Evaluating the Impact of Fishery-Related Claw Removal On Diet, Consumption Rate, Energetics and Reproduction In the Florida Stone Crab (Menippe Spp.)

Jessica Mary Hogan
University of South Carolina

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EVALUATING THE IMPACT OF FISHERY-RELATED CLAW REMOVAL ON DIET, CONSUMPTION RATE, ENERGETICS AND REPRODUCTION IN THE FLORIDA STONE CRAB (*MENIPPE SPP.*)

by

Jessica Hogan

Bachelor of Science
Hawaii Pacific University, 2011

Submitted in Partial Fulfillment of the Requirements
for the Degree of Master of Science in
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Accepted by:
Blaine Griffen, Major Professor
Tammi Richardson, Thesis Reader
Dennis Allen, Thesis Reader
Lacy Ford, Vice Provost and Dean of Graduate Studies
DEDICATION

I would like to dedicate this work to my husband, Daniel Hogan, for his support and encouragement throughout this process.
ACKNOWLEDGEMENTS

This research would not have been possible without the encouragement and assistance of my thesis committee, family, and friends. First, I would like to express my sincere gratitude to my thesis advisor, Dr. Blaine Griffen, for his support throughout the progression of my degree. I would also like to thank my committee members, Dr. Tammi Richardson and Dr. Dennis Allen, for their assistance during my research and graduate education. I would like to thank my husband, Daniel Hogan, for his dedication to helping me succeed. And lastly, I would like to thank my lab members and the staff at the Baruch Institute for Marine and Coastal Sciences for their help with various aspects of this research.
ABSTRACT

Many global fisheries are overexploited and working towards the development of sustainable fishing methods. Claw based crab fisheries, such as the Florida stone crab (*Menippe mercenaria*, *M. adina*, and hybrids) fishery, use unique fishing techniques that reduce the overall mortality of harvested organisms. For example, the Florida stone crab fishery is regulated by requiring that fishermen only harvest crab claws and requires that fishermen return the live crab to the water following harvesting. This process takes advantage of the ability of crabs to autotomize and regenerate their claws, and enables crabs to re-enter the fishery in subsequent years if they survive. Though this fishery is currently considered to be sustainable, fishery-related claw loss may negatively influence the population through multiple pathways. The objectives of this study were to demonstrate how fishery-related claw loss influences Florida stone crab diet choice, consumption over time, and energy allocation following simple dynamic energy budget theory, with the ultimate goal of determining how these factors influence the reproduction of harvested individuals. I demonstrated that one-clawed Florida stone crabs do not switch their diet to more easily managed food items, such as algae or sponge, following claw removal. However, I found that one-clawed crabs consume fewer bivalves than two-clawed crabs, and they do not improve in their ability to crack mussels over time, suggesting that decreased foraging capacity will remain until the regenerative molt. I found that one-clawed Florida stone crabs do not alter their energy storage
patterns prior to the reproductive season, suggesting that the energy for both reproduction and claw removal will be derived from the same energy stores. Lastly, I found that regenerating a crusher claw has the potential to take energy away from reproduction; however, the energetic implications of decreased consumption following claw loss far outweigh the energetic costs of claw regeneration. The results of this study indicate that Florida stone crabs are likely to suffer from severe energetic constraints resulting from claw removal, which could limit growth, claw regeneration, reproduction and survival of harvested crabs.
# Table of Contents

**DEDICATION** .................................................................................................................. iii

**ACKNOWLEDGEMENTS** .................................................................................................. iv

**ABSTRACT** ....................................................................................................................... v

**LIST OF TABLES** .............................................................................................................. viii

**LIST OF FIGURES** .......................................................................................................... ix

**INTRODUCTION** .............................................................................................................. 1

**METHODS** ..................................................................................................................... 7

**RESULTS** ........................................................................................................................ 17

**DISCUSSION** .................................................................................................................. 30

**REFERENCES** ................................................................................................................ 36

**APPENDIX A** .................................................................................................................. 42
LIST OF TABLES

Table 1. Distribution of crab sizes in experiments ................................................. 7
Table 2. LMER model results ..................................................................................... 20
Table 3. Calculation of daily energy intake ................................................................. 28
Table 4. Calculation of basic metabolic requirements ................................................. 29
Table A.1. Parameters included in the Lefkovitch matrix model .............................. 43
Table A.2. Stage and ages used in model ................................................................. 44
Table A.3. Equations used in the Lefkovitch matrix model ...................................... 47
LIST OF FIGURES

Figure 1. Dynamic energy budget model.......................................................... 4
Figure 2. Phenology for female Florida stone crabs........................................... 5
Figure 3. Geukensia demissa length to mass .................................................. 10
Figure 4. Diet Choice following claw removal.................................................. 18
Figure 5. Trends in consumption following claw removal .................................. 21
Figure 6. Average consumption of one and two clawed individuals..................... 22
Figure 7. Energy storage and reproductive investment prior to reproduction ......... 23
Figure 8. Energy required for claw regeneration................................................. 24
Figure 9. Reproductive energy lost due to claw regeneration .............................. 26
Figure 10. Reproductive energy lost from different factors ................................. 27
Figure A.1 Lefkovitch matrix model for the Florida stone crab population .......... 44
INTRODUCTION

Many fisheries around the world are heavily exploited. Over fifty percent of global fisheries are considered to be fully exploited, with yet another thirty percent of fisheries considered as overexploited (FAO 2012). Research is making progress towards successful fisheries management strategies (Beddington et al. 2007) and the degree of overexploitation has decreased for a number of fisheries (Worm et al. 2009, NRDC 2013); however, the sustainability of global fisheries is still a major concern (Pauly et al. 2002, Mora et al. 2009).

Many fisheries have adapted unique fishery techniques or regulations to address sustainability concerns. Claw-based crab fisheries are one such class of fisheries. These fisheries occur globally; including fisheries based on the crabs *Menippe spp.* (Bert et al. 1978), *Chaceon affinis* (Robinson 2008), *Cancer pagurus* (Fahy et al. 2004) and *Uca tangeri* (Oliveira et al. 2000). Rather than harvesting the entire organism, these fisheries only harvest crab claws, taking advantage of the ability of crabs to autotomize (voluntarily shed) and regenerate their claws (Patterson et al. 2008). This method of capture decreases the instantaneous mortality rate of the harvested crabs (Davis et al. 1978), and allows the harvested crabs to re-enter the fishery after they regenerate their claws (Bert et al. 1978).
The Florida stone crab (*Menippe adina, M. mercenaria*, and hybrids) fishery is an example of a claw-based fishery and is the fifth most valuable crab fishery in the United States (NMFS 2011). This fishery occurs along most of the southern coasts of the United States, though the majority of commercial landings come from the state of Florida. The commercial Florida stone crab fishery began in the early 1960s (Bert et al. 1978), and landings quickly increased to a maximum during the late 1990s (Muller et al. 2006). However, the annual catch per unit effort (CPUE) has been declining since the fishery’s inception, falling from a high of nearly 23 pounds of claws per trap to less than 5 pounds per trap today (Muller et al. 2011). A notable decline (approximately 37%) in the CPUE occurred in the early 1970s, which is when fishery regulations were adjusted to allow the removal of both claws (Muller et al. 2011) and to allow claw removal from females (Bert et al. 1978).

