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Fishery and Biological Characteristics of Jonah Crab (*Cancer borealis*) in Rhode Island Sound

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FISHERY AND BIOLOGICAL CHARACTERISTICS OF
JONAH CRAB (*CANCER BOREALIS*) IN RHODE
ISLAND SOUND
BY
CORINNE L. TRUESDALE

A THESIS SUBMITTED IN PARTIAL FULFILLMENT OF THE
REQUIREMENTS FOR THE DEGREE OF
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MASTER OF SCIENCE THESIS

OF

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ABSTRACT

Jonah crab (*Cancer borealis*) is a demersal crustacean distributed throughout continental shelf waters from Newfoundland to Florida. The species supports a rapidly growing commercial fishery in southern New England, where landings of Jonah crab have increased more than six-fold since the early 1990s. However, management of the fishery has lagged its expansion; the first Fishery Management Plan for the species was published in 2015 and a stock assessment has not yet been created due to a lack of available data concerning the species' life history and fishery. Fishing effort in the crab fishery is necessarily tied to fishing effort for American lobster (*Homarus americanus*), and the structure of this mixed crustacean fishery further complicates efforts to manage each of its component species.

In the first manuscript of this thesis, a fishery-dependent sea sampling protocol was developed and implemented in Rhode Island Sound to (1) describe biological characteristics of the Jonah crab in Rhode Island Sound and (2) begin to characterize catch per unit effort in the Jonah crab fishery. With these methods, seasonal patterns in carapace width frequency and sex ratios were described for the commercial trap fishery, along with biological characteristics including shell disease condition, reproductive condition and allometric growth relationships. This study provides a unique description of commercial catch before discards and provides a more comprehensive description of the population than is available with dockside sampling methods. Conducting this type of data collection across the range of the species would substantially expand available data that is considered essential for constructing a stock assessment.

The second manuscript describes growth characteristics of Jonah crab in Rhode Island Sound from data gathered during a laboratory study and via sea sampling in the commercial fishery. Description of the growth rates of exploited marine species is essential to understanding the impacts of fishing pressure on these resources and to predicting population abundances. Because crustaceans grow only during discrete molting events, description of growth per molt along with molting probabilities is necessary for estimating absolute growth rates of crustaceans. The results of this project provide characterization of growth per molt for male and female Jonah crabs along with description of molting seasonality for mature males.

This thesis provides essential knowledge concerning growth, seasonal catch patterns and basic biological description of the Jonah crab to fishery managers charged with regulating the resource. To date, knowledge of the species has been limited enough to preclude the creation of a thorough stock assessment; these results provide marked progress in meeting the data needs for such an assessment.

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PREFACE

This thesis was formatted in accordance with the manuscript format guidelines established by the Graduate School of the University of Rhode Island. The first manuscript is formatted for the journal *North American Journal of Fisheries Management*, with coauthors M. Conor McManus and Jeremy S. Collie. The second manuscript is formatted for the *Journal of Crustacean Biology*, with coauthors M. Conor McManus and Jeremy S. Collie.

TABLE OF CONTENTS

ABSTRACT	ii
ACKNOWLEDGEMENTS.....	iv
PREFACE.....	vi
TABLE OF CONTENTS.....	vii
LIST OF TABLES	ix
LIST OF FIGURES	xi
MANUSCRIPT 1.....	1
ABSTRACT	2
INTRODUCTION.....	3
METHODS	4
<i>Data Collection</i>	<i>4</i>
<i>Data Analysis.....</i>	<i>6</i>
RESULTS	7
<i>Biological Data Summary.....</i>	<i>7</i>
<i>Length-to-Weight Relationship.....</i>	<i>8</i>
<i>Fishery characteristics and catch per trap</i>	<i>8</i>
DISCUSSION	10
ACKNOWLEDGEMENTS.....	13
FUNDING	14
LITERATURE CITED	14
TABLES.....	16
FIGURES.....	21

MANUSCRIPT 2.....	29
ABSTRACT	30
INTRODUCTION.....	31
METHODS	33
<i>Molt increments.....</i>	<i>33</i>
<i>Molting seasonality</i>	<i>35</i>
<i>Commercial fishery biological sampling.....</i>	<i>36</i>
RESULTS	36
<i>Molt increments.....</i>	<i>36</i>
<i>Molting seasonality</i>	<i>37</i>
<i>Commercial fishery biological sampling.....</i>	<i>38</i>
DISCUSSION	38
ACKNOWLEDGEMENTS.....	43
FUNDING	43
LITERATURE CITED	43
TABLES.....	47
FIGURES	49

LIST OF TABLES

TABLE	PAGE
Table 1-1. Dates and Jonah crab sample sizes for commercial fishery sea sampling program.....	16
Table 1-2. Summary of females observed with sperm plugs (evidence of having recently mated), listed by sample date.....	17
Table 1-3. Most common bycatch species in traps targeting Jonah crab, listed by season. Limited to species that were encountered a minimum of three times in a fishing day. Rock crabs (<i>Cancer irroratus</i>) and American lobsters (<i>Homarus americanus</i>) were encountered throughout the fishing season.....	18
Table 1-4. Allometric growth model coefficients for males and females with 95% confidence intervals. The allometric growth power function was linearized to derive the equations listed. Both coefficients are significantly different between males and females ($p < 0.001$).....	19
Table 1-5. Estimated coefficients of linear and categorical predictors for quasi-Poisson GLM.....	20
Table 2-1. Sampling dates of monthly molt probability study. When sample dates occurred during the last 10 days of the month, data were binned into the subsequent month (for example, crabs collected on August 29 were labeled as September molts).	47
Table 2-2. Molt condition of males sampled from commercial catches, determined according to three factor scale: 1= Just molted, carapace is soft; 2=Newly molted, with brittle carapace (abdominal segments are still pliable); 3= shell hard, no evidence	

of recent molt. Percent of total number of males indicated in parentheses. Percent of total number of males indicated for each molt condition.....48

LIST OF FIGURES

FIGURE	PAGE
Figure 1-1. Map of sampling region. Crabs were collected from NMFS statistical areas 539 and 537, north of 41° N latitude and west of 71° W latitude. Specific fishing locations are not presented to protect confidentiality of data.....	21
Figure 1-2. Carapace width frequency barplots of male Jonah crabs caught in commercial fishery by sample date, binned in 10-mm size increments. Mean carapace width (mm) indicated on left side of each subplot in blue. Proportion of males caught exceeding legal minimum size indicated on right side of each subplot in dark red....	22
Figure 1-3. Carapace width frequency barplots of female Jonah crabs caught in commercial fishery by sample date, binned in 10-mm size increments. Mean carapace width (mm) indicated on left side of each subplot in blue. Proportion of crabs caught that were female is indicated in dark green on right side of each subplot.....	23
Figure 1-4. Shell disease condition for male and female Jonah crabs, 6/30/2016 to 8/4/2017. Sample sizes given within bars. Disease levels assessed on four factor scale adapted from that defined in Sindermann et al., 1989: Absent: no visible dark spots on carapace; Minor: <10% of carapace covered in dark spots; Moderate: 10-50% of carapace covered in dark spots; Severe: >50% of carapace darkened.....	24
Figure 1-5. Proportion of crabs that were female within commercial traps, calculated from all crabs that were randomly sampled within each day, 6/30/2016-8/4/2017. Proportions given above each bar.....	25
Figure 1-6. Carapace width to weight relationship for male and female Jonah crabs, plotted with fitted allometric growth models (see Table 4 for model parameters).....	26

Figure 1-7. Catch per trap of Jonah crab and lobster in trawls with a mixture of traps targeting each. “Circle vents” indicates traps configured to target Jonah crab; “Both vents” indicates traps configured to target lobster. Results plotted for 6/30/16 (N=12 crab traps, 18 lobster traps) and 8/23/16 (N=30 crab traps, 30 lobster traps).....27

Figure 1-8. Selected GLM for Jonah crab catch per trap in crab-targeting traps (model coefficients in Table 5). Model predictions plotted with observed data against lobster catch per trap to provide visualization of variance explained by the selected GLM. Red dashed line added to show isolated effect of lobster catch per trap (temperature fixed at 10 °C, soak time fixed at 6 days).....28

Figure 2-1. Map of sampling region. Crabs were collected from NMFS statistical areas 539 and 537, north of 41° N latitude and west of 71° W latitude. Specific fishing locations are not presented to protect confidentiality of data.....49

Figure 2-2. Residuals of growth per molt linear regression (mm) plotted against time in captivity before molting. Molts occurring after 30 days in the laboratory (orange points) were removed from analysis due to the low bias of these molt increments.....50

Figure 2-3. Pre-molt vs. post-molt carapace width (mm) male (blue) and female (red) Jonah crabs observed molting in the laboratory. Coefficients of the selected model ($R^2=0.96$) plotted for males and females as solid blue and dotted red lines, respectively. One-to-one replacement line provided as reference, in black.....51

Figure 2-4. Molt increments by pre-molt carapace width showing changes in growth per molt with increase in carapace width. Males are indicated in blue and females are in red, with linear regressions fitted to each sex. Linear regressions for both sexes are significantly different from zero ($p<0.05$).....52

Figure 2-5. Occurrence of ecdysis in male Jonah crabs, by size bin and month collected, September 2016 to August 2017. Orange and blue proportions indicate crabs that did and did not molt, respectively, within 30-day observation period. Sample sizes are indicated in white within each size bin.....53

Figure 2-6. Carapace width density plot of commercially-caught male (blue) and female (red) Jonah crabs in study area. Green line represents legal minimum size for commercial fishery.....54

MANUSCRIPT 1

Biological characteristics and fishery dynamics of Jonah crab (*Cancer borealis*) in Rhode Island Sound

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ABSTRACT

Jonah crab (*Cancer borealis*) supports a growing fishery in southern New England. However, management of the species has lagged its commercial popularity, and no stock assessment currently exists due to a lack of available data on Jonah crab life history and fishery dynamics. To describe inshore fishery dynamics, 13 sea sampling trips were conducted from June 2016 to August 2017 on commercial fishing vessels targeting Jonah crab in Rhode Island Sound. Jonah crab biological data, including carapace width, sex, ovigerous condition, and shell condition were recorded for 9,465 individuals caught in commercial traps. Catch composition was described for a random subset of traps within each trawl and the effects of fishery-dependent and environmental variables were analyzed with respect to Jonah crab catch per trap using generalized linear models (GLMs). Sex ratios and length frequencies of commercial catch display seasonal trends wherein females are most frequently caught in August and September and larger males are more abundant in summer and autumn months. Results of GLM analysis indicate that lobster catch, temperature, vessel effects and soak time are significant in predicting Jonah crab catch per trap. The results presented here directly contribute to a range-wide understanding of the biology of Jonah crab and characteristics of its commercial fishery, which are necessary to the creation of a stock assessment for the species. Further, this project serves as a pilot monitoring program which could be implemented to collect biological data in other regions within the species' range.

