names and contact information for harvesters that called in and placing their names into a raffle prize contest at the completion of the study. All recapture data were analyzed to determine recapture rates of each treatment. For purposes of this study, these data were only intended to be used to compare to our lab results. Detailed movement patterns will be further analyzed in a subsequent manuscript assessing sub-lethal effects of claw removal using acoustic telemetry.

2.7. Data analyses

Where data satisfied normality assumptions, a series of Student's t-tests were used to compare distributions. In cases where data did not meet normality assumptions but had equal variance, a non-parametric Wilcoxon's rank-sum test was carried out. A generalized linear model (GLM) with binomial distribution and logit function was used to assess the effects of temperature (factor-1), wound width (factor-2), and shell condition (factor-3) on the binary response (i.e., dead or alive) after each of the four trials. To investigate the effect these variables had on the duration of survival, a parametric survivorship analysis was used to calculate survival data over an event-time response. In construction of both models, we combined temperature for trials with mean temperatures within 0.5 °C, and we grouped our four trials by temperature for modeling as follows: December (6 °C, two trials), February 3 °C, one trial) and June (12 °C, one trial). Additionally, wound width was binned for models based on preliminary data which showed that claws generally detached in three locations which were associated with binned wound sizes as follows: 1) small, coxa intact = 7−13 mm; 2) medium coxa removed with claw = 14−20 mm; and 3) and large body cavity exposed = 21−27 mm). Crab haemolymph data were evaluated for potential differences in glucose or lactate levels between our three treatment levels (fixed factor-1) at each of three sampling periods (fixed factor-2). A 3 × 3 full factorial design was used and analyzed as a split-plot (SP) ANOVA (whole-plot: treatment, sub-plot: time, $df_{total} = 9$); contrasts between groups were compared using the Tukey's HSD function. We tested the assumptions of normality, independence, and homogeneity of variance and used a Kuskal Wallis *H*-test where these assumptions were not supported. All reported error is represented as standard error of mean (sem) and JMP Pro 14.0 (SAS Institute Inc., Cary, NC) was used for all statistical analyses.

3. Results

3.1. Manual declawing (laboratory trials)

A total of four trials (2014−2015) were conducted to assess mortality associated with manual crab declawing. One additional trial was run to assess changes in crab haemolymph chemistry associated with this practice. Seawater temperatures for each of our four trial periods ranged from 3 to 12 °C. In total, 240 crabs were evaluated (controls, $n = 40$; 1-claw removal, $n = 100$; 2-claw removal, $n = 100$). Crab sizes (mean CW $= 139.2 \pm 0.45$ mm) and weights (mean $= 433.4 \pm 4.0$ g) allowed us to determine claw weights for both claws which, on average, accounted for 28 % of total crab body weight. Mortality rates for all treatments were as follows: Controls = 16 %, 1-claw removed = 51 %, and 2-claws removed = 70 %. There was a significant difference in mortality between controls and 1-claw, as well as controls and 2-claw, but not between one and two-claw treatments (Wilcoxon pairs test, $p < 0.05$, Fig. 2). Wound widths for both 1-claw and 2-claw removals ranged from 3.0 to 26.6 mm, with a mean of 14.5 ± 0.2 mm, and there was a significant negative relationship between wound width and fluid loss ($r = 0.40$, $p = < 0.001$).

A generalized linear model (GLM), with the three categorical independent variables (temperature, wound width, and shell condition) were all significant terms with respect to their binary response to mortality (i.e. dead or alive, Table 2). Parametric survivorship curves based on a continuous response (i.e. days) revealed temperature and wound width as the significant terms determining duration of survival (Table 3, Fig. 3). A general pattern emerges where higher temperatures and larger wound sizes contribute to a higher probability of mortality, most likely due to greater haemolymph loss.