Stock assessments have determined that the Florida stone crab fishery has been overfished for at least the past fifteen years (Muller and Bert 1997, Muller and Bert 2001, Muller et al. 2006, Muller et al. 2011). In an effort to combat overfishing, the state of Florida implemented the passive-reduction stone crab trap limitation program in the 2002-2003 fishing season. This program is designed to passively reduce the number of traps in the stone crab fishery by not selling additional trap certificates and by decreasing the number of trap certificates received when they are transferred between owners. The goal of the program is to reach 600,000 traps in the fishery, a goal that will take 37 years to reach at the current rate of trap reduction (Muller et al. 2011). Though the number of traps in the fishery has been declining since this program was implemented (total fishing effort from 2002 to 2010 declined by 16.5%, roughly 260 thousand traps), the CPUE has
remained consistently low (Muller et al. 2011). The lack of increase in CPUE with the declining number of traps suggests that the population is not positively responding to decreased fishing pressure. Thus, current management strategies may not be as sustainable as intended.

Fishery-related claw removal may negatively impact stone crabs due to mortality (Davis et al. 1978), the energetic costs of claw regrowth, reduced energy intake associated with diet or foraging changes, and via decreased reproductive output (reviewed in Juanes and Smith 1995). The goal of this research was to determine how fishery-related claw removal influences the Florida stone crab population from an energy budget theory perspective (Kooijman 2009). To do this, I follow the conceptual model of energy intake and utilization established by dynamic energy budget theory (van der Meer 2006), exploring how claw loss may influence energetics at each stage of this process (Figure 1). First, I examined how claw loss may influence stone crab energy intake (Figure 1, #1). Florida stone crabs have large claws that represent up to fifty percent of their body weight (Davis et al. 1978), allowing the crabs to specialize in consuming hard-shelled bivalve prey (Yamada and Boulding 1998). Claw loss in other crab species is known to reduce consumption rates and alter diets (Smith and Hines 1991, Brock and Smith 1998, Patterson et al. 2008, Delaney et al. 2011). Thus, it is likely that removing a claw will similarly limit the foraging capabilities of single-clawed stone crabs, potentially causing them to reduce their consumption, consume smaller prey, or alter their diet to consume more manageable foods such as algae or plant material (Bender 1971). Further, even after initial claw regeneration, consumption is likely to be limited to smaller prey
items due to the smaller size of the regenerated claw (Cheung 1976), which may take up to three years to fully regenerate (Savage and Sullivan 1978).

I had no reason to believe that claw removal would alter the efficiency of assimilating consumed food and therefore do not examine this aspect of energetics.

Figure 1 Conceptual dynamic energy budget model for Menippe spp. with corresponding elements addressed by this study (modified from van der Meer 2009). \( \kappa \) represents the energy required for growth and maintenance, and \( 1-\kappa \) represents the energy remaining that may be allocated to reproduction.

Second, I examined whether claw loss altered the energy storage of Florida stone crabs (Figure 1, #2). In crustaceans, the energy used for molting and reproduction is generally stored in the hepatopancreas (Kennish 1997). Legal sized female stone crabs (84 mm carapace width (CW) or larger) use this energy reserve once annually for molting in the fall or winter (Gerhart and Bert 2008), causing the impact of claw loss to persist
until the next annual molt. The molting period of female crabs occurs during the early months of the fishing season (Figure 2), increasing the likelihood that one-clawed female crabs will not regenerate their claw until after the next spawning season. Consequently, reproduction and claw regeneration create two simultaneous energetic demands that must be met by energy stores. Energy budget theory assumes that growth and maintenance demands must be met prior to energy allocation for reproduction ($\kappa$, Figure 1, #3), implying that female stone crabs may alter the allocation of energy over winter, from gonad development to energy storage, in preparation for regenerating their lost claw.

![Figure 2](image-url)  
**Figure 2** Annual timeline of events for the female Florida stone crab. Phenology created from published data (mating: Savage 1971, spawning: Bert et al. 1986, molting: Cheung 1969 & Gerhart and Bert 2008, fishery dates: Muller et al. 2011).

Third, I examined the energy required for limb regeneration (Figure 1, #3) and its energetic consequences for reproduction (Figure 1, #4). When a crab loses its claw, the amount of energy required for growth and maintenance ($\kappa$) increases. In lizards that autotomize and regrow their tails, regrowth can demand up to 56% of total stored energy (Vitt et al. 1977). As the amount of energy put towards regrowth ($\kappa$) increases with claw
regeneration, the amount of energy available for reproduction consequently decreases (1-κ). Decapods commonly decrease their reproductive output while regenerating a limb (Juanes and Smith 1995, Maginnis 2006), suggesting that this energy balance strategy is also likely seen in Florida stone crabs. However, the energetics of limb regrowth have not previously been examined for this species of crab.

I tested the following hypotheses. First, that stone crabs will alter their diet to a more readily consumable prey type following claw loss (i.e. algae, as suggested by Bender 1971), and that the consumption of bivalves would be lower for individuals with a single claw (as demonstrated for other molluscivorous crabs: Smith and Hines 1991, Brock and Smith 1998, Patterson et al. 2008, Delaney et al. 2011), thus decreasing overall energy intake. Second, since many crabs have the capacity to adapt new foraging strategies (Micheli 1995), I also hypothesized that individuals with a single claw will become more efficient at consuming prey over time, thus partially compensating for altered diets or reduced foraging following claw loss. Third, I hypothesized that energy allocation to storage would increase over winter, consequently decreasing the amount of energy put towards reproductive output. And fourth, I hypothesized that allocating energy to claw regeneration, and the energy lost from decreased consumption, would substantially decrease the amount of energy available for reproduction in one-clawed Florida stone crabs.
METHODS

1. Energy Intake

1.1 Diet Choice

I conducted the energy intake experiments at Baruch Institute’s Marine Field Laboratory, in Georgetown, SC. I evaluated the influence of claw loss on Florida stone crab diet choice using a short term study in May 2012. I collected a total of 38 crabs (Table 1) from North Inlet Estuary (33°20'N, 79°10'W) for use in the experiment and removed the larger, crusher claw from 19 of these crabs within 24 hours of their capture. Two crabs perished immediately following claw removal. The remaining crabs were housed in individual containers within flow-through aquaria, allowing water temperature and salinity to fluctuate with ambient conditions. The experiment was conducted over four 72-hour trials (blocked by time) during a two week period. I included a control in each block to account for any consumption-independent changes in biomass of the provided diet items.

Table 1 Mean carapace widths (CW) ± standard deviations and sexes of crabs used in each experiment.

<table>
<thead>
<tr>
<th>Experiment</th>
<th>CW_{all} (mm)</th>
<th>CW_{males} (mm)</th>
<th>n_{males}</th>
<th>CW_{females} (mm)</th>
<th>n_{females}</th>
</tr>
</thead>
<tbody>
<tr>
<td>Diet Choice</td>
<td>90.7 ± 10.6</td>
<td>97.2 ± 9.2</td>
<td>14</td>
<td>86.6 ± 9.4</td>
<td>22</td>
</tr>
<tr>
<td>Consumption and Efficiency</td>
<td>92.0 ± 8.3</td>
<td>93.0 ± 10.0</td>
<td>9</td>
<td>91.0 ± 6.8</td>
<td>10</td>
</tr>
<tr>
<td>Energy Storage</td>
<td>95.5 ± 16.9</td>
<td></td>
<td></td>
<td>95.5 ± 16.9</td>
<td>19</td>
</tr>
</tbody>
</table>
I provided the crabs with six diet options that are commonly found in oyster reefs within North Inlet Estuary: eastern oysters (*Crassostrea virginica*), hard clams (*Mercenaria mercenaria*), ribbed mussels (*Geukensia demissa*), green algae (*Ulva spp.*), red algae (*Gracilaria spp.*), and the sun sponge (*Hymeniacidon heliophila*). Due to large differences in the mass to volume ratio between these food items, I varied the amount of each of these food items provided in an attempt to standardize the relative volume of consumable tissue across diet types. I determined the initial blotted wet weight of each food item prior to placement in the aquaria. After 72 hours I removed all unconsumed tissue and determined the final blotted wet weight of each food item separately. While using wet weights is less accurate than using dry weights, it was necessary because crabs were fed living organisms (initial dry weight could not be determined without sacrificing the provided organisms).