INTRODUCTION

The Jonah crab, *Cancer borealis*, is a brachyuran crustacean distributed in northwest Atlantic coastal waters (Haefner, 1977) and a significant contributor to marine trophic webs (Leland, 2002; McKay and Heck, 2008; Stehlik, 1993; Ojeda and Dearborn, 1991). Limited evidence suggests that the species migrates seasonally across the continental shelf (Jeffries, 1966; Krouse, 1980; Stehlik et al., 1991). Previous studies also found evidence of depth dependence in the size distribution of Jonah crab (Carpenter, 1978; Krouse, 1980). However, there is an overall paucity of data concerning distribution of the species including spatial and temporal dynamics (ASMFC, 2015).

Jonah crab have long been caught as a bycatch species in the American lobster (*Homarus americanus*) fishery. However, the decline of the lobster fishery in southern New England—along with the increased market demand for crab—have caused a rapid increase in targeted fishing for Jonah crab. A mixed crustacean fishery has emerged in which fishers seasonally switch between targeting lobster and Jonah crab by modifying fishing traps and changing fishing location.

The first Fishery Management Plan (FMP) for the Jonah crab fishery was published in 2015, motivated by concerns about the sustainability of this rapidly growing yet unregulated fishery. In the FMP, a legal minimum size for harvest was established for Jonah crab at 4.75” carapace width (121.65 mm). Additionally, fishing permits for Jonah crab became tied to the lobster fishery in the FMP; fishers may target and land Jonah crab only if they hold a lobster trap allocation or can prove

participation in the crab fishery before a specified control date (ASMFC, 2015). To date, no legal distinction exists between lobster and Jonah crab traps.

Knowledge of the Jonah crab's life history and biology is limited; existing literature on the species is temporally and spatially sporadic, and further data collection is needed to inform the creation of a range-wide stock assessment (ASMFC, 2015). As part of the FMP, state and federal agencies are required to conduct port and/or sea sampling programs to collect biological data from commercially harvested Jonah crab. To this end, we developed a pilot sea sampling program to collect fishery-dependent data from Jonah crab caught in the commercial fishery in Rhode Island Sound. Data were collected year-round to elucidate seasonal patterns in Jonah crab biology. Length-to-weight relationships were modelled for males and females to characterize allometric growth in the species. Catch per trap of Jonah crab was analyzed with respect to measured fishery-dependent and environmental variables. Collectively, these results build upon the limited knowledge of the Jonah crab and address data needs for informed management of the resource.

METHODS

Data collection

At-sea data collection was conducted during normal fishing operations on commercial fishing vessels targeting Jonah crabs in Rhode Island Sound in National Marine Fisheries Service (NMFS) statistical areas 537 and 539 north of 41° N latitude and west of 71° W longitude (Figure 1). From each trawl, the following fishing effort information was recorded: latitude and longitude, water depth, habitat type (as reported by the vessel operator based on depth sounder readings and local ecological

knowledge), bait species, soak time, trap dimensions and escape vent configurations. When feasible, all traps within a trawl were sampled for catch composition; when census sampling was not possible, a systematically random subset of the traps within a trawl were sampled. In these traps, Jonah crab, American lobster, Atlantic rock crabs (*Cancer irroratus*), and other bycatch species were quantified.

Biological measurements were collected from a random subset of the Jonah crabs caught within each trawl. A systematic random sample frame was used to select a subset of traps in the trawl, within which all Jonah crabs were sampled. From each of these specimens the following measurements were collected: sex, carapace width, ovigerous condition, presence of sperm plugs in females indicating recent mating (see Elner et al., 1985), and shell disease condition. Carapace width was measured as the widest width of the carapace, in mm, including anterolateral teeth. All carapace measurements were taken with digital Vernier calipers and rounded to the nearest 0.1 mm. A subset of the Jonah crabs caught were collected and weighed to the nearest gram on a digital electronic scale.

Shell disease syndrome is defined as black-spot lesions on the exoskeleton (Vogan et al., 2008). It varies in cause, appearance, and severity between crustacean species but has not been described for Jonah crab. We assessed shell disease on a four-factor scale adapted from that described for deep sea crab crabs, *Chaceon quinquedens*, by Sindermann et al. (1989) (see caption of Figure 4). Shell disease was described according to the following factor levels: Absent: no visible dark spots on carapace; Minor: <10% of carapace covered in dark spots; Moderate: 10-50% of carapace covered in dark spots; and Severe: >50% of carapace darkened.

An Onset HOBO Tidbit temperature logger (Model UTBI-001) was deployed on a trap in the general sampling area to capture the region's seasonal temperature pattern. Temperature readings were recorded at a minimum frequency of once every 4 hours. Bottom temperature was averaged over the day of harvest to be used in analysis of temperature effects on catch per trap.

Data Analysis

The relationship between carapace width and weight was defined with a power function using the formula

$$W = a CW^b$$

where W represents the weight in g, CW represents the carapace width in mm, and a and b are fitted parameters representing the condition factor and the allometric factor, respectively (Quinn and Deriso, 1999). The power function was linearized and parameters were estimated using least squares regression.

A generalized linear model (GLM) was employed to estimate the effects of the following variables on Jonah crab catch per trap in traps that were configured to target Jonah crab: vessel (as a factor); bottom temperature on the day of trap haul; soak time in days; depth; lobsters per trap; total bycatch excluding lobster; and interactive effects of latitude and longitude. Habitat type and bait species remained constant throughout the study and were therefore excluded from this analysis. Traps were controlled for trap length (i.e., traps that were 4 feet in length rather than the standard 3 feet were excluded) and traps for which counts of all species were not taken were excluded. Stepwise model selection was used to remove nonsignificant covariates until the selected model was chosen.

RESULTS

Biological catch summary

A total of 8535 male and 930 female Jonah crabs were biologically sampled throughout the study period (Table 1). The average carapace width for males was 126.1 mm (s.d.=9.0) and the average carapace width of females was 104.9 mm (s.d.=11.3). The size ranges of males and females caught were 75.0-158.7 mm and 63.2-129.2 mm, respectively.

Of the females sampled throughout the year, 3.8% were above the legal minimum size established for the commercial fishery. The sex ratio of the catch was variable but was consistently male-dominated; relatively few females ($\leq 10\%$) were caught throughout the year with the exception of sample dates on 8/29/2016, 9/22/2016 and 11/1/2016 (47%, 15%, 20%) (Figure 5). During months when females were more abundant in the catch, larger size classes (>100 mm) dominated the size distributions of females that were caught (Figure 3). None of the females observed throughout the study were ovigerous. Females with sperm plugs were encountered infrequently but had the highest prevalence in the months of January, February and May (Table 2). All females with sperm plugs had recently molted as indicated by a pliability of the shell and overall light color.

Overall, 75.0% of the males caught exceeded the legal minimum size threshold, though this proportion varied throughout the study period (Figure 2). Large males (>130 mm) represented the highest proportion of the catch of males in between August and November. The mean size of males was lowest from November to May.

In general, shell disease presented as black spotting on the exoskeleton without lesions and obvious degradation of the shell; lesions were limited to the most severe cases of shell disease. Shell disease exhibited a seasonal pattern of occurrence in males, with lowest rates of disease occurring in August and September (Figure 4). The pattern of shell disease occurrence in females appears seasonal as well, with lowest shell disease rates occurring between January and June (Figure 4). However, female patterns are potentially confounded by seasonal low catch rates of female crabs.

Length-to-Weight Relationship

Analysis of the length-to-weight relationship indicated significant differences in both the condition factor and allometric factor between males and females ($p < 0.05$, Table 4). An allometric factor $b = 3$ indicates isometric growth (Quinn and Deriso, 1999). This parameter is 2.94 for females and 3.12 for males in the Jonah crab population, indicating negative and positive allometric growth, respectively, although these values are close to isometry. The power function condition factor, a , found by exponentially transforming a from the linearized equation, is 9.42×10^{-5} for males and 2.06×10^{-4} for females. Although this coefficient is higher for females than for males, the allometric factor, b , has a greater influence on relative weight-at-length between females and males.

Fishery characteristics and catch per trap

Most common bycatch species in traps targeting Jonah crab were black sea bass (*Centropristis striata*), unidentified eels, rock crabs (*Cancer irroratus*), sculpins (*Myoxcephalus spp.*), and scup (*Stenotomus chrysops*) (Table 3). Species composition

of bycatch varied throughout the year, but overall catch rates of finfish species were low.

One of the methods fishers use to target Jonah crab rather than lobster is to modify trap escape vents so that crabs are less likely to exit the traps. Traps used throughout this study were outfitted with both rectangular vents measuring $5\frac{3}{4}$ " by $1\frac{7}{8}$ "-2" wide and double circular escape vents of $2\frac{5}{8}$ " diameter. When targeting crabs, the rectangular vents were blocked off and the circular vents left open; when targeting lobsters, both vents were left accessible. To observe the effects of these vent modifications on Jonah crab catch per trap, trawls were selected in which at least two traps of each type were sampled for catch composition. These trawls were isolated to two sampling dates—6/30/2016 and 8/23/2016—because trawls with a mixture of trap types were encountered and sampled throughout the study period only on these days. Comparison of catch per trap of lobsters and Jonah crabs between these vent configuration types indicates a significantly higher Jonah crab catch per unit effort for those traps that were adjusted to target them (Figure 7).

A quasi-Poisson GLM was selected to model the effects of measured covariates on Jonah crab catch per trap. This model, composed of a Poisson-distributed error component and a natural log link function, also incorporates a parameter to account for dispersion of the response variable. Of the variables investigated, soak time, temperature, lobster catch per trap and vessel differences were found significant and were included in the final model (Table 5). Depth, latitude and longitude, and non-lobster bycatch were not found significant and were excluded from

the analysis. The model explained 28.1% of the deviance in Jonah crab catch per trap (Figure 8).

DISCUSSION

The seasonal trends in sex ratio of Jonah crab commercial catch resemble those described by Stehlik et al. (1991), who compiled Northwest Atlantic Shelf survey data from the Northeast Fisheries Science Center and found that Jonah crab sex ratios favored females in the fall and males in the winter and spring. Stehlik and colleagues suggested these differences in sex composition may have been due to sex-specific migrations or to changes in catchability related to reproduction. The absence of ovigerous females throughout this study align with findings of previous research; egg-bearing females have been rarely encountered and compose a notably low proportion of Jonah crabs sampled in research studies, sometimes leading to the assumption that females are absent from the study area (Haefner, 1977; Wenner et al., 1992).

However, low activity levels and resultant low catchability have been documented for ovigerous females of other *Cancer* species (Naylor et al., 1999); thus, the seasonality of spawning and distribution of ovigerous females likely cannot be fully assessed in a fishery-dependent study such as the present one. Sastry and McCarthy (1973) reported ovigerous Jonah crabs in Narragansett Bay in July, but methods used to collect these crabs were not reported. The increased catch of large females in the late summer and fall may be due to post-hatching increases in feeding and activity of mature females.