3.2. Crab haemolymph assays

We found that both haemolymph constituents (lactate and glucose, uM/L) did not significantly differ at time-0 ($p = 0.32$) or time-1 ($p = 0.18$) but did deviate at time-2 or 24 h post-claw removal (*SPANOVA*; $F_{2,57} = 0.56$, $p < 0.01$). Our treatment factor (claw removal) was significant ($F_{2,57} = 0.31$, $p < 0.001$) between controls and 1- and 2-claw removal, but not between claw removals (1 vs. 2). This was the case for both lactate (control mean $= 847 \pm 168$ μM/L; 1-claw mean $= 1237 \pm 124$ μM/L; 2-claw mean $= 1428 \pm 156$ μM/L, $p < 0.001$) and glucose (control mean $= 284 \pm 67$ μM/L; 1-claw mean $= 568 \pm 55$ μM/L; 2-claw mean $= 478 \pm 71$ μM/L, $p = 0.016$, Fig. 4).

3.3. Manual vs. mechanical declawing trials

3.3.1. Laboratory

Mortality rates for controls was 10 % (1/10), compared with 87 % (13/15) mortality for manually declawed crabs and 40 % (6/15) for crabs that had their claws removed mechanically using a tool. Overall, manually removed claws resulted in significantly more mortality compared with mechanically removed claws (χ^2 test, $p = 0.0031$). Additionally, crabs with mechanically removed claws had significantly smaller wound sizes (16.8 ± 0.38 mm), compared to crabs where manual claw removal was used (25.5 ± 1.46 mm, Wilcoxon $p < 0.0001$). There was also significantly less fluid loss during mechanical (5.79, ± 1.15 g) versus manual (16.5 ± 2.1 g, Wilcoxon $p < 0.0001$) claw removal, and there was a significant negative relationship between wound size and fluid loss ($r = 0.67$, $p < 0.0001$).

3.3.2. Field

A total of 464 crabs were tagged, subjected to the same treatments as described above for the laboratory study and released at two different locations in July and August of 2018. Crabs with claws removed mechanically had significantly smaller wound sizes compared to crabs that had claws removed by hand (Wilcoxon $p < 0.0001$). A total of 29 crabs (6.25 %) were recaptured and of these 23 were controls (4.96 %

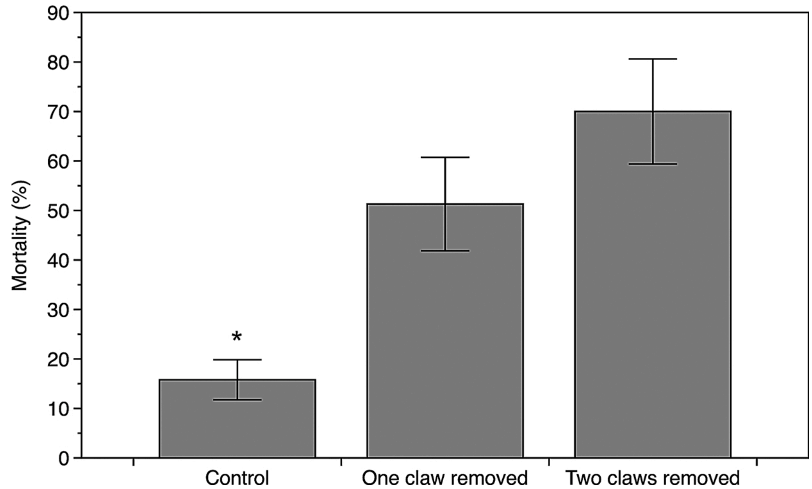

Fig. 2. Comparative mortality rates of Jonah crabs by treatment 1) control; 2) 1-claw removed; and 3) 2-claws removed. An '*' above bars indicate significant difference with Wilcoxon pairs test ($p < 0.05$). *P*-values as follows: One-claw to control= -0.0304, two-claw to control = -0.0304, one-claw to two-claw = -0.2454.

Table 2
Generalized Linear Model effect tests (a); and parameter estimates (b), indicating temperature, wound size, and shell condition were all significant terms in a binomial response (i.e. alive or dead). Significant terms denoted with asterisk.

a.

Source	DF	L-R ChiSq	Prob > ChiSq
Temperature	2	13.26	0.0013*
Wound size	3	50.34	<0.001*
Shell condition	2	7.88	0.0194*

b.