I analyzed the amount consumed of each food type using a multivariate linear mixed effects model (LMER in R), with the logarithm of wet weight consumed for each diet item as response variables, number of claws, sex, and CW as predictor variables, and date block as a random factor. This was followed by individual LMERs using the same variables to examine each diet item separately.

1.2 Consumption amount and efficiency

I used a long-term foraging study (June 2012 – August 2012) to simultaneously assess how claw loss influences the amount of food consumed and whether one-clawed stone crabs become more efficient at foraging over time. I collected a total of nineteen crabs from North Inlet estuary (Table 1). These crabs were divided into five different 5-mm size classes and were each fed mussels (*Geukensia demissa*) *ad libitum* until
declawing. At the start of the experiment (June 4th, 2012), I declawed 14 of the 19 crabs. Five crabs, one from each size class, were not declawed and served as control crabs in the experiment. Both sexes were represented in each 5-mm size class, and both sexes were included in both one (7 males, 7 females) and two clawed treatments (2 males, 3 females). I replaced any crabs that perished from claw removal within the first four weeks of the experiment (n = 3) using new crabs collected from the field. Three crabs died following the initial four week period and were frozen for analyses, but were not replaced.

I provided all crabs with a diet of five live ribbed mussels (*Geukensia demissa*) daily. The mussels used in the experiment ranged from 55 to 75 mm in length and were scaled with respect to crab size classes. The mussels provided to each crab were consistent within 1 mm for the duration of the experiment. I measured the length of all mussels provided and used the length of each mussel to calculate the predicted initial dry weight with a separately-determined linear regression ($r^2 = 0.6527$, Figure 3). I marked each mussel with a small dot of nail polish to distinguish individual mussels. Fragments of consumed mussels were dried daily at 60 °C for 24 hours to determine the post-consumption dry weight.

For each day in the experiment I recorded the total number of mussels cracked. Additionally, I calculated the total amount of tissue consumed (predicted initial dry weight (g) – post-consumption dry weight (g)) from each mussel. Using this information, I calculated the average consumption efficiency for each crab as the total mussel tissue consumed (g) divided by the total predicted dry weight (g) of the cracked mussels. By analyzing the number of mussels cracked and the average daily efficiency, I was able to
differentiate between two aspects of prey handling: the ability to crack prey items and the ability to remove tissue from prey once cracked.

![Graph](image.png)

**Figure 3** *Geukensia demissa* length (mm) to dry mass (g) collected from the intertidal salt marsh in North Inlet estuary, Georgetown, SC (n=103). The dashed line represents the generated linear regression (adj. $r^2=0.6527$, $p<0.01$).

I analyzed the number of mussels cracked and average consumption efficiency separately using linear mixed effects models (LMER in R). I removed three crabs from the analysis due to lack of consumption for seven days or more (two 1-clawed individuals and one 2-clawed individual). Removing these individuals from the analysis did not influence the qualitative trends in the data. However, removal of these crabs reduced overall variation. Environmental variables (temperature, salinity) and crab characteristics (number of claws, days in the experiment, size-class, and sex) were included in the initial analysis as predictor variables, and crab identification number was used as the random factor to account for daily repeated measurements. I used backwards model selection (until all parameters included were significant), and AIC values to determine the best-
fitting models. This analysis for the daily number of mussels cracked resulted in two models that were not distinguishable (parameter estimates were within 2 AIC values) from the model with only significant parameters remaining. I therefore used full model averaging (using AIC parameter weights of all generated models) to estimate the final model parameter values.

2. Energy Storage prior to Reproduction

The commercial Florida stone crab fishing season is open from October 15\textsuperscript{th} to May 15\textsuperscript{th}, which results in female crabs being declawed prior to the next reproductive season (Figure 2). Crabs that lose a claw may preferentially allocate energy into storage, in preparation for replacing the missing claw, rather than allocating energy to reproductive development. To determine if energetic storage of female crabs differed over winter between one and two-clawed individuals, I conducted a simple experiment from December 2011 to April 2012 within an indoor recirculating aquarium at the University of South Carolina. I collected a total of 22 female crabs from North Inlet estuary (Table 1) and paired them based on CW to control for any size effects. After a two week acclimation period, I removed the larger, crusher claw from one crab in each pair. Three individuals died immediately following claw loss and were not analyzed further. I fed the 19 remaining crabs (11 two-clawed, 8 one-clawed) a diet of crushed ribbed mussels (\textit{Geukensia demissa}, collected from the salt marsh in North Inlet) twice per week and removed the mussel remains after 24 hours. The temperature of the aquaria mimicked daily coastal water temperatures (determined by temperature readings of the Oyster Landing water quality station in North Inlet Estuary) and ranged between 10 and 24 °C over the course of the experiment. I maintained salinity between 32-37. Excess
protein in the recirculating aquarium was removed with a protein skimmer and I also exchanged approximately five gallons of the aquaria water biweekly to regulate water quality. Crabs were maintained in these conditions for a total of 119 days (17 weeks). Crabs that died after the first week of the experiment (two 1-clawed, one 2-clawed) were frozen for later analyses.

At the conclusion of the experiment, I removed the ovaries and hepatopancreas from each crab by dissection and determined the dry weight of each of these organs and of the total crab after drying to constant weight at 70 °C. I then determined the hepatosomatic index (HSI) and gonadosomatic index (GSI) for each crab. These two indices represent the proportion of the body weight allocated to the hepatopancreas (HSI, energy storage) and to the gonads (GSI, reproductive investment) (Kennish 1997, Griffen et al. 2011). Claw weights were not included in the HSI or GSI calculations to allow for accurate comparisons between one- and two-clawed treatments and to avoid variation resulting from any potential previous claw loss and regeneration. I conducted a separate analysis of covariance (ANCOVA) for HSI and GSI, with number of claws (one or two claws) as the factor, the number of days that individual crabs were in the experiment (to account for crabs that died during the experiment, n=3) and CW as covariates.

3. Energetic Requirements of Claw Replacement

Limb regeneration is an energetically demanding process, requiring up to 56% of total energy available for growth in some species (Vitt et al. 1977). The reallocation of energy to limb regeneration can greatly limit the energy available for growth and reproduction (Juanes and Smith 1995, Maginnis 2006). I used calorimetry to determine the energetic cost of claw regeneration by calculating the energy necessary to regenerate
a crusher claw to full pre-autotomy size, assuming that the energy required to regrow a claw is equivalent to the energy content of the claw itself. This is a conservative assumption if claw loss causes long term stress that elevates resting metabolic rates. I only considered the regenerated muscle tissue of the claw in the following calculations, as crabs must regenerate exoskeleton material annually during molts (Williams et al. 2009) regardless of claw-loss.

I determined the energetic content of crab claw muscle tissue (kJ g\(^{-1}\)) using a Parr 6725 micro oxygen-bomb calorimeter and using triplicate subsamples of muscle tissue (0.024 ± 0.002 g) from the minor claw of 10 crabs (I am assuming that crabs initially regenerate a cutter claw (Savage and Sullivan 1978)). There was no trend in energetic content (kJ g\(^{-1}\)) of muscle tissue with CW (adj. \(r^2 = 0.179, p = 0.1295\)), so an average value (17.5 ± 1.9 kJ g\(^{-1}\)) was used in further calculations.