In Boothbay Harbor, Maine, Krouse (1980) described a seasonal peak in research trap catch per unit effort (CPUE) in the fall which diminished rapidly in the winter and hypothesized this decline to be due to fishing mortality or emigration. The

length frequencies of male Jonah crabs in the present study followed a similar pattern. The mean size of male Jonah crabs was highest in the late summer and fall and decreased through the spring until June (Figure 2). The molting season for mature males in this region occurs during the late spring and early summer (Truesdale et al., *in prep*). Fishing and natural mortality may cause large male abundance to slowly decline throughout the year until the molting season brings new recruits to large size classes. Alternatively, ontogenetic seasonal migrations may cause these shifts in mean size of males in commercial traps, yet the migration paths are poorly understood (ASMFC, 2015). Seasonal patterns in length frequency distribution may also be influenced by changes in predominant target species (Table 1) wherein trap configuration affects trap size selectivity. These effects were not investigated in the present study.

Length-weight relationships in male and female Jonah crabs indicate that both sexes experience nearly isometric growth. Visually, the growth curves for males and females are quite similar until a carapace width of approximately 95 mm (Figure 6). Males have larger claws than females, and this point of divergence most likely results from morphological differences between mature males and females. Size at maturity for Jonah crabs is not well described in southern New England, but previous studies indicate that males reach sexual maturity between 90 and 100 mm and females reach sexual maturity by 80-90 mm in Norfolk Canyon (Carpenter, 1978; Wenner et al., 1992).

The divergence in Jonah crab catch rates between traps with different escape vent configurations indicates that CPUE metrics, such as those calculated by Pezzack

et al. (2011) for the Canadian Jonah crab fishery, would not be an accurate proxy for abundance in the mixed crustacean fishery in southern New England. There is no legal distinction between lobster and Jonah crab traps (ASMFC, 2015), and spatial and temporal differences in target species likely confound trends in CPUE that might be calculated from vessel logbook data, particularly as targeted fishing for Jonah crab has increased over the past two decades.

Jonah crab catch in crab-targeting traps is influenced by temperature, fisher behavior (vessel differences), catch of lobsters and soak time. Latitude, longitude and depth were not found significant in the chosen model, which is attributed to the small sampling area and depth range at which Jonah crabs were caught. Bottom temperature on day of capture ranged between 5.38°C and 14.04°C for traps included in GLM analysis, and the selected GLM indicates that temperature had a positive effect on Jonah crab catch within this temperature range. These temperatures closely match the preferred temperature range for the species provided in other field and laboratory investigations (Carpenter, 1978; Haefner, 1977; Jeffries, 1966).

Antagonistic interactions between lobsters and Jonah crabs have been documented in previous studies, and Jonah crabs have been observed avoiding interaction with lobsters by choosing suboptimal substrates (Fogarty, 1978; Richards, 1992). Avoidance of traps containing lobsters is assumed to be the cause of negative correlation between Jonah crab and lobster catch per trap.

Effects of various habitat types on Jonah crab catch per trap could not be tested because fishers targeted Jonah crabs exclusively in flat, muddy sediment during the study. Preference for fishing in this habitat type did not align with previous study of

Jonah crabs in Narragansett Bay and Boothbay Harbor, which found that Jonah crab preferred coarse gravel and rocky substrate (Jeffries 1966; Fogarty, 1978; Krouse, 1980). However, this preference for a muddy fishing substrate aligns with research conducted by Wenner et al. (1992) on the continental slope of the southeastern United States wherein Jonah crabs were found in highest abundance on soft bioturbated ooze substrates. Further research is necessary to understand spatial and seasonal dynamics of habitat preference by Jonah crabs.

Results of this year-round sampling program indicate seasonal trends in Jonah crab commercial catch length frequencies and sex ratios, along with evidence of the effects of environmental and fishery-dependent parameters on catch per unit effort. The sea sampling protocol developed here may serve as a template for other fishery-dependent sampling programs throughout the range of the species; collection of similar data types across a larger region may aid in describing spatial dynamics of Jonah crab. Given the increasing importance of the fishery, such efforts will aid efforts to understand the impacts of fishery exploitation on the resource.

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Table 1. Dates and Jonah crab sample sizes for commercial fishery sea sampling program.

Date	Stat Area	Males	Females	Predominant Target Species
6/30/2016	537	320	8	Both
7/25/2016	537	290	31	Both
8/23/2016	539	807	62	Both
8/29/2016	537	482	435	Both
9/22/2016	539	522	92	Lobster
11/1/2016	537	538	138	Both
11/5/2016	539	816	22	Jonah crab
12/14/2016	539	1154	64	Jonah crab
1/16/2017	539	829	41	Jonah crab
2/28/2017	539	817	11	Jonah crab
5/30/2017	539	1183	14	Jonah crab
6/28/2017	539	467	0	Jonah crab
8/4/2017	539	310	12	Lobster

Table 2. Summary of females observed with sperm plugs (evidence of recent mating), listed by sample date.

Date	Number sampled	Number with sperm plugs	Carapace Width Range (mm)
8/23/2016	62	1	96.0
11/1/2016	138	1	105.2
12/14/2016	64	1	102.1
1/16/2017	41	11	87.5-107.4
2/28/2017	11	3	94.1-103.6
5/30/2017	14	8	74.0-100.7

Table 3. Most common bycatch species in traps targeting Jonah crab, listed by season. Limited to species that were encountered a minimum of three times in a fishing day. Rock crabs (*Cancer irroratus*) and American lobsters (*Homarus americanus*) were encountered throughout the fishing season.

Autumn (Sept-Nov)	Winter (Dec-Feb)	Spring (Mar-May)	Summer (Jun-Aug)
black sea bass	sculpin	eels	black sea bass
scup		black sea bass	scup
tautog		scup	

Table 4. Allometric growth model coefficients for males and females, with 95% confidence intervals of parameters. The allometric growth power function was linearized to obtain the equations listed. Both coefficients are significantly different between males and females ($p < 0.001$).

	Equation	α	α confint 95%	b	b confint 95%	R^2	N. obs	Size range (mm)
Male	Log WT= $\alpha + \beta(\log CW)$	-9.27	[-9.58, -8.97]	3.12	[3.05, 3.18]	0.970	284	53.4-155.1
Female	Log WT= $\alpha + \beta(\log CW)$	-8.49	[-8.81, -8.17]	2.94	[2.87, 3.01]	0.975	171	59.5-126.0

Table 5. Estimated coefficients of linear and categorical predictors for final quasi-Poisson GLM.

Explanatory Variable	Estimate	Std. Error	t value	Pr(> t)
Lobster catch per trap	-0.079	0.014	-5.440	***
Soak time	-0.009	0.003	-3.318	***
Temperature	0.074	0.010	7.172	***
Vessel	0.427	0.066	6.465	***

Dispersion parameter for quasipoisson family taken to be 3.161

Significance code: p<0.001 (***)

Deviance explained=0.281

N traps=462

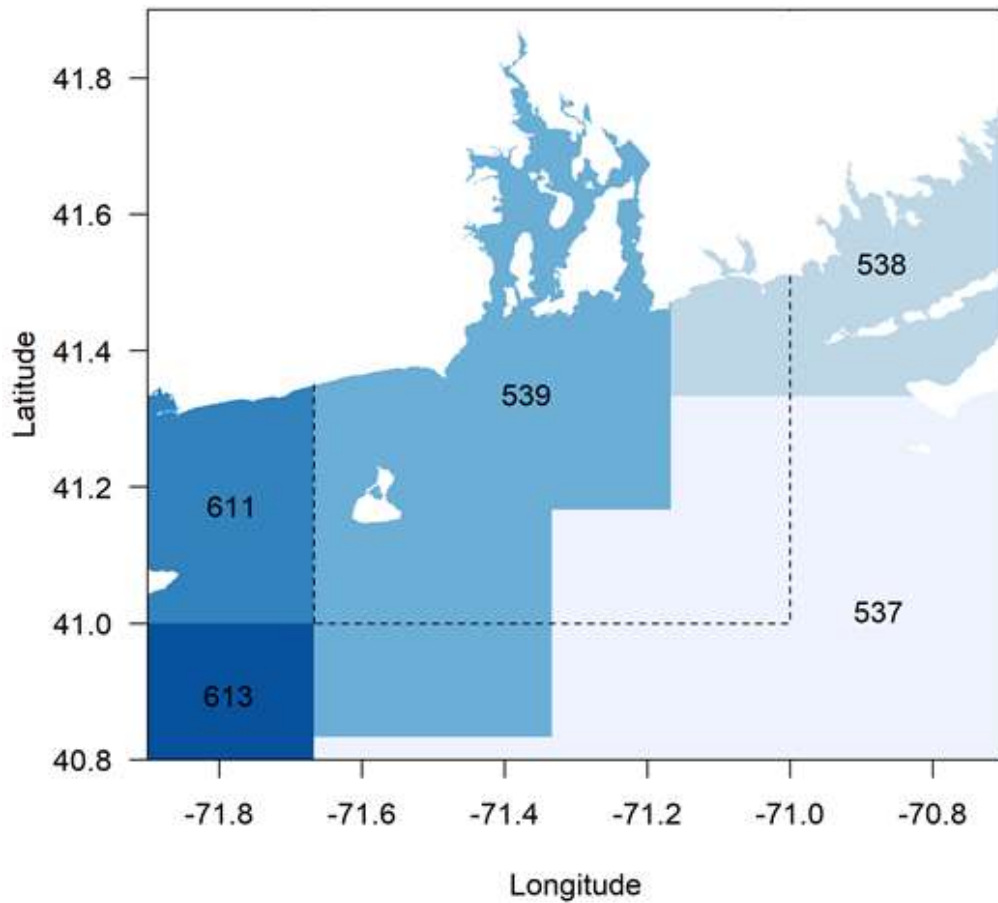


Figure 1. Map of sampling region. Crabs were collected from NMFS statistical areas 539 and 537, north of 41° N latitude and west of 71° W longitude. Specific fishing locations are not presented to protect confidentiality of data.