Model	Estimate	Std Error	L-R ChiSq	Prob > ChiSq	Lower CL	Upper CL
Intercept	−1.00	0.49	5.23	0.0222*	−2.16	−0.13
Temperature (3 °C)	0.67	0.27	6.30	0.0121*	0.14	1.21
Temperature (6 °C)	0.32	0.23	1.87	0.1716	−0.14	0.78
Wound size (large)	−2.90	0.80	32.31	<.0001*	−5.09	−1.65
Wound size (medium)	−0.21	0.34	0.34	0.5586	−0.84	0.61
Wound size (small)	1.19	0.45	8.06	0.0045*	0.35	2.17
Shell cond (medium)	0.38	0.43	0.88	0.3472	−0.38	1.44
Shell cond (new)	−1.48	0.81	4.31	0.0379*	−3.53	−0.08

Table 3
Likelihood ratio tests for parametric survivorship curves indicating treatment, temperature, and wound size as significant terms in the model. See Fig. 3 for depiction of modeled survival by temperature and wound size.

Source	DF	L-R ChiSq	Prob > ChiSq
Treatment	2	11.37	0.0034
Temperature	3	60.99	<0.0001*
Wound size	3	32.96	<0.0001*
Shell condition	2	4.76	0.0925*

recaptured), six had their claws removed with a tool (1.29 % recaptured) and 0% of those that had their claws removed manually were recaptured. There was a significant difference in recapture rate between mechanically and manually declawed crabs (χ^2 test, $p = 0.0048$).

4. Discussion

Gaining a better understanding of the implications of live claw removal in the expanding Jonah crab fishery was the driving motivation for this study. As expected, claw removal affected survivorship but water temperature, wound size, and shell condition modulated overall mortality. However, we were able to significantly decrease mortality rates by using a tool to mechanically declaw crabs, a method that appears to show some promise for potential broad-scale commercial use.

4.1. Crab mortality

Overall, our results are comparable with crab mortality rates for one of the largest and economically lucrative crab fisheries, stone crab (*Menippe mercenaria*), where declawing studies show mortality rates from 28 to 100% (Savage and Sullivan, 1978; Simonson and Hochberg, 1986). In a related study, Davis et al. (1978) reported crab mortality rates of 23 % and 51 % with one or two claws removed, respectively. More recently, Gandy et al. (2016) reported mortality rates of 62.9 %, 40.8 %, and 12.8 % for 2, 1, and 0 claws removed, respectively. Therefore, for both stone crabs and Jonah crabs claw removal-induced mortality is substantial and could have a significant impact on the sustainability of such fisheries.

4.2. Factors influencing mortality

We used both generalized linear model analysis and parametric survivorship curves to better understand factors influencing mortality in declawed crabs. In both models, temperature and wound width were significant terms. Furthermore, wound width was significantly correlated with fluid loss, suggesting that the size of the wound has a direct effect on the amount of haemolymph that is lost. One factor that likely comes into play is the efficacy of the harvester to remove claws resulting in 'clean (or natural) breaks' (i.e. between the merus and the coxa, see Fig. 1), which result in smaller wound sizes and less fluid loss, thus, lower mortality. In our study, we had one trained operator for all manual claw removals, although 'bad breaks' (i.e. at the base of the coxa and often into the body sinus cavity, Carloni, personal observation) still occurred. We suspect that even the most competent harvesters occasionally induce large wounds that would increase the likelihood of subsequent mortality. This relationship between wound size and morality has also been shown in other studies with stone crabs as well (e.g. Davis et al., 1978; Simonson and Hochberg, 1986; Duermit et al., 2017).