The mass of crusher muscle (g) was determined as a power function of CW (Mass (g) = 6.022×10\(^{-7}\) CW\(^{3.55}\), \(r^2=0.556\)). The energetic content of the muscle tissue (kJ g\(^{-1}\)) was multiplied by crusher mass (g) to determine total energetic investment (kJ) required by claw regeneration to full pre-autotomy size.

4. Energetic Requirements of Reproduction

The amount of energy used to regenerate a claw must be re-allocated from reproduction or growth. In Florida stone crabs, previous studies have demonstrated that growth per molt decreases during claw regeneration (measured by CW increase: Savage and Sullivan 1978, Sullivan 1979), indicating that some of this energy may be re-allocated from growth. However, following the simple dynamic energy budget framework presented above, I assumed that all energy will be reallocated first from
reproduction, and that reduced growth will only occur if energy requirements exceed those that can be met by reducing reproduction. To determine the reduction in fecundity that may be expected due to claw regeneration, I determined the energetic content of Florida stone crab eggs and scaled the energy needed for claw regeneration to the number of eggs forfeited, using the energy content of claw muscle determined in part 3 above, as follows.

I first determined the energy content (kJ g⁻¹) of field collected egg masses (n=13, run in triplicate) using the calorimetry methods described in the previous section. There was no trend in energetic content (kJ g⁻¹) of egg tissue with CW (adj. r² < 0.001, p=0.7864), so an average value (25.8 ± 0.774 kJ g⁻¹) was used in further calculations. I subsequently determined the number of eggs in a given egg mass (g) from the same crabs. However, I did not use eggs from three of these crabs due to degradation of the eggs. I dried the eggs from the remaining 10 samples for 72 hours at 65 °C, and counted the number of eggs in a pre-weighed sample (approximately 2 mg) of egg tissue by moistening the eggs, placing the samples onto a gridded counter plate, and counting the eggs under a dissecting scope. I then divided the mass of the eggs (no. eggs g⁻¹) by the energetic content of the eggs (kJ g⁻¹) to yield the number of eggs per kJ of energy. There was no trend in the number of eggs per kJ with CW (adj. r² < 0.001, p=0.900), so an average value (4469 ± 418 eggs kJ⁻¹) was used in further calculations. To calculate the number of eggs that crabs will forfeit to regenerate a crusher claw, I multiplied the average number of eggs per kJ of egg tissue by the energy required to regenerate crusher muscle tissue (kJ).
I also estimated the number of eggs forfeited when additionally accounting for decreased consumption as determined in Part 1 above. To do this, I first estimated the amount of energy consumed by one and two clawed crabs daily for mussels (used in this study) or oysters (common prey consumed in the natural environment, Menzel & Hopkins 1955). I used laboratory-based consumption rates for mussels and oysters, as field consumption rates available in the literature were usually confounded with other factors (i.e. disproportionately small prey provided: O’Connor et al. 2008, or multiple prey types provided: Macreadie et al. 2011). The estimated number of mussels and oysters consumed daily for two-clawed individuals was 2.7 day$^{-1}$ (present study) and 3.2 day$^{-1}$ (Brown and Haight 1992) respectively. I assumed that one-clawed individuals of all CW suffer the same foraging limitation seen in this study (47%, with no increasing trend over time, see Results) for both mussels and oysters. Thus, the number of mussels or oysters consumed daily was decreased by 47% for one-clawed crabs. I determined the daily energy consumed (kJ) of each prey type by multiplying the daily consumption of mussel or oyster mass (g) by the energetic content (kJ g$^{-1}$) of its tissue. I also estimated the energetic consumption needed to meet basic metabolic demands, and compared this to the energy consumed by two and one-clawed individuals.

Next, to demonstrate the reproductive consequences of decreased consumption, I converted the annual energetic loss due to reduced consumption of one-clawed individuals to its energetic equivalent in eggs. I calculated this by multiplying the average number of eggs per kJ, as described in the preceding paragraph, by the amount of energy one-clawed crabs will not be able to consume over one year following claw removal (consumption of two-clawed crabs minus the consumption of one-clawed crabs). I used a
period of one year because this is approximately the length of time from the opening of
the fishing season until the end of the next spawning season.
RESULTS

1. Energy Intake

1.1 Diet Choice

The amount of non-bivalve prey (Ulva spp., Gracilaria spp., and Hymeniacidon heliophila) consumed by all crabs was small (Figure 4). Some H. heliophila tissue was lost over the course of the study, but this loss was primarily due to tissue decomposition in some replicates and was not greater than the tissue lost in the crab-free controls (glm, $p=0.390$). Additionally, consumption of Mercenaria mercenaria was very low. One-clawed crabs consumed significantly less of the overall provided diet than two-clawed crabs (multivariate lmer, estimated effect of claw removal ± 1 SE -0.214 ± 0.0935, $t = -2.292, p = 0.029$). Analyses of individual prey types revealed that single clawed crabs consumed significantly less G. demissa tissue (lmer, -0.298 ± 0.133, $t = -2.231, p = 0.033$) and C. virginica tissue (lmer, -0.231 ± 0.089, $t = -2.604, p = 0.0137$) than two-clawed crabs. However, there was no difference between one and two clawed crabs for the very minor consumption of Mercenaria mercenaria (-0.055 ± 0.0595, $t = -0.929, p=0.360$), Ulva spp. (-0.01 ± 0.002, $t = -0.495, p=0.624$), Gracilaria spp. (0.00 ± 0.035, $t = -0.004, p=0.997$), or H. heliophila tissue (-0.022 ± 0.031, $t = -0.718, p=0.478$). Sex and carapace width had no influence on consumption of any of these prey types ($p > 0.2$ in all models).
Figure 4 The average consumption of provided diet species (wet mass (g)) for one (n=19) and two clawed (n=17) crabs during the diet choice experiment (mean ± SE).
1.2 Consumption amount and efficiency

The number of mussels consumed and the average consumption efficiency varied daily over the course of the experiment (Figure 5). Single clawed crabs cracked fewer mussels than two-clawed crabs (estimated effect of claw removal = -0.8214, Table 2 & Figure 5A) for the duration of the experiment. On average, single-clawed Florida stone crabs cracked 47% fewer mussels than two-clawed crabs (Figure 6). Average daily temperature (estimated effect of average daily temperature = 0.0168) and size class (estimated effect of size class = 0.1212) positively influenced the number of mussels cracked daily, though their influence was low in comparison to claw removal. The number of days in the experiment (to account for crabs introduced on different dates), average salinity, and sex had little influence on the number of mussels cracked (Table 2). There was no increase in the number of mussels cracked over the course of the experiment for one or two clawed crabs (estimated effect size of days since experiment start < 0.0001). The average daily consumption efficiency of cracked mussels showed minor increases over the course of the experiment (estimated effect of days in experiment ± 1 SE = 0.0007 ± 0.0002, t = 3.599, p< 0.001, Table 2 & Figure 5B). These minor increases were likely driven by environmental factors (estimated effect of average daily salinity ± 1 SE = 0.006 ± 0.002, t = 2.629, p = 0.009), as there was no difference between increases in average daily efficiency seen for one and two clawed crabs (claw number not present in the final model based on AIC).
Table 2 Linear mixed effect models (LMER in R) selected by AIC for the number of mussels cracked (full model average) and average daily efficiency over the course of the consumption experiment (section 1.2). The reference state for claw was two-clawed individuals and the reference state for sex was female. Asterisks indicate significant factors in the final model (included only significant parameters).