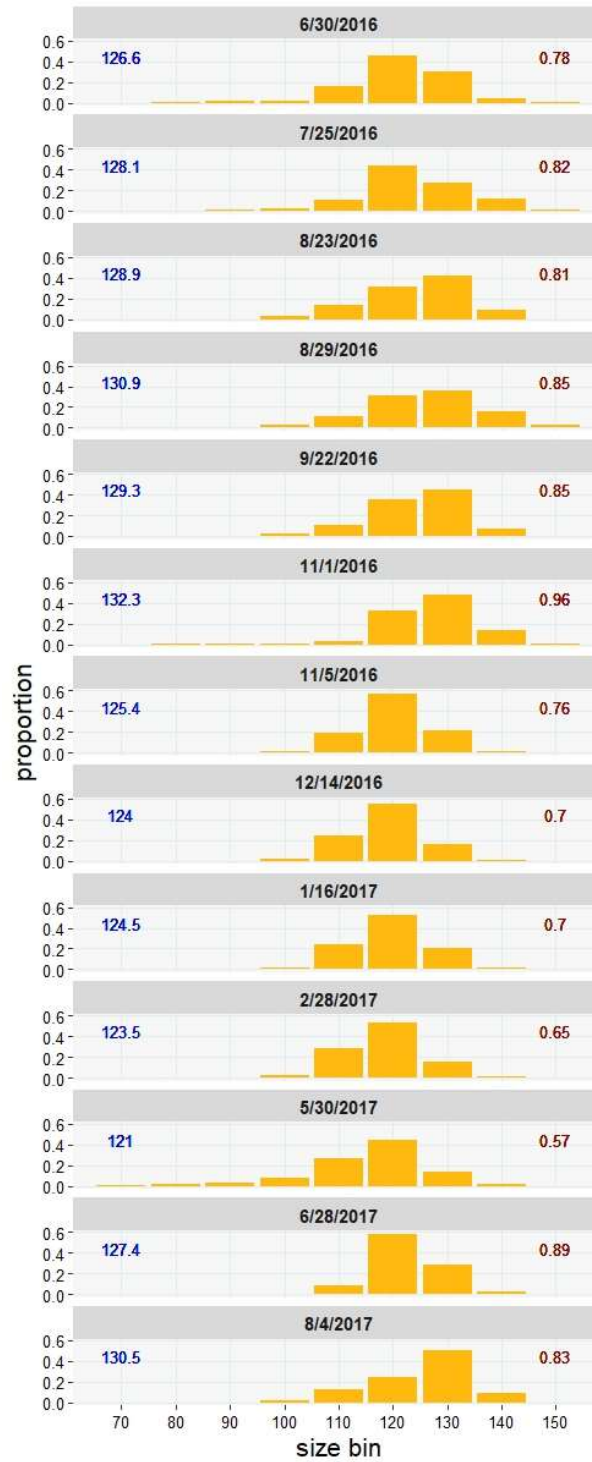


Figure 2. Carapace width frequency barplots of male Jonah crabs caught in the commercial fishery by sample date, binned in 10-mm size increments. Mean carapace width (mm) is indicated on left side of each subplot in blue. Proportion of males caught exceeding legal minimum size is indicated on right side of each subplot in dark red.

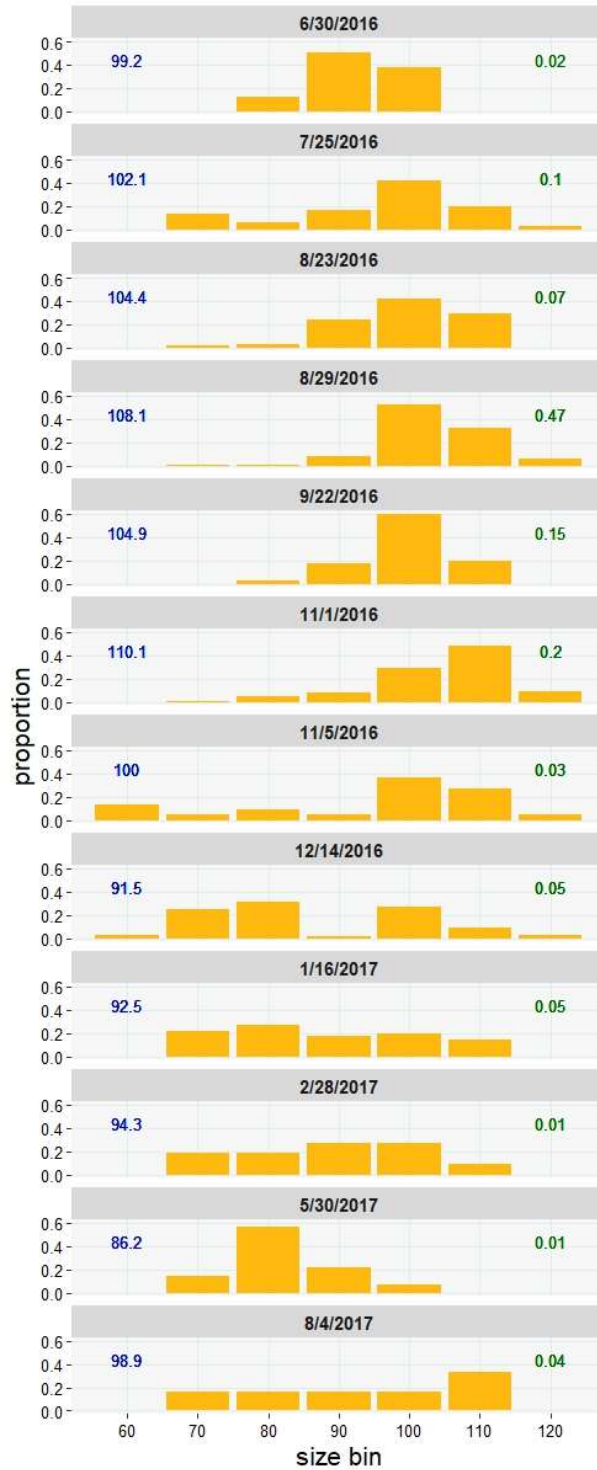


Figure 3. Carapace width frequency barplots of female Jonah crabs caught in the commercial fishery by sample date, binned in 10-mm size increments. Mean carapace width (mm) is indicated on left side of each subplot in blue. Proportion of crabs caught that were female is indicated in dark green on right side of each subplot.

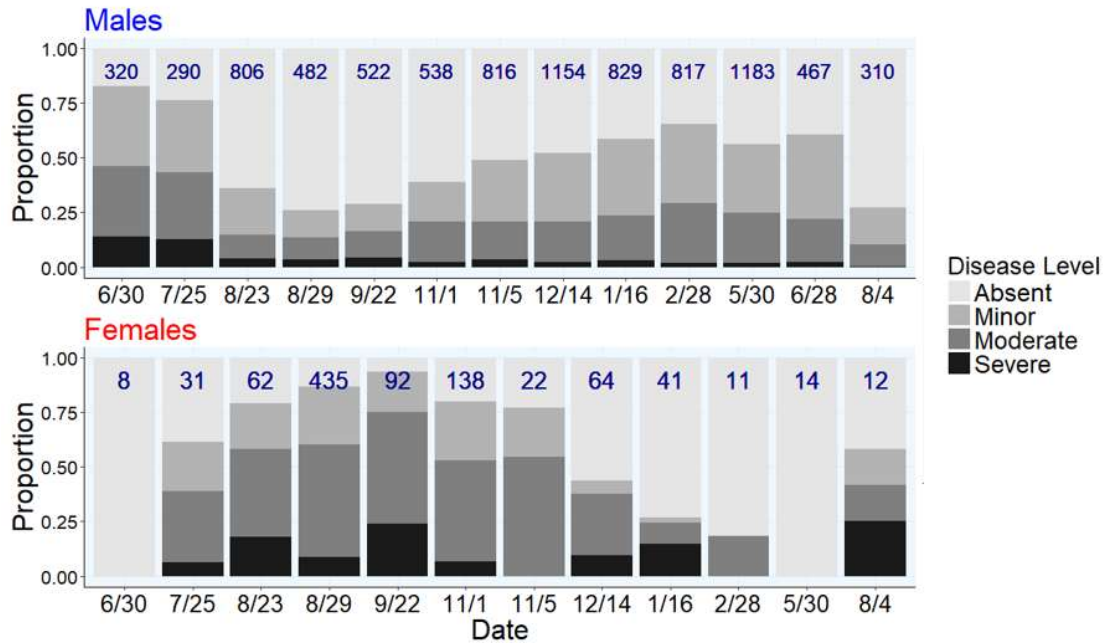


Figure 4. Shell disease condition for male and female Jonah crabs, 6/30/2016 to 8/4/2017. Sample sizes given within bars. Disease levels assessed on four factor scale adapted from that defined in Sindermann et al., 1989: Absent: no visible dark spots on carapace; Minor: <10% of carapace covered in dark spots; Moderate: 10-50% of carapace covered in dark spots; Severe: >50% of carapace darkened.

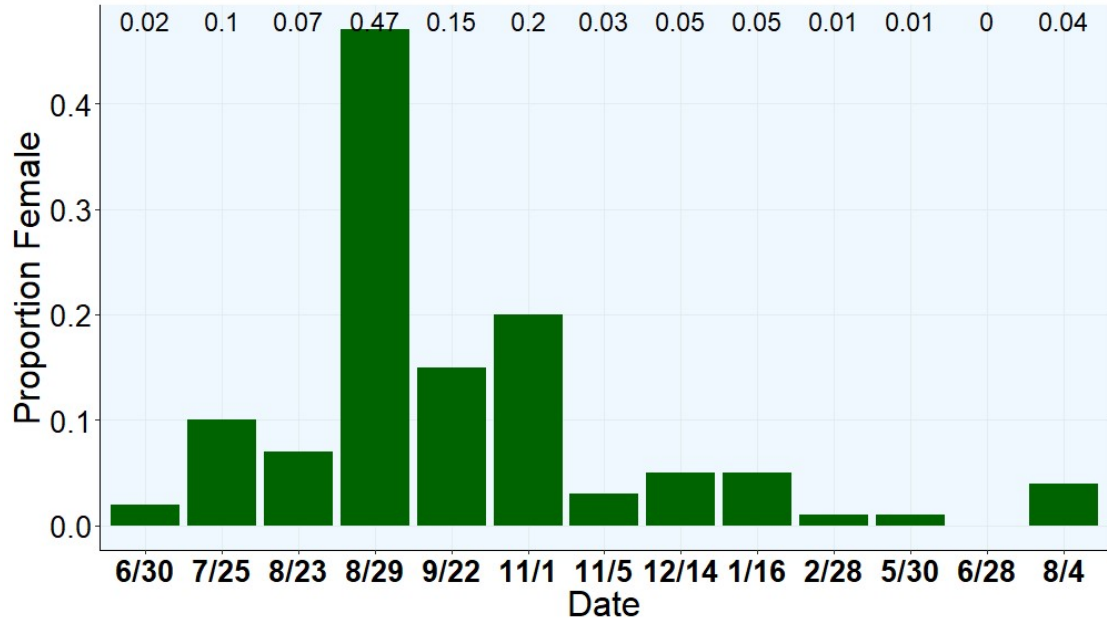


Figure 5. Proportion of crabs that were female within commercial traps, calculated from all crabs that were randomly sampled within each day, 6/30/2016-8/4/2017. Proportions given above each bar.