The importance of wound width and the location of break in survival

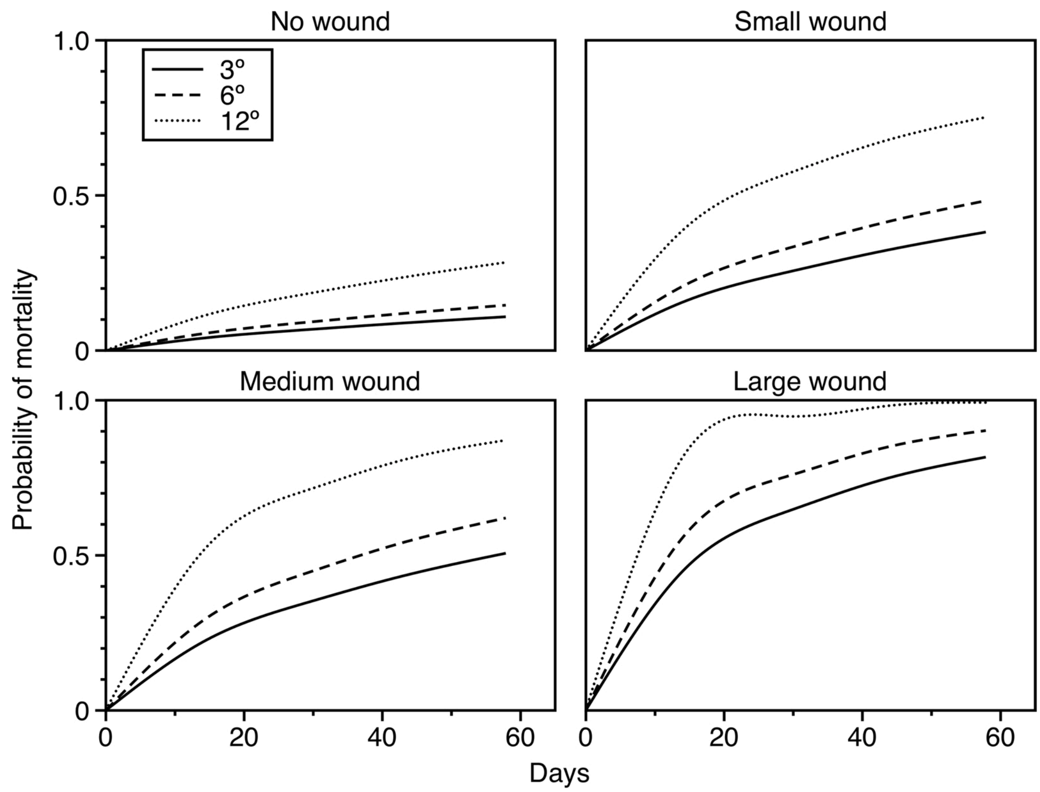

Fig. 3. Probability of mortality based on different wound sizes (i.e. no wound, small, medium and large) at three different temperatures. A pattern emerges where higher temperatures and larger wound size contribute higher probability of mortality.

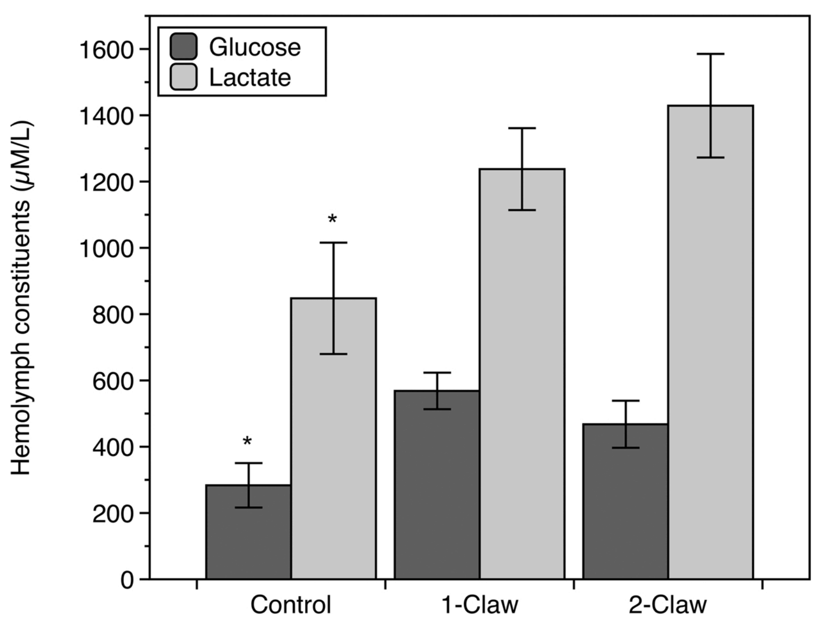

Fig. 4. Haemolymph assays for mean crab lactate and glucose levels (measured in uM/L ± sem) for crabs ($n = 22$ each for 1- and 2-claw removal; $n = 15$ controls, not declawed) at time-2 or 24 h post-declaw event. An '*' above bars represent significant differences (glucose, $p = 0.016$; lactate, $p < 0.001$) between treatments.