<table>
<thead>
<tr>
<th>Model</th>
<th>Intercept</th>
<th>Days Since Start</th>
<th>Days in Exp.</th>
<th>Average Temp</th>
<th>Average Salinity</th>
<th>Claw</th>
<th>Size Class</th>
<th>Sex</th>
</tr>
</thead>
<tbody>
<tr>
<td>Number Cracked</td>
<td>0.2580*</td>
<td>-0.0007</td>
<td>0.0007</td>
<td>0.0168</td>
<td>-0.0003</td>
<td>-0.8214*</td>
<td>0.1212</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>Average Daily Efficiency</td>
<td>-0.1088</td>
<td>0.0007*</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>0.0056*</td>
</tr>
</tbody>
</table>


Figure 5 A) The average number of ribbed mussels cracked by one and two clawed crabs and B) the average daily consumption efficiency of cracked mussels for one (n=12) and two clawed crabs (n=4) over the duration of the summer consumption amount and efficiency experiment initiated on June 4th, 2012 (section 1.2). Error bars represent standard error.
Figure 6 The average number of mussels cracked per day for one (n=12) and two (n=4) clawed crabs (mean ± SE) for the duration of the consumption and efficiency experiment (11 weeks).
2. Energy Storage prior to Reproduction

Energy was not preferentially reallocated to energy storage following claw loss. Specifically, there was no difference in the HSI of one-clawed (mean ± SD = 0.045 ± 0.012) and two-clawed (0.0421 ± 0.023) female crabs (ANCOVA, F1,17 = 0.099, p = 0.757, Figure 7) held over winter. There was also no difference in the GSI of one (0.015 ± 0.008) or two clawed (0.021 ± 0.017) female crabs over winter ( F1,17 = 0.664, p = 0.426). Carapace width and days in the experiment did not influence crab HSI (both p > 0.15) or GSI (p > 0.16).

Figure 7 Boxplot of the final hepatosomatic index (HSI) and gonadosomatic index (GSI) for the energy storage prior to reproduction experiment. The medians are represented as the horizontal line, with boxes representing 25% and 75% quartiles. Whiskers reflect 95% CI. Two-clawed crabs (n=11) are represented by white bars, and one-clawed crabs (n=8) are represented by grey bars.
3. Energetic Requirements of Claw Replacement

The energy required to regenerate crusher claw muscle tissue to full pre-autotomy size increased as a power function of CW (Energy (kJ) = 1.05×10^{-5} CW^{3.545}, Figure 8), causing the energy required for regeneration to be much greater for large, reproductive crabs.

**Figure 8** The amount of energy required by claw regeneration to full pre-autotomy size for female Florida stone crabs.
4. Energetic Requirements of Reproduction

The number of eggs forfeited while regenerating a crusher claw increased as a power function of CW (Figure 9). The amount of eggs lost by small crabs was relatively limited. However, large crabs (greater than 100 mm CW) will lose the amount of energy necessary to spawn over 500,000 eggs. However, while these energetic effects of claw regeneration are substantial, they are dwarfed by much larger impacts of persistent diet reductions. Specifically, the amount of energy lost due to persistent decreased consumption (47% reduction reported here) was approximately 90 times greater than energetic costs of claw regeneration alone (Figure 10). This resulted in an estimate of nearly 70 million eggs forfeited due to decreased consumption over a single year – an amount that greatly exceeds the total annual reproductive potential of this species (Ros et al. 1982).

The amount of energy consumed by two-clawed crabs daily via mussel (73.2 kJ day\(^{-1}\)) or oyster tissue (88.2 kJ day\(^{-1}\), Table 3) exceeds the amount of energy needed to meet basic metabolic demands (70.6 kJ day\(^{-1}\), Table 4). However, when consumption is decreased to the extent demonstrated in this study (47%), crabs will be highly limited energetically by consuming only either mussel (38.8 kJ day\(^{-1}\)) or oyster tissue (46.8 kJ day\(^{-1}\), Table 3).
Figure 9 The number of eggs forfeited (solid line) due to claw regeneration for the carapace width (CW) range of reproductive female crabs (60 + mm CW) based on dynamic energy budget theory. The dashed lines represent ± 1 SD.
Figure 10 The average number of eggs forfeited for single-clawed, legal-sized female Florida stone crabs (84 + mm CW) during claw regeneration and various levels of decreased oyster consumption, assuming all energy is first drawn from reproduction. The dashed line indicates a generalized estimate of yearly reproductive output for legal sized female stone crabs (2 million eggs yr\(^{-1}\), based on Ros et al. 1982 and Porter 1960), and values that fall above this dashed line reflect energetic costs that exceed yearly reproductive output.
Table 3: Calculations of the daily number of mussels and oysters consumed for two and one-clawed crabs and their energetic equivalent, assuming a 47% reduction in consumption.

<table>
<thead>
<tr>
<th></th>
<th>Two-Clawed</th>
<th>One-Clawed</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>percent consumption</strong></td>
<td>(100%)</td>
<td>(53%)</td>
<td>present study</td>
</tr>
<tr>
<td><strong>mussels</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>number consumed</td>
<td>2.74</td>
<td>1.45</td>
<td>present study</td>
</tr>
<tr>
<td>dry mass of mussel tissue</td>
<td>1.46 (g)</td>
<td>1.46 (g)</td>
<td>Franz 1993</td>
</tr>
<tr>
<td>energy of mussel tissue</td>
<td>18.3 (kJ g(^{-1}))</td>
<td>18.3 (kJ g(^{-1}))</td>
<td>McKinney et al. 2004</td>
</tr>
<tr>
<td>energy consumed daily</td>
<td>73.2 (kJ day(^{-1}))</td>
<td>38.8 (kJ day(^{-1}))</td>
<td></td>
</tr>
<tr>
<td><strong>oysters</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>number consumed</td>
<td>3.2</td>
<td>1.70</td>
<td>Brown and Haight 1992</td>
</tr>
<tr>
<td>dry mass of oyster tissue</td>
<td>1.39 (g)</td>
<td>1.39 (g)</td>
<td>Dame 1972</td>
</tr>
<tr>
<td>energy of oyster tissue</td>
<td>19.8 (kJ g(^{-1}))</td>
<td>19.8 (kJ g(^{-1}))</td>
<td>Krishnamoorthy et al. 1978</td>
</tr>
<tr>
<td>energy consumed daily</td>
<td>88.2 (kJ day(^{-1}))</td>
<td>46.8 (kJ day(^{-1}))</td>
<td></td>
</tr>
</tbody>
</table>
Table 4 Calculations used to determine energy intake needed daily (in the number of mussels and oysters) for an median sized legal female Florida stone crab (102 mm CW, Gerhart and Bert 2008).