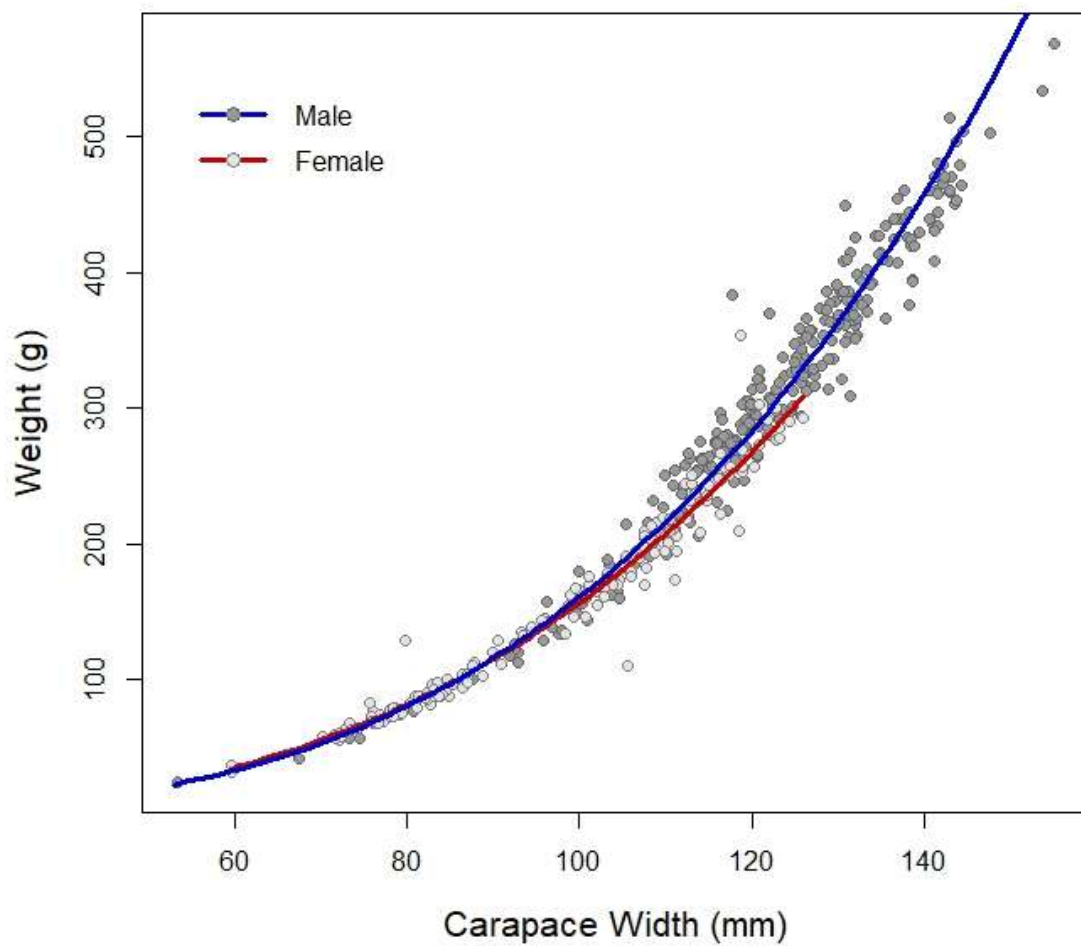


Figure 6. Carapace width to weight relationship for male and female Jonah crabs, plotted with fitted allometric growth models (see Table 4 for model parameters).

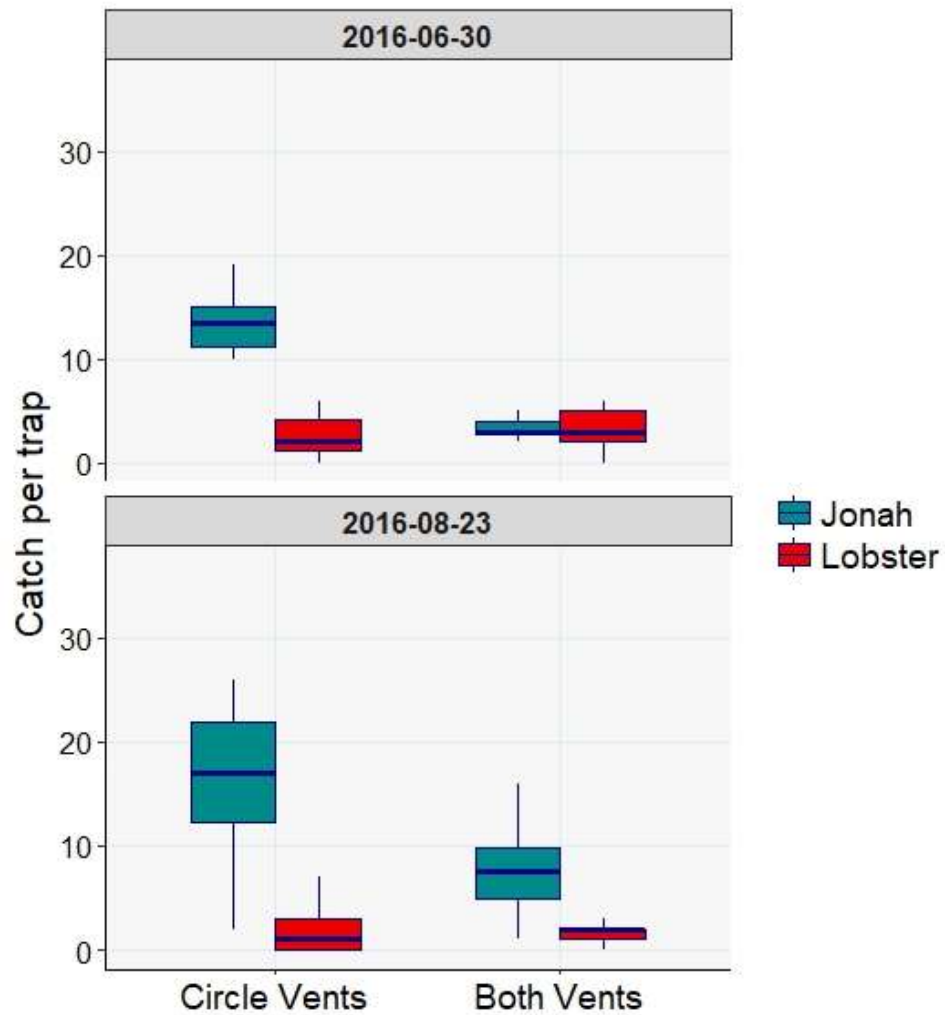


Figure 7. Catch per trap of Jonah crab and lobster in trawls with a mixture of traps targeting each. “Circle vents” indicates traps configured to target Jonah crab; “Both vents” indicates traps configured to target lobster. Results plotted for 6/30/16 (N=12 crab traps, 18 lobster traps) and 8/23/16 (N=30 crab traps, 30 lobster traps).

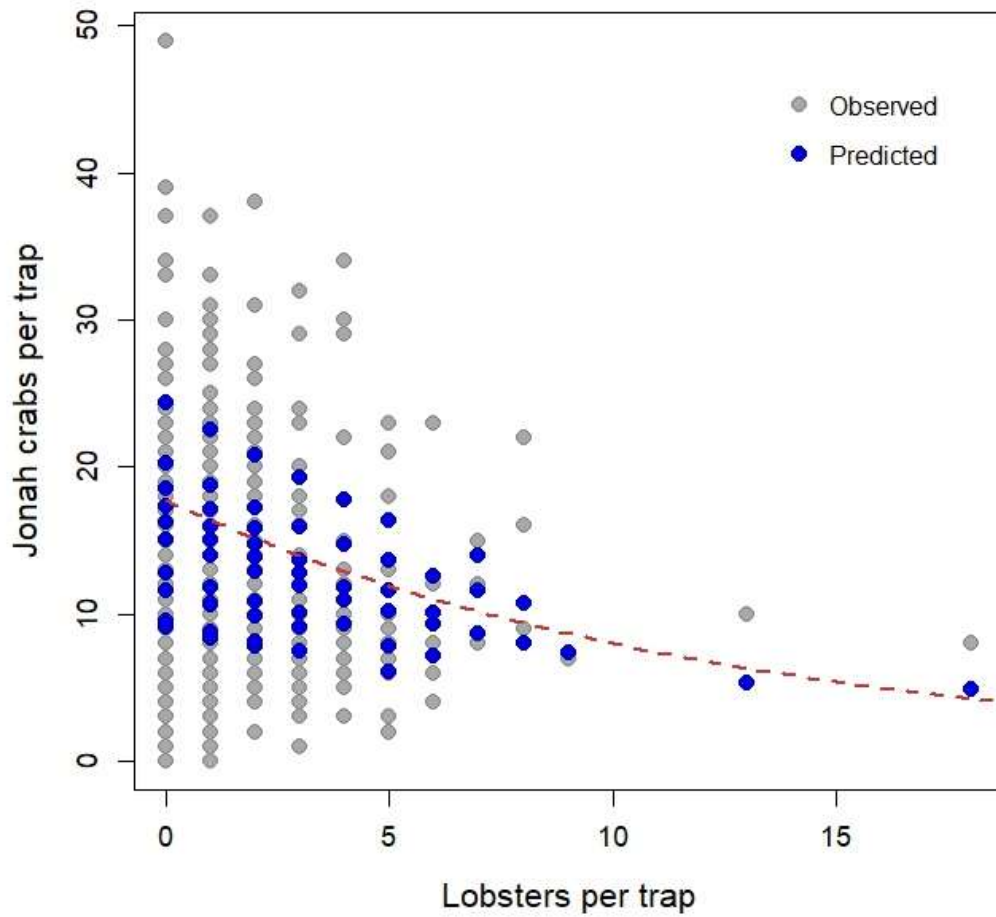


Figure 8. Final GLM predicting Jonah crab catch per trap in crab-targeting traps (model coefficients in Table 5). Model predictions plotted with observed data against lobster catch per trap to provide visualization of variance explained by the selected GLM. Red dashed line added to show isolated effect of lobster catch per trap (temperature fixed at 10 °C, soak time fixed at 6 days).

MANUSCRIPT 2

Growth of Jonah crab (*Cancer borealis*) in Rhode Island Sound

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ABSTRACT

The Jonah crab, *Cancer borealis*, supports a rapidly growing commercial fishery in southern New England. However, the species is poorly understood and lack of data concerning its life history, including growth dynamics, hinders the creation of a thorough stock assessment for the species. In this study, the incremental growth and seasonality of molting in Jonah crabs from Rhode Island Sound was examined in specimens collected from commercial traps and monitored in flow-through seawater tanks. Regression analysis from molt increments of 119 female and 91 male crabs indicates growth dimorphism in mature Jonah crabs, with diverging trends in proportionate growth with size between the sexes at the sizes observed. Molting seasonality and size-dependent molt probabilities in male Jonah crabs were studied via periodic sampling and observation of male specimens across a range of 10-mm carapace width size bins throughout a year-long period. A discrete molting season was identified in June for male Jonah crabs smaller than 120 mm. Molting probability decreased with increasing carapace width and males larger than 120 mm did not molt during the year-long study, suggesting that *C. borealis* has determinate growth or that there are ontogenetic migrations in the species. The results presented here provide the first published growth data for *C. borealis* and are highly applicable to management efforts for the species.

INTRODUCTION

The Jonah crab, *Cancer borealis*, is a brachyuran crustacean distributed in continental shelf waters from Newfoundland to Florida (Haefner, 1977). Spatial dynamics of Jonah crab populations are not well described but previous research suggests they are structurally complex, displaying seasonal inshore-offshore movements and apparent sex segregations corresponding to water depth and offshore distance (Jeffries, 1966; Krouse, 1980; Stehlik et al., 1991). Additionally, previous studies found evidence of depth dependence in the size distribution of Jonah crab (Carpenter, 1978; Krouse, 1980). Small Jonah crabs were observed to be absent from inshore, shallow waters in Maine and Rhode Island where larger individuals were frequently caught (Krouse, 1980). In the Mid-Atlantic Bight, Haefner (1977) found crabs less than 40 mm in carapace width to be distributed predominantly at depths between 75 and 150 m, while individuals between 41 and 80 mm were found exclusively at depths greater than 150 m. Such descriptions of the seasonal and spatial dynamics of Jonah crab are sporadic, and further research is required to fully understand spatial dynamics and migration patterns for the species (ASMFC, 2015).