of declawed animals motivated us to find a technique to try and promote smaller wounds (analogous to what is observed in some crabs caught *in-situ* with natural breaks) when removing claws from individual crabs. Utilizing mechanical snips to remove claws led to significantly less mortality compared with manual claw removal (87 % vs. 40 %, respectively) most likely because using a tool created smaller wounds and at least 50 % less fluid loss. Although this technique still requires extensive field-testing, our results suggest it could be used by commercial harvesters to mitigate some of the mortalities associated with claw removal at sea.

Temperature was also a pervasive factor driving mortality in declawed Jonah crabs. Both our GLM and survivorship curves demonstrated increased mortality with higher temperatures (Fig. 3). This same pattern of increased probability of mortality with increased temperature holds true not only for animals with small, medium, and large wound sizes, but also for control animals. Like most marine crustaceans, temperature affects most, if not all physiological processes and may dramatically influence survivorship (reviewed in Hochachka and Somero, 2002). It was not too surprising then that temperature was a noteworthy driver in both of our model explorations, as even the most modest temperature increases in our trials were enough to alter mortality rates substantially (Table 2, Fig. 3). It should also be pointed out that over the course of this study we subjected Jonah crabs to temperatures that were indicative of a seasonal suite of temperatures ranging from 3 °C (winter) to 12 °C (spring/summer) in our region. Due to logistical challenges, we were not able to conduct trials at maximum (summertime) temperatures, but with typical annual ranges of 15–18 °C in southern coastal Maine and New Hampshire waters (NERACOOS, 2020), we suspect mortality rates to have risen even higher over this time period. By comparison, in a field-based cage study with stone crabs, Gandy et al. (2016) looked at mortality over a range of temperatures (12.2–28.1 °C) in the Gulf coast of Florida and determined that for each degree increase in temperature, crab mortality increased by a factor of 1.33 (and a factor of 2.29 with two claws removed).

Along with temperature, shell condition (i.e. old, medium, or new shell) was a significant term in our GLM, but not in the survivorship analysis (Table 3). New shell (i.e. recently molted) crabs exhibited higher mortality rates during declawing, likely due to the vulnerable nature of decapod crustaceans during their post-molt period where they are recovering from ecdysis and continuing to harden over time. Ecdysis is both a physiologically- and biochemically-taxing event on decapod crustaceans (see review in Chang, 1995), and we suspect that crabs may be prone to higher mortality, especially with respect to the impact of claw removal. Even though new shelled crabs tended to be more pliable during claw removal (pers. observation), we also observed larger wounds associated with these animals due to the 'soft' nature of their shells, especially around the claw articulation points, resulting in more haemolymph loss. Additional studies might consider a continuum of shell conditions to help delineate any potential window of time where claw harvesting could least impact crabs. For example, evidence points towards the changing mechanical properties of crustacean shells over time (e.g. cuticle and tensile strength, crack blunting, and mineralization; Tarsitano et al., 2006; Gadgey and Bahekar, 2017). Thus, older shells may be more forgiving under conditions of manual claw breakage, and this is something that we also captured in our findings.