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Value</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>energy needed daily (kJ)</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>basic metabolic rate</td>
<td>$8.5 \times 10^{-6} \text{ (L O}_2\text{ g}^{-1}\text{ min}^{-1})$</td>
<td>Ayers 1938</td>
</tr>
<tr>
<td>× mass of crab</td>
<td>284 (g)</td>
<td>Sullivan 1979</td>
</tr>
<tr>
<td>× conversion to energy</td>
<td>20.3 (kJ L O$_2$^{-1})</td>
<td>used in Hughes &amp; Goldman</td>
</tr>
<tr>
<td>= energy per min</td>
<td>0.049 (kJ min$^{-1}$)</td>
<td>1970</td>
</tr>
<tr>
<td>= or energy per day</td>
<td>70.6 (kJ day$^{-1}$)</td>
<td></td>
</tr>
<tr>
<td><strong>convert to mussels needed daily</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>energy content of mussel tissue</td>
<td>18.3 (kJ g$^{-1}$)</td>
<td>McKinney et al. 2004</td>
</tr>
<tr>
<td>÷ dry mass of mussel (64.5 mm)</td>
<td>1.46 (g)</td>
<td>size: present study</td>
</tr>
<tr>
<td>= mussels</td>
<td>2.64 (day$^{-1}$)</td>
<td>mass: Franz 1993</td>
</tr>
<tr>
<td><strong>convert to oysters needed daily</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>energy content of mussel tissue</td>
<td>19.8 (kJ g$^{-1}$)</td>
<td>Krishnamoorthy et al. 1978</td>
</tr>
<tr>
<td>÷ dry mass of oyster (47.5 mm)</td>
<td>1.39</td>
<td>size: Rindone &amp; Eggleston</td>
</tr>
<tr>
<td>= oysters</td>
<td>2.56 (day$^{-1}$)</td>
<td>2011</td>
</tr>
<tr>
<td></td>
<td></td>
<td>mass: Dame 1972</td>
</tr>
</tbody>
</table>
DISCUSSION

Energy Intake

The results of this study indicate that Florida stone crabs drastically reduce energy intake following claw removal. Some crab species change their diet to include more plant material following claw loss (Juanes and Smith 1995), and previous studies have suggested that Florida stone crabs consume algal or plant material (Bender 1971). Additionally, crabs may be able to compensate for decreased consumption of preferred prey prior to claw regeneration by altering their foraging strategy to include other animal prey types (i.e. polychaetes, gastropods, fish or bivalve remains) or smaller prey. Patterson et al. (2008) found that single clawed Cancer pagurus consumed more fish and fewer bivalves following claw loss, demonstrating that crabs will primarily consume their preferred prey, but may consume other prey out of necessity following claw loss. Using a limited set of alternative foods available in intertidal areas of South Carolina (algae and sponges) I did not observe any diet switching in this study. Similarly, I have not noticed diet switching in gut content analyses of field collected one-clawed crabs (Hogan, unpub. data).

Though one-clawed crabs did not alter their diet following claw removal, I found that these crabs consumed approximately 47% fewer mussels following claw loss, with no increasing trend over 77 days (Figures 5 & 6). I found that the main barrier to bivalve consumption was the initial cracking phase, presumably due either to mechanical
limitation of the remaining cutter claw (Cheung 1976) or simply to reduced handling capabilities with a single claw. After cracking the mussels, both one and two clawed crabs were able to remove bivalve tissue equally (Figure 5B). This suggests that single-clawed crabs are just as efficient in manipulating soft tissue as two-clawed crabs, which is likely because Florida stone crabs commonly use their walking legs to manipulate prey (Savage and Sullivan 1978). It is possible that this level of reduced consumption will continue until the next molting event when a new claw is regenerated (approximately one year), and could greatly limit the energy available for both reproduction and growth during claw regeneration. Decreased consumption may also extend beyond the initial regenerative molt due to the reduced size of the regenerated claw, as demonstrated by Elner (1980) for *Carcinus maenas*; but the primary energetic costs of changes in foraging are likely to occur prior to the initial claw regeneration. In areas where it is a legal practice to remove both claws from legal sized crabs (i.e., Florida), harvested crabs will be completely dependent on foraging with their walking legs, which may further intensify foraging limitation.

Reproductive Consequences of Claw Loss

I found no evidence that single clawed Florida stone crabs preferentially allocate energy to storage prior to the reproductive season (Figure 7). This indicates that crabs do not accumulate additional energetic stores in preparation for claw regeneration, and also means that crabs will draw upon the same energy store for both reproduction and claw regeneration. Thus, following simple dynamic energy budget theory (Figure 1) the energy available for reproduction is likely to be decreased by (at a minimum) the energy required to regenerate a claw.
The energetic content of Florida stone crab muscle tissue determined in this study (17.5 kJ g\(^{-1}\)) was similar to that of previous research (18.8 kJ g\(^{-1}\); Sushchenya and Claro 1970). I found that reproductive female stone crabs will lose the energy to produce over 500,000 eggs (Figure 9) during claw regeneration. Very large crabs will be impacted to a much greater extent, losing the energy to generate over one million eggs at 120 mm CW. Though reduced fecundity because of claw regeneration in Florida stone crabs has not been quantified, other crab species have been demonstrated to decrease their reproductive output following claw loss (reviewed in Juanes and Smith 1995). For example, the brood size of field collected velvet swimming crabs (Necora puber) was approximately 45% less for crabs missing limbs (Norman and Jones 1987), confirming that the reproductive consequences for crustaceans of missing a limb are high.

Though the decrease in the amount of energy available for reproduction due to the energetic demands of claw regeneration is substantial, this cost is small relative to the persistent cost of reduced consumption over an annual basis prior to claw regeneration (Figure 10). If crabs in the field do not compensate for decreased bivalve consumption by altering their foraging, they will lose much more energy than is generally allocated to reproduction (approximately 30 times more). For example, if I consider only a 1% decrease in consumption (much less than the 47% observed here), including both this energy reduction and the energy required by claw regeneration together, Florida stone crabs will have little to no energy left for reproduction (Figure 10). This conclusion is conservative in that it could be exacerbated by imperfect assimilation efficiency of consumed food.
If the amount of energy lost due to decreased consumption or claw regeneration is greater than the amount of energy allocated towards reproduction (30 times more in the present study), the energy available for growth and maintenance is also likely to be decreased. This appears to commonly be the case for Florida stone crabs, as field-collected crabs regenerating a single claw grow 11% less than crabs with two normal sized claws, and crabs regenerating two claws grow 31% less (Savage and Sullivan 1978). This decreased annual growth further decreases reproductive output in future years since Florida stone crabs, similar to most crab species, have size-dependent fecundity (Hines 1982, Ros et al. 1982). All of these factors make it unlikely that harvested Florida stone crabs, especially crabs with both claws harvested, will contribute to reproduction and population growth.

Conclusions

Decreased consumption, a lack of energy stores, and reallocating energy to claw regeneration will limit the energy available for growth and reproduction of Florida stone crabs regenerating a claw. The extent of the energetic constraint will depend on many factors, including the number of claws removed, crab size, and the degree of decreased consumption. If the energetic demands of decreased consumption and claw regrowth are even a fraction the size of those measured here, it is likely that harvested crabs will have little to no energy available to reproduce. Thus, the mismatch of increasing energetic demands for claw regrowth while simultaneously reducing energy intake through lowered feeding rates would appear to be an unsustainable combination. Though I have only considered one-clawed crabs in this study, harvesting both claws is legal in Florida, and crabs with both claws harvested are likely to be impacted to a much greater extent by
further reductions in foraging ability and increased predation risk. This, in addition to the much higher injury-related mortality rate of individuals with both claws harvested (47%, Davis et al. 1978), makes it unlikely that these crabs will survive to reproduce. Further, mating is competitive in Florida stone crabs (Wilber 1989) making it unlikely that clawless male crabs will be able to successfully compete for mates. All of the above factors are likely to contribute to consistently low catch per unit effort even though fishery pressure is declining (Muller et al. 2011). It is essential that resource managers continue to evaluate fishery regulations to ensure fishery stocks will not be depleted by present day fishing methods. As in most fisheries, sustainability is a hard goal to achieve and maintain, and will require much more research to ensure the existence of this fishery for future generations.