Cancer borealis supports a rapidly growing commercial fishery in southern New England, where landings have increased nearly seven-fold since the 1990s (ASMFC, 2015). Management of the fishery has lagged this substantial growth—the first fishery management plan for the species was published in 2015. A stock assessment has yet to be published, and lack of fundamental biological data—including description of growth and maturity—precludes the creation of such an assessment (ASMFC, 2015). The commercial fishery is male-dominated; the species

is sexually dimorphic, and the larger size of males increases their marketability and likelihood of exceeding the legal minimum size of 4.75" (121.65 mm), established in 2015 (ASMFC).

Understanding growth of exploited marine species is essential to quantitative fisheries stock assessments (Chang et al., 2012). However, description of growth in crustaceans is challenging because it is discontinuous, occurring only during periodic molting events. Characterizing absolute growth requires knowledge of the size increase during each molt (molt increment) and the time between molting events (intermolt period). Historically, collecting these parameters has been accomplished via tag-recapture studies, laboratory observation, and cohort analysis of wild populations (Hartnoll, 1982). Each of these methods comes with limitations, and none are universally robust across crustacean species. Tag-recapture studies demand substantial resources and ensuring retention of tags through the molt can be difficult (Hartnoll, 1982). Size-frequency analysis relies heavily on assumptions about reproductive timing and migration and becomes less reliable for large and long-lived species (Hartnoll, 1982; Kilada et al., 2017). Laboratory studies are comparatively practical, but holding crustaceans in an artificial environment has been shown to influence growth (Wainwright and Armstrong, 1993; Stone et al., 2003; Somerton et al., 2013). Direct aging methods have been studied for multiple crustacean species, but these methods are new and are infrequently represented in the literature (Kilada et al., 2017).

In this study, we describe the growth per molt of *Cancer borealis* and characterize the molting seasonality of mature males of the species. Molt increments

were collected by short-term observation of crabs in a laboratory setting, and growth seasonality and molting probabilities were explored via periodic sampling and observation throughout a year-long study period. Comparison with data collected by field sampling on commercial Jonah crab fishing vessels corroborates laboratory findings and supports assumptions made regarding the validity of the data collection methods employed.

METHODS

Molt increments

Jonah crabs were collected from commercial fishing traps deployed in Rhode Island Sound south of Narragansett Bay, in National Marine Fisheries Service (NMFS) statistical areas 537 and 539 north of 41° N latitude and west of 71° W longitude (Figure 1), from April 18, 2016 to August 4, 2017. Crabs were voluntarily collected by fishermen and sea samplers during commercial fishing operations on vessels targeting Jonah crab. Specimens were kept in flow-through seawater tanks at one of two facilities: the Marine Research Facility at the University of Rhode Island (URI) in Narragansett, Rhode Island, and wet lab facilities at the Department of Environmental Management (RIDEM) in Jamestown, Rhode Island. In both facilities, crabs were kept in flow-through seawater tanks directly sourced with ambient seawater from the mouth of Narragansett Bay. To reduce differences between *in situ* temperatures and more extreme Narragansett Bay water temperatures, seawater was heated during the coldest winter months and chilled during the peak of summer with the goal of maintaining water temperatures between 5° C and 17° C. Diel light cycles were provided by windows situated near the holding tanks, and artificial light was reduced by blocking

out overhead lights with black plastic sheeting. Crabs were fed to satiation once weekly with scup, herring or squid (*Stenotomus chrysops*, *Clupeidae*, and *Loligo pealei*, respectively).

Crabs that molted in the laboratory were isolated in individual compartments and allowed to harden for a minimum of three days before being measured post-molt. Growth was assessed by measuring carapace width—the widest width of the carapace including anterolateral teeth—before and after molting. Carapace measurements were taken with digital Vernier calipers and rounded to the nearest 0.1 mm.

Growth increments were modeled with ordinary least squares linear regression of post-molt carapace width against pre-molt carapace width (Hiatt, 1948). Interactive effects of year (2016 or 2017), laboratory water temperature at time of molt, sex, laboratory treatment (URI or RIDEM), and statistical area of capture were tested using step-wise model selection to investigate the effects of these variables on growth per molt. Comparison between the two laboratory facilities was intended to represent non-measured effects of various laboratory treatments (e.g. flow rate, water quality), and NMFS statistical area was included to investigate differences between Jonah crabs caught closer (statistical area 539) and farther (statistical area 537) from shore.

In addition to the molt increments collected in the laboratory, 24 molt increments (16 male, 8 female) were collected by fishermen or sea samplers from crabs that molted in commercial traps. These newly molted crabs could be matched with their recently shed exuvium based on individual carapace markings and anterolateral tooth structure. The exuvium was measured to obtain pre-molt carapace width. Molt increments collected at sea in this manner were introduced to the selected

growth per molt model; at-sea collection versus laboratory collection was incorporated as a factor to test for significant differences in growth per molt between data collection methods.

Molting seasonality

Jonah crabs were collected in NMFS statistical areas 539 and 537 from commercial traps between August 23, 2016 and August 4, 2017 (Table 1, Figure 1). Effort was made to sample monthly during the study period, but February, April, and May were missed due to weather and logistical limitations. Male and female crabs were collected across the range of size classes (defined as 10-mm size bins) caught in commercial traps; crabs from common size classes were collected from randomly selected traps, and rare size classes were opportunistically collected. Specimens were measured, tagged with individual identification numbers, and kept in flow-through seawater tanks at URI as was done for molt increment collections.

Crabs were held in the laboratory to observe binary molt response—whether or not an individual crab molted within a 30-day period after capture (Chang et al. 2012). The chosen observation period was intended to minimize laboratory bias, as other crab growth studies found a significant reduction in growth per molt for crabs that were retained in the laboratory more than 30 days before molting (Somerton et al., 2013; Stone et al., 2003).

Crabs that died in the lab before molting were excluded from analysis. Binary molt responses were aggregated by size bin and by month according to the dates and months listed in Table 1. Comparison of relative molting probabilities between months

and size classes across the study period was conducted to explore molting seasonality and ontogenetic changes in growth.

Commercial fishery biological sampling

On the dates listed in Table 2, a sea sampler was deployed on commercial fishing vessels targeting Jonah crab in NMFS statistical areas 539 and 537 as described above. A random subset of the traps hauled throughout each fishing day were sampled, and all crabs within selected traps were processed. For each sampled crab, the carapace width was measured with digital Vernier calipers and rounded to the nearest 0.1 mm. Molt condition was recorded for each crab on a 3-factor scale: just molted, shell soft to the touch (1); recently molted with brittle shell, abdominal segments bend when pressure is applied (2); and hard shell, abdominal segments do not give with pressure (3).

RESULTS

Molt increments

Coefficients for the linear relationship between pre-molt and post-molt size were found to be significantly different between males and females (Figure 3). Year, lab temperature at time of molt, statistical area of capture, and lab treatment were not found significant and were not incorporated into the chosen model. Growth per molt was not found to be significantly different between crabs that molted in traps and those that molted in the laboratory, so increments collected at sea were incorporated into the model. The regression for males was described as

$$\text{PostCW}=1.22*\text{PreCW}+5.47$$

and female growth per molt was described as:

$$\text{PostCW}=0.94*\text{PreCW}+23.31$$

where PostCW represents the post-molt carapace width in mm, and PreCW represents the pre-molt carapace width ($R^2=0.96$).

All molt increments from crabs that were held in the laboratory for more than 30 days before molting were excluded from analysis of growth per molt. This decision was validated by incorporating long-term (>30 days after capture) molts into the chosen model and plotting residuals of post-molt carapace width against time in captivity before molting (Figure 2). The final growth per molt analysis incorporated 119 increments collected from females ranging in post-molt carapace width from 73.2 to 112.6 mm and 91 increments collected from males ranging between 97.0 and 149.1 mm (Figure 3).

Molt increments (absolute increase in size through molt event) exhibit diverging trends between the sexes at the size ranges observed (Figure 4). Female molt increments decrease with increasing carapace width, while molt increments of males are positively correlated with carapace width.

Molting seasonality

Year-round observations of male crabs in the laboratory indicate a clear seasonal pattern in molting probability, with most observed molts occurring during the June observation period (Figure 5). Molt probabilities in this month decreased consistently with increasing size bin: 100% (3/3) in the 80-90 mm size bin; 92.9% (13/14) in the 90-100 mm size bin; 42.9% (3/7) in the 100-110 mm size bin; 8.3% (1/12) in the 110-120 mm size bin; and 0% of crabs 120 mm and larger (0/29). None of the crabs larger than 120 mm molted throughout the year-long study period.

Female Jonah crabs occurred in commercial traps sporadically throughout the year and sample sizes were highly inconsistent between months, precluding description of molting seasonality. Alternative sampling methods may be employed in the future to allow for description of female molting seasonality.

Commercial fishery biological sampling

Carapace width and molt conditions were described for 9465 crabs in total. The mean carapace width for females was 104.9 mm (s.d.=11.3, n=930), and the mean carapace width for males was 126.1 mm (s.d.=9.0, n=8535) (Figure 6).

Male molt condition exhibited a strong seasonal trend, with newly molted individuals being caught exclusively in late May, when 16.1% of males caught were soft (molt condition=1). Brittle shell males (molt condition=2) appeared as a substantial portion of the commercial catch in June and July (6.9-14.1%) (Table 2). Catch of females was highly variable throughout the year, and female molt conditions were not included in this analysis due to seasonally low sample sizes.

DISCUSSION

We present growth increment information for Jonah crab through laboratory and field-based estimates. The sexual dimorphism in growth per molt of the Jonah crab aligns with previous study of the growth of the species, although this data is limited to a single unpublished study with a small sample size (Ordzie and Satchwill, 1984). In Dungeness crabs, molt increments are similar between males and females until sexual maturity is reached, at which point males exhibit higher proportional growth than females (Wainwright and Armstrong, 1961). Differences in growth per molt between the sexes after maturity has been shown for many other crab species

(Gerhart and Bert, 2008; Hartnoll, 1982; Moriyasu et al., 1987), and is attributed to differential investment in reproduction (Hartnoll, 1982). Few studies have described size at maturity for Jonah crabs. According to available literature, females reach sexual maturity by 80-90 mm in Norfolk Canyon (Carpenter, 1978; Wenner et al., 1992). Moriyasu et al. (2002) found that males reach gonadal maturity at 69 mm on the Scotian Shelf, while Carpenter (1978) found males to reach sexual maturity between 90 and 100 mm in Norfolk Canyon. Most of the molt increments collected in this study were from crabs molting to sizes exceeding these maturity thresholds, and the clear dimorphism in growth per molt may be attributed to this divergence in reproductive investment between males and females. Because few juvenile crabs of either sex were observed, ontogenetic shifts in growth per molt could not be assessed here.