We validated our studies with physiological indicators of stress (haemolymph glucose and lactate) and determined that, like other studies (e.g., Patterson et al., 2007) glucose and lacate levels were markedly elevated for declawed crabs compared with our control treatments (i.e. handled only crabs), remaining elevated for at least 24-hr (but possibly longer) post claw removal. Lactate tends to be a valid indicator of a general stress response in crustaceans and is the primary end-product of anaerobic metabolism while increased glucose tends to induce hyper-glycaemia (Albert and Ellington, 1985). Both these biomarkers are considered physiological modulators that work to increase blood oxygen affinity from a stressor and are very sensitive to changes in elevated temperatures (Ocampo et al., 2003). The continued warming in the Gulf of Maine (Pershing et al., 2015) is projected to adversely impact many commercially important species including lobsters and crabs (Staudinger et al., 2019) and will likely put added physiological stress on biological processes (through increased temperatures) that make these species more vulnerable to fishery-based mortality.

4.3. Fishery-simulated mortality

We attempted to apply our laboratory trial outcomes in the field by conducting a fisheries-simulated study. Through a mark-recapture study we determined that 1.25 % of Jonah crabs with mechanically removed claws were recaptured compared with no crabs with manually removed claws. Furthermore, 4.8 % of control (claw-intact) crabs were recaptured indicating that, in general, declawed crabs were captured less often than control crabs. Our results are congruent with stone crab recapture rate studies that are low as well (Savage and Sullivan, 1978; Duermit et al., 2017). For example, Ehrhardt et al. (1990) reported recapture rates of 1.2 % for declawed crabs compared with 10.5 % for control crabs. It is not clear if recapture rates are low for declawed crabs because of mortality, or they are less active and feed less, so they are less 'catchable', as demonstrated by Duermit et al. (2017); this study showed declawed crabs were less motivated to feed and therefore entered traps less often. Orrell et al. (2019) also reported that declawed stone crabs spent disproportionately less time feeding and were physiologically more taxed (i.e. increased metabolic rates) than control crabs that entered traps more readily. Acoustic telemetry studies are currently underway to determine if declawed Jonah crabs released back into their natural habitat are less active and move less than control crabs.

4.4. Fishery management considerations

The expanding Jonah crab fishery in the Northwest Atlantic is likely partially a result of changing ecosystems and shifting species dynamics. These changes are seen even more starkly in southern New England where lobster stock declines (Atlantic States Marine Fisheries Commission, (ASMFC, 2015) have driven some harvesters to switch to alternative species like Jonah crab (Mercer et al., 2018). Although at present, the majority of Jonah crabs are harvested whole (ASMFC, 2015), it is currently legal to remove claws at sea in many jurisdictions and our results help to promote a more thorough understanding of the biological impacts of this practice that are crucial to the long-term sustainability of this resource. A core goal in fisheries management is to effectively assess stock health and discard mortality (see Stoner, 2012 for review). The durability and tolerance of Jonah crabs to handling and transport are generally robust, however continuing to understand both acute and chronic stress responses to manual declawing trauma are vital in future practices as well as the broad ecological consequences of limb removal (Juanes and Smith, 1995).

In this study, we examined the implications of claw removal on overall mortality and physiological stress; however, we also evaluated claw removal techniques and the factors that exacerbate mortality, which include a trifecta of warm temperature, large wound size, and new shell condition. When harvesting whole crabs, a 100 % mortality rate is incurred; in our research, we found that a best-case scenario under laboratory conditions was a 70 % crab mortality rate when removing both claws. Finally, by employing a declawing tool, commercial harvesters can significantly decrease wound size and thus mortality. Based on our research, there may be tangible strategies to help mitigate mortality associated with declawing and these criteria should be considered by fisheries scientists and managers when drafting future management plans for this species. We are currently conducting a series of companion studies that will help to further determine a variety of sub-lethal effects on claw removal that include mating performance, feeding, and activity (Dorrance et al., submitted). Collectively, these studies will provide a more comprehensive understanding of the impacts of Jonah crab claw harvesting and help to guide improved fisheries management of this rapidly growing fishery in New England waters.

CRediT authorship contribution statement

Jason S. Goldstein: Conceptualization, Methodology, Data curation, Formal analysis, Writing - review & editing, Writing - original draft. **Joshua T. Carloni:** Conceptualization, Methodology, Data curation, Formal analysis, Writing - review & editing.

Declaration of Competing Interest

The authors report no declarations of interest.

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Appendix A. Supplementary data

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