**Future Directions**

More research is needed to determine possible ways of improving current fishery regulations in order to maximize the fishing potential of the Florida stone crab population while ensuring its persistence. The following data are needed to assess the implications of Florida stone crab fishery-related claw loss on a population scale. First, researchers need to determine how long-term foraging changes influence Florida stone crab energetics. It is particularly important that researchers determine the magnitude and duration of decreased bivalve consumption under natural conditions, and determine if crabs switch their foraging strategy to compensate for this. Second, by generating a simple matrix model (Appendix A), I found that juveniles may play a large role in sustaining the fishery. However, data on juvenile Florida stone crabs in the field is currently lacking. We need to determine the extent of brood loss, larval mortality vs. larval recruitment, and the mortality of juveniles
in the field to better understand overall population dynamics. Finally, we need to know more about the mortality of harvested individuals. Instantaneous mortality of Florida stone crabs experiencing claw removal in the laboratory is relatively low (single claw removal: 34% in the present study, 28% in Davis et al. 1978; double claw removal: 47% in Davis et al. 1978), however, mortality in the field is likely to be much higher due to long term metabolic costs due to foraging difficulty and increased predation risk. If survivorship (or reproduction) after claw removal in the field is low, then this fishery practice may be equivalent to simply removing those individuals from the population.
REFERENCES


Sushchenya, L.M & R. Claro. (1970). Quantitative regularities of feeding and their connection with the balance of energy of the commercial crab *Menippe mercenaria* (Say). Published for Smithsonian Institute and Natural Science Foundation by the Indian Natural Science Document Center, New Delhi, India, pp. 292-310.


APPENDIX A

Matrix Model

The strict regulations of the Florida stone crab fishery were designed to minimize the influence of the fishery on the harvested population. However, it is still unclear how the current fishery regulations influence overall stone crab population dynamics. To evaluate how claw loss influences overall population dynamics, I generated a simple Lefkovitch matrix model for the Florida stone crab population using data available in the literature (Table A.1) and from the present study. Matrix models have been used to successfully evaluate the management strategies for a variety of systems. One primary example of this is a paper written by Crouse, Crowder and Caswell (1987) that used a Lefkovitch (or stage-based) matrix model to analyze conservation practices for the loggerhead turtle population. Through the use of their generated model, the authors determined that conservation practices were misguided and suggested that conservationists needed to re-evaluate their management approaches. Following the framework provided in their paper, and the equations provided in Caswell (1989), I developed a Lefkovitch matrix model (Figure A.1) and used this model to directly evaluate how claw loss influences population dynamics.
Table A.1 Parameters used in the Lefkovitch Matrix model and their numerical value used in the present study.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Value</th>
<th>Definition</th>
<th>Used in</th>
<th>References</th>
</tr>
</thead>
<tbody>
<tr>
<td>$\sigma_l$</td>
<td>0.0001</td>
<td>larval survival</td>
<td>$F_{(all)}$</td>
<td>Thorson 1946, McConaugha 1992</td>
</tr>
<tr>
<td>$\sigma_j$</td>
<td>0.09</td>
<td>juvenile survival</td>
<td>$P_{j}, G_{j}$</td>
<td>estimate (expected to be low: Bert et al. 1978)</td>
</tr>
<tr>
<td>$\sigma_{sl}$</td>
<td>0.704</td>
<td>sub-legal survival</td>
<td>$P_{sl}, G_{sl}$</td>
<td>Bert et al. 1986</td>
</tr>
<tr>
<td>$\sigma_{l1}$</td>
<td>0.704</td>
<td>small legal survival</td>
<td>$P_{l1}, G_{l1}$</td>
<td>Bert et al. 1986</td>
</tr>
<tr>
<td>$\sigma_{l2}$</td>
<td>0.601</td>
<td>large legal survival</td>
<td>$P_{l2}$</td>
<td>Bert et al. 1986, Restrepo 1989</td>
</tr>
<tr>
<td>$T_j$</td>
<td>2</td>
<td>duration of juvenile stage</td>
<td>$P_{j}, G_{j}$</td>
<td>Gerhart and Bert 2008</td>
</tr>
<tr>
<td>$T_{sl}$</td>
<td>2</td>
<td>duration of sub-legal stage</td>
<td>$P_{sl}, G_{sl}$</td>
<td>Gerhart and Bert 2008</td>
</tr>
<tr>
<td>$T_{l1}$</td>
<td>2</td>
<td>duration of small legal stage</td>
<td>$P_{l1}, G_{l1}$</td>
<td>Gerhart and Bert 2008</td>
</tr>
<tr>
<td>$T_{l2}$</td>
<td>2</td>
<td>duration of large legal stage</td>
<td>$P_{l2}$</td>
<td>Gerhart and Bert 2008</td>
</tr>
<tr>
<td>$C_{Wj}$</td>
<td>30</td>
<td>average carapace width of juveniles</td>
<td>$F_{j}$</td>
<td>Gerhart and Bert 2008</td>
</tr>
<tr>
<td>$C_{Wsl}$</td>
<td>72</td>
<td>average carapace width of sub-legals</td>
<td>$F_{sl}$</td>
<td>Gerhart and Bert 2008</td>
</tr>
<tr>
<td>$C_{Wl1}$</td>
<td>89.5</td>
<td>average carapace width of small legals</td>
<td>$F_{l1}$</td>
<td>Gerhart and Bert 2008</td>
</tr>
<tr>
<td>$C_{Wl2}$</td>
<td>107.5</td>
<td>average carapace width of large legals</td>
<td>$F_{l2}$</td>
<td>Gerhart and Bert 2008</td>
</tr>
<tr>
<td>$b_l$</td>
<td>0.8</td>
<td>brood survival</td>
<td>$F_{(all)}$</td>
<td>Kuris 1991</td>
</tr>
<tr>
<td>$b$</td>
<td>4</td>
<td>egg batches</td>
<td>$F_{(all)}$</td>
<td>Porter 1960</td>
</tr>
<tr>
<td>$r$</td>
<td>0.72</td>
<td>regenerative survival claw loss probability of juveniles</td>
<td>$P_{j}$</td>
<td>Davis 1978</td>
</tr>
<tr>
<td>$p_{jl}$</td>
<td>0.12</td>
<td>claw loss probability of sub-legal</td>
<td>$P_{sl}$</td>
<td>Wilber 1995</td>
</tr>
<tr>
<td>$p_{l1}$</td>
<td>0.12</td>
<td>claw loss probability of small legal</td>
<td>$P_{l1}$</td>
<td>Sullivan 1979</td>
</tr>
<tr>
<td>$p_{l2}$</td>
<td>0.185</td>
<td>claw loss probability of large legal</td>
<td>$P_{l2}$</td>
<td>Sullivan 1979</td>
</tr>
<tr>
<td>$R_{j}$</td>
<td>0.718</td>
<td>Length of regenerative claw for juveniles (% of original)</td>
<td>$d$</td>
<td>Savage and Sullivan 1978</td>
</tr>
<tr>
<td>$R_{sl}$</td>
<td>0.718</td>
<td>Length of regenerative claw for sub-legals (% of original)</td>
<td>$d$</td>
<td>Savage and Sullivan 1978</td>
</tr>
<tr>
<td>$R_{l1}$</td>
<td>0.647</td>
<td>Length of regenerative claw for small legals (% of original)</td>
<td>$d$</td>
<td>Savage and Sullivan 1978</td>
</tr>
<tr>
<td>$R_{l2}$</td>
<td>0.647</td>
<td>Length of regenerative claw for large legals (% of original)</td>
<td>$d$</td>
<td>Savage and Sullivan 1978</td>
</tr>
<tr>
<td>$Cal_{Exo}$</td>
<td>3773.0</td>
<td>Calories in exoskeleton tissue</td>
<td>$d$</td>
<td>present study</td>
</tr>
<tr>
<td>$Cal_{Mus}$</td>
<td>4179.3</td>
<td>Calories in muscle tissue</td>
<td>$d$</td>
<td>present study</td>
</tr>
<tr>
<td>$Cal_{Egg}$</td>
<td>6174.6</td>
<td>Calories in egg tissue</td>
<td>$d$</td>
<td>present study</td>
</tr>
<tr>
<td>Calcium%</td>
<td>0.822</td>
<td>Percent Calcium in exoskeleton</td>
<td>$d$</td>
<td>present study</td>
</tr>
<tr>
<td>Cu&lt;sub&gt;me&lt;/sub&gt;</td>
<td>0.206</td>
<td>ratio of muscle to exoskeleton tissue for the cutter claw</td>
<td>$d$</td>
<td>present study</td>
</tr>
<tr>
<td>Cr&lt;sub&gt;me&lt;/sub&gt;</td>
<td>0.202</td>
<td>ratio of muscle to exoskeleton tissue for the crusher claw</td>
<td>$d$</td>
<td>present study</td>
</tr>
<tr>
<td>$\lambda$</td>
<td>1.00</td>
<td>initial estimate of lambda</td>
<td>$\lambda$</td>
<td></td>
</tr>
</tbody>
</table>
Since most factors relating to crab growth, reproduction, and survival are size related (rather than age related) I distributed the model into four stages that had common characteristics. The stages included in the model were juveniles, sub-legal adults (reproductively mature crabs that are not yet harvestable size), small legal adults and large legal adults (Table A.2).