The 30-day observation time limit employed in this study is assumed to sufficiently minimize laboratory bias by limiting observed growth events to crabs that were likely preparing for ecdysis at the time of capture. Molt stages of crustaceans have been classified into multiple intermolt and pre-molt stages so that molt timing can be predicted for marine crustaceans (Drach, 1939). Pre-molt stages D₀-D₄ describe successive levels of active preparation for ecdysis, and Stage D₁ is the first stage after which a subsequent molt event is inevitable (ie. physiological preparation for molting cannot be halted) (Miller and Hankin, 2004). Studies of premolt setal development stages have estimated the time to molt from Stage D₁ as 60 days for *Cancer magister* (Miller and Hankin, 2004); 18-40 days (depending on temperature treatment) for *Homarus americanus* (Aiken, 1973); and 6-9 weeks for *Chionocetes opilio*

(O'Halloran and D'Or, 1988). Molt stage timing estimates are not currently available for *C. borealis*, however, based on these other species, we assume that it takes a number of weeks to physiologically prepare for ecdysis. Thus, seasonal molt timing recorded in this study is assumed to be reflective of *in situ* molt timing, as crabs molting within 30 days of capture are likely to have been in late D-Stage preparation for ecdysis when caught. This assumption is corroborated by the alignment of laboratory seasonal molt timing observations with shell conditions recorded from crabs caught in commercial traps (Table 2). Similarly, the growth per molt observed in the laboratory is assumed to be representative of *in situ* growth because any biases introduced in the laboratory are minimized by sufficiently limiting holding time. Alignment between lab-collected molt increments and increments measured from crabs that molted in traps supports this assumption (Figure 7). When incorporated into regression analysis, no significant difference was found between increments collected at sea and those collected in the laboratory.

Juvenile growth rates have not been described for *Cancer borealis* and the age at recruitment for the species is unknown. However, quantification of the growth per molt and molting seasonality of adult male *C. borealis* provides a potential opportunity to predict recruitment in subsequent years. For instance, male crabs at 95.4 mm are the smallest we would expect to recruit into the commercial fishery at their next molt, becoming larger than the legal minimum size of 121.65 mm (ASMFC, 2015). If an annual molt is assumed for crabs of this size and mortality can be estimated, subsequent year recruitment prediction may be possible. Pre-recruit surveys

may thus be a practical means of monitoring and predicting the magnitude of the Jonah crab resource (Caputi et al., 2014).

The small sample sizes for small size classes in the monthly observation study were a consequence of collecting specimens using fishery-dependent methods—smaller individuals are less susceptible to commercial crab traps, which are outfitted with escape vents to allow small individuals to exit. The sample sizes within each size bin are somewhat representative of their relative abundance in commercial traps, with deviations due to deaths during the observation period. The anomalously large sample size in the 90 mm size bin for June may be caused by pre-molt behavior. The traps from which the crabs were collected were set in flat, muddy habitat, and would be expected to provide some of the only available shelter. Crabs are most vulnerable to predation and cannibalism after molting (Romano and Zeng, 2016; Ryer et al., 1997, Sotelano et al., 2016), and previous studies have shown that shelter availability reduces post-molt mortality for crustaceans (Marshall et al., 2005; Zhang et al., 2018). We hypothesize that Jonah crabs about to molt seek shelter in traps. This is the proposed explanation for having high representation in the 90 mm size class for June only, when 13 of 14 of the sampled individuals molted. The inherent bias that this behavior introduces to the molting probabilities is recognized; however, the relative probabilities between size classes are still expected to be reflective of the population *in situ*. Thus, decreasing molt probabilities with size is accepted as a characteristic of the wild population. Similarly, observations of molting seasonality would not be affected by this behavior; the relative molt frequency between months supports a clear seasonal pattern notwithstanding the potential bias of trap-seeking behavior.

Monthly molt probability observations are interpreted to indicate an annual molt period in the summer for male Jonah crabs between 90 and 110 mm. Molting events become much less common in male crabs larger than 110 mm (Figure 5), aligning with observations of other brachyuran crabs for which the intermolt period increases as crabs grow larger (MacKay and Weymouth, 1934; Hartnoll, 1982). Molt events in crabs larger than 120 mm were quite rare: over the course of the entire study, only one crab larger than 120 mm (120.6 mm) molted in the laboratory. The Jonah crab may thus be a species that experiences a terminal molt, or determinate growth—individuals molt to a certain size or through a predetermined number of instars, rather than continuing to molt indefinitely (see Hartnoll, 1985). Length frequencies in the commercial fishery (Figure 6) lend support to this hypothesis. Using the Hiatt model that was fitted to molt increments, a male crab at 120 mm would be expected to grow to 151 mm during its next molt. Crabs larger than 120 mm composed 77.67% of the male crabs caught in the commercial fishery (6629/8535) yet crabs larger than 150 mm composed only 0.37% of males caught in the commercial fishery (32/8535). The discordance in abundance between these size classes in the commercial fishery indicates that *C. borealis* may experience determinate growth. Ontogenetic migrations from the study area provide an alternative to this terminal molt hypothesis, and are supported by the available literature showing size segregation in Jonah crab populations (Carpenter, 1978; Krouse, 1980). These distributions are not well characterized across the range of the species, and further investigation of movement patterns is necessary to evaluate these hypotheses for the absence of molting in large male Jonah crabs.

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Table 1. Sampling dates of monthly molt probability study. When sample dates occurred during the last 10 days of the month, data were binned into the subsequent month (for example, crabs collected on August 29, were labeled as September molts).

Capture Date	Month Bin	Statistical Area
8/23/2016	Sept	539
8/29/2016	Sept	537
9/22/2016	Oct	539
11/1/2016	Nov	537
11/5/2016	Nov	539
12/14/2016	Dec	539
1/16/2017	Jan	539
2/28/2017	Mar	539
5/30/2017	Jun	539
6/28/2017	Jul	539
8/4/2017	Aug	539

Table 1. Molt condition of males sampled from commercial catches, determined according to three factor scale: 1= Just molted, carapace is soft; 2=Newly molted, with brittle carapace (abdominal segments are still pliable); 3= shell hard, no evidence of recent molt. Percent of total number of males indicated for each molt condition.

Sample Date	Statistical Area	Males Sampled	Molt Condition (%)		
			1	2	3
6/30/2016	537	320	0	7.2	92.8
7/25/2016	537	290	0	14.1	85.9
8/23/2016	539	807	0	1.2	99.9
8/29/2016	537	482	0	0	100.0
9/22/2016	539	522	0	0	100.0
11/1/2016	537	538	0	0	100.0
11/5/2016	539	816	0	0	100.0
12/14/2016	539	1154	0	0.1	99.9
1/16/2017	539	829	0	1.2	99.9
2/28/2017	539	817	0	0	100.0
5/30/2017	539	1183	16.1	2.2	81.7
6/28/2017	539	467	0	6.9	93.1
8/4/2017	539	310	0	0	100.0

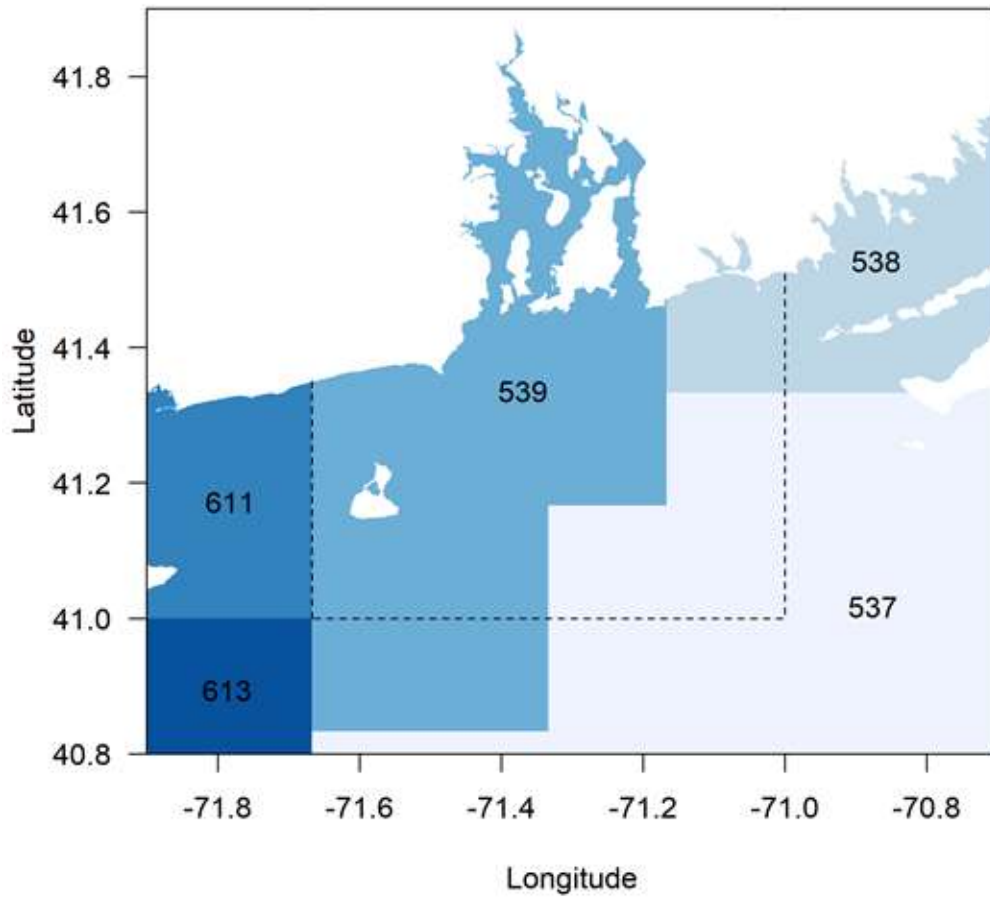


Figure 1. Map of sampling region. Crabs were collected from NMFS statistical areas 539 and 537, above 40° N latitude. Specific fishing locations are not presented to protect confidentiality of data.