**Table A.2** Stages and corresponding size and age ranges incorporated into the matrix model (based on Gerhart and Bert 2008).

<table>
<thead>
<tr>
<th>Stage</th>
<th>Carapace width (mm)</th>
<th>Age (years)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Juveniles</td>
<td>0 to 60</td>
<td>0 to 2</td>
</tr>
<tr>
<td>Sub-legal</td>
<td>61 to 84</td>
<td>2 to 4</td>
</tr>
<tr>
<td>Small legal</td>
<td>85 to 95</td>
<td>4 to 6</td>
</tr>
<tr>
<td>Large legal</td>
<td>96 to 120</td>
<td>6 to 8</td>
</tr>
</tbody>
</table>
Individuals may transition through matrix stages with the probability $G$ (survival and growth), or remain in their current stage with the probability $P$ (survival and no growth) (Figure A.1). These two parameters were estimated using stable-stage duration methods presented in Caswell 1989 (Table A.3, eqns. 1-3). I calculated the fecundity ($F$) of individuals as a function of size, using the average carapace width of each stage to calculate stage-based fecundity (Ros et al. 1981, Table A.3, eqn. 5). I incorporated claw loss into the model by generating a two state matrix, allowing individuals to transition between one and two clawed states with probabilities $p$ (claw loss) and $r$ (regeneration). The fecundity of one-clawed individuals was decreased by the reduction in fecundity ($d$) estimated from calorimetry calculations described above. I calculated a maximum and minimum value for $d$ (Table A.3). The minimum value for $d$ simply incorporated the energetic demands of claw regeneration. The maximum value for $d$ incorporated the energetic demands of claw regeneration and additional energetic costs due to decreased consumption (approximately 47%, present study). When data for *Menippe spp.* was lacking, I incorporated values for similar species into the model.

The eigenvalues of the matrix model were calculated to determine the relative growth of the population (represented by the dominant eigenvalue, lambda). Additionally, asymptotic, transient, ergodicity, and sensitivity analyses were conducted. The results of the initial sensitivity analysis indicated that juvenile survivorship was the most influential parameter. Since we do not have a good estimate on what juvenile survival is in the field, I scaled juvenile survivorship to 9%, for both the maximum and minimum reductions in fecundity models, to generate an initial lambda of one. I also conducted manual sensitivity analyses to determine the influence manipulating the
reduction in fecundity of one-clawed individuals \((d)\) and increased fishing pressure \((p)\) on the overall population growth rate. The generated Lefkovitch matrix was ergodic and approached lambda quickly (within 6 time steps). Elasticity analysis (or the proportional sensitivity) indicated that juvenile \(G\) (growth and survival) was the most important factor influencing the growth of the system. Other variables influential to the model outcome were sub-legal \(F\) (fecundity), sub-legal \(P\) (survival with no growth) and sub-legal \(G\) (growth and survival). All other parameters had an order of magnitude less of an influence on the population growth rate.

The results of these model simulations are preliminary and require much more detailed parameter estimates to be used accurately in estimating the effects of claw removal on population dynamics. However, using the current parameter estimates, decreasing the fecundity of one-clawed individuals had a limited effect on the population (generally < 0.1%). Increasing fishery pressure, while reducing fecundity of one-clawed individuals by 16%, had a stronger influence on the population dynamics (up to 6% decrease in population growth rate). Parameters that are essential to the development of this model for Florida stone crabs are brood loss, larval recruitment, juvenile survivorship, the prevalence of crab harvesting, and harvested crab fecundity and survival. Nevertheless, the use of matrix models such as this may be beneficial to fisheries managers to more thoroughly understand the impact of claw harvesting on the overall Florida stone crab population.
Table A.3 Equations used to generate parameters in the Matrix Model.

<table>
<thead>
<tr>
<th>#</th>
<th>Description</th>
<th>Equation</th>
<th>Reference</th>
</tr>
</thead>
</table>
| 1  | \( \Upsilon \)  | \[
\left( \frac{\sigma^T}{\lambda} - \frac{\sigma^{T-1}}{\lambda} \right) \\
\left( \frac{\sigma^T}{\lambda} - 1 \right)
\] | Caswell 1989, equation 4.66  |
| 2  | \( P \)         | \( \sigma (1 - \Upsilon) \)                                              | Caswell 1989, equation 4.61 |
| 3  | \( G \)         | \( \sigma \Upsilon \)                                                 | Caswell 1989, equation 4.60 |
| 4  | \( F \)         | \( f_i b P_i + f_{i+1} b P_{i+1} \)                                   | Caswell 1989, equation 4.91 |
| 5  | \( f \)         | \(-431083 + 8720 \, CW_i\)                                             | Ros et al. 1981             |
| 6  | \( DW_{Eggs} \) | \(-4.8958 + 0.1079 \, CW_i\)                                           | present study               |
| 7  | \( DW\, Cr \)   | \(0.0000797 \, L_{Cr}^{2.7839}\)                                       | present study               |
| 8  | \( L_{Cr} \)    | \(1.130 \, CW_i\)                                                    | present study               |
| 9  | \( DW_{Cu} \)   | \(0.0000328 \,(R_i \, L_{Cr})^{2.9503}\)                              | present study               |
| 10 | Regen Cals      | \( Cal_{Mus} \, DW_{Cu} \, Cu_{me} + Calcium\% \, Cal_{Exo} \, DW_{Cu} \,(1 - Cu_{me}) \) | present study               |
| 11 | Crush Cals      | \( Cal_{Mus} \, DW_{Cr} \, Cr_{me} + Calcium\% \, Cal_{Exo} \, DW_{Cr} \,(1 - Cr_{me}) \) | present study               |
| 12 | Regen Cals Net  | \( Regen \, Cals - Crush \, Cals \)                                   | present study               |
| 13 | \( d \)         | \( \frac{Cal_{Egg} - Regen \, Cals \, Net}{Cal_{Egg}} \)              | present study               |