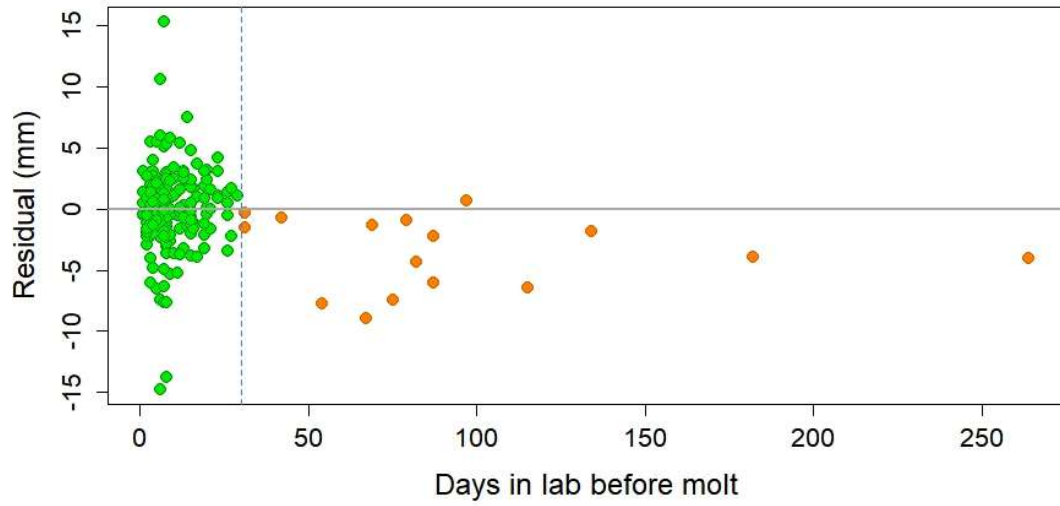


Figure 2. Residuals of growth per molt linear regression (mm) plotted against time in captivity before molting. Molts occurring after 30 days in the laboratory (orange points) were removed from analysis due to the low bias of these molt increments.

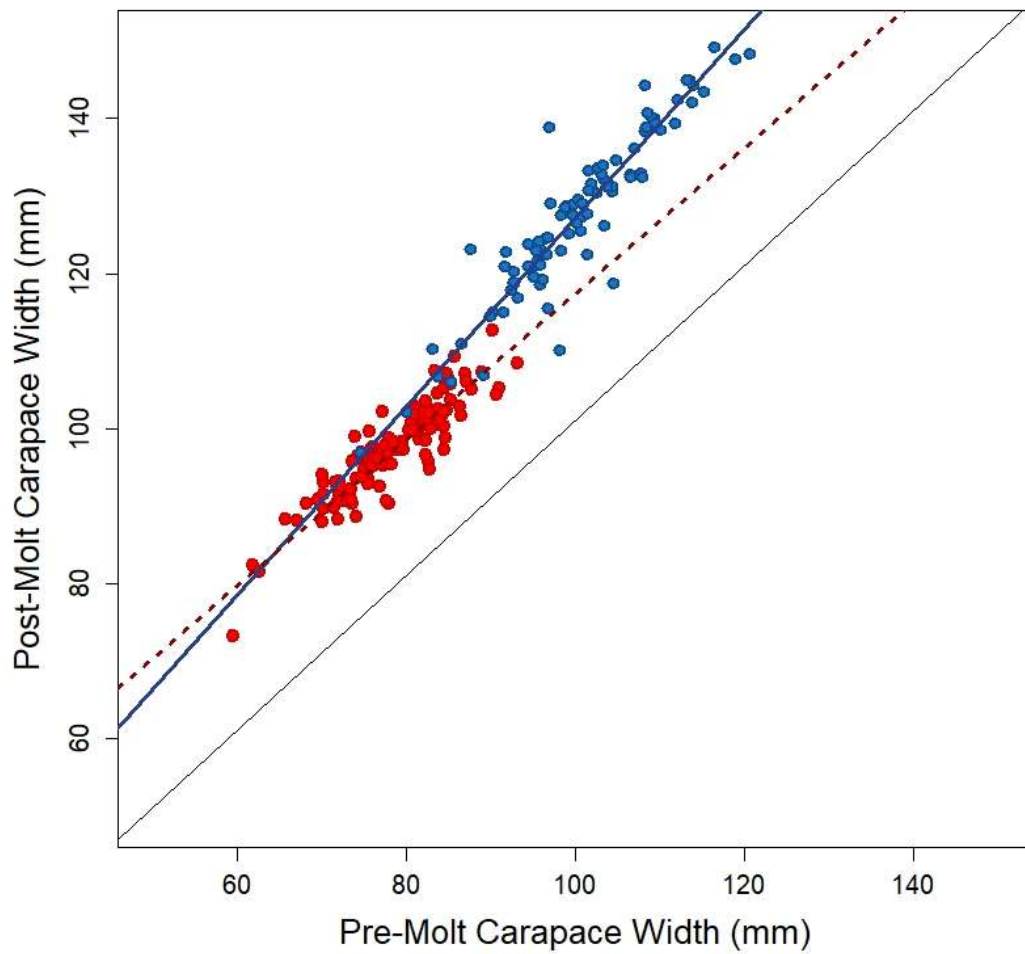


Figure 3. Pre-molt vs. post-molt carapace width (mm) male (blue) and female (red) Jonah crabs observed molting in the laboratory. Coefficients of the selected model ($R^2=0.96$) plotted for males and females as solid blue and dotted red lines, respectively. One-to-one replacement line provided as reference, in black.

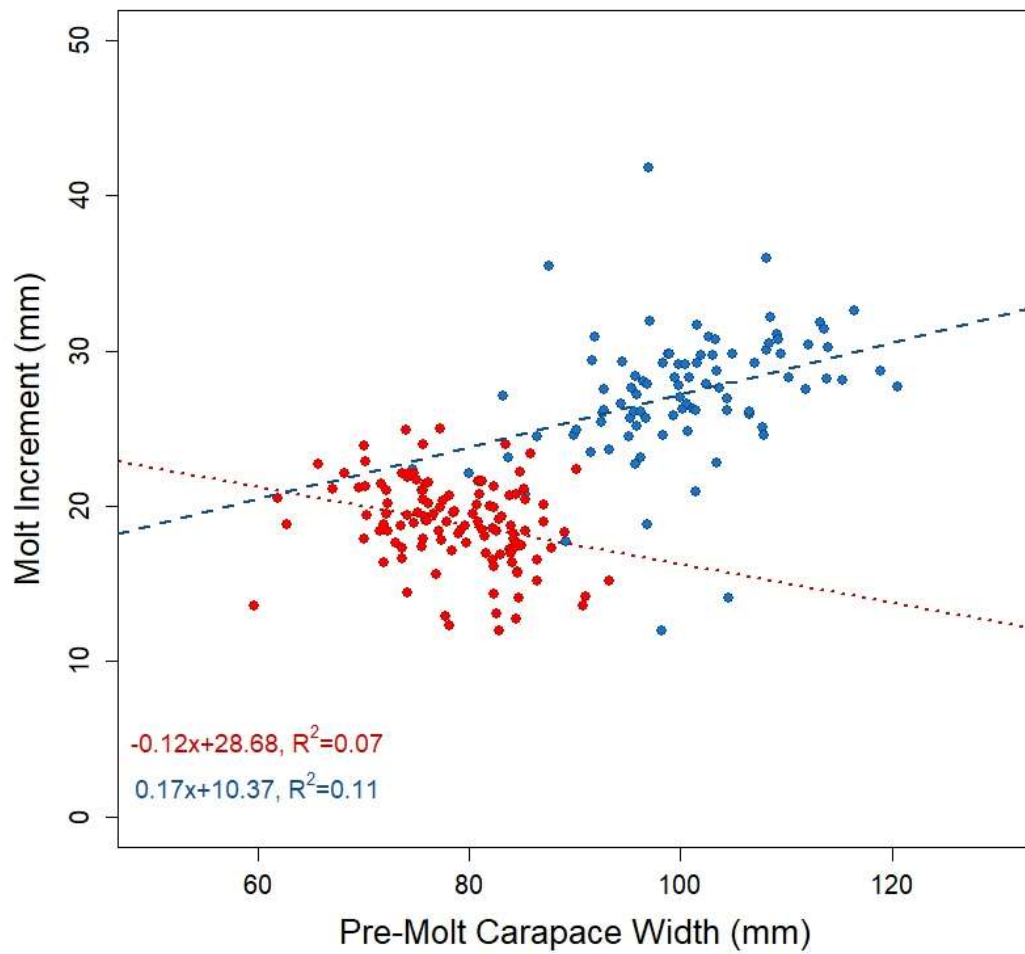


Figure 4. Molt increments by pre-molt carapace width showing changes in growth per molt with increase in carapace width. Males are indicated in blue and females are in red, with linear regressions fitted to each sex. Linear regressions for both sexes are significantly different from zero ($p < 0.05$).

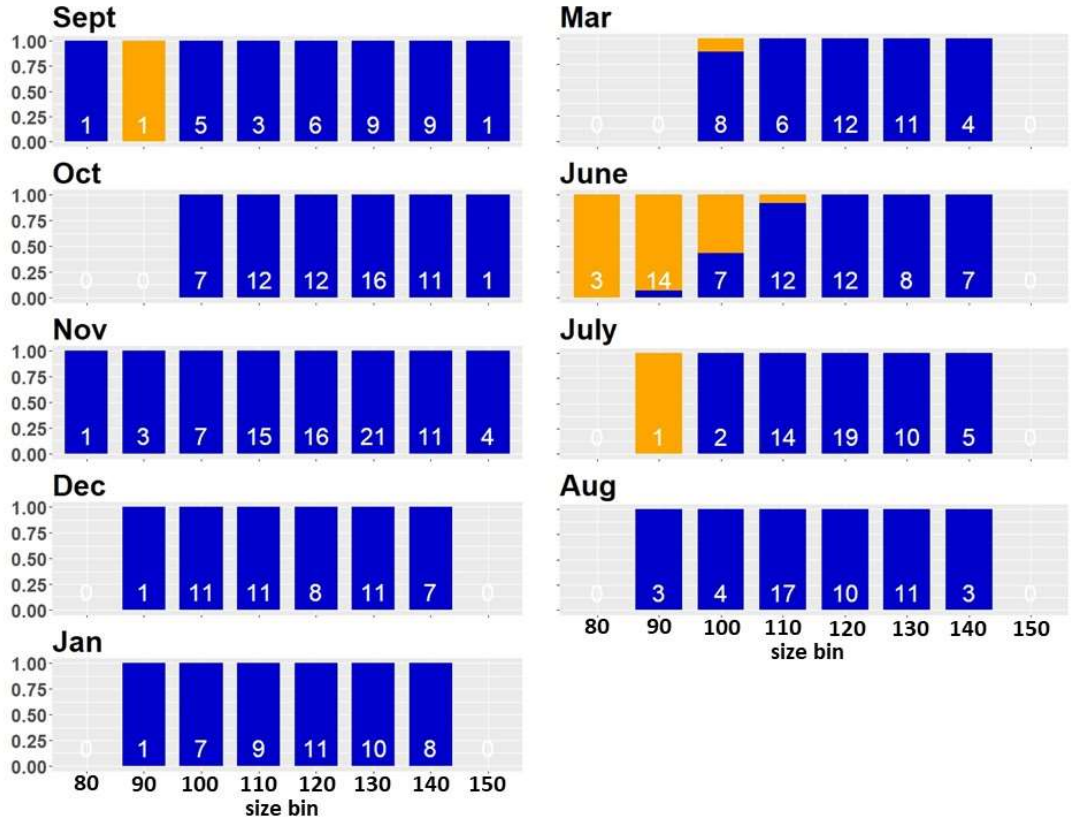


Figure 5. Occurrence of ecdysis in male Jonah crabs, by size bin and month collected, September 2016 to August 2017. Orange and blue proportions indicate crabs that did and did not molt, respectively, within 30-day observation period. Sample sizes are indicated in white within each size bin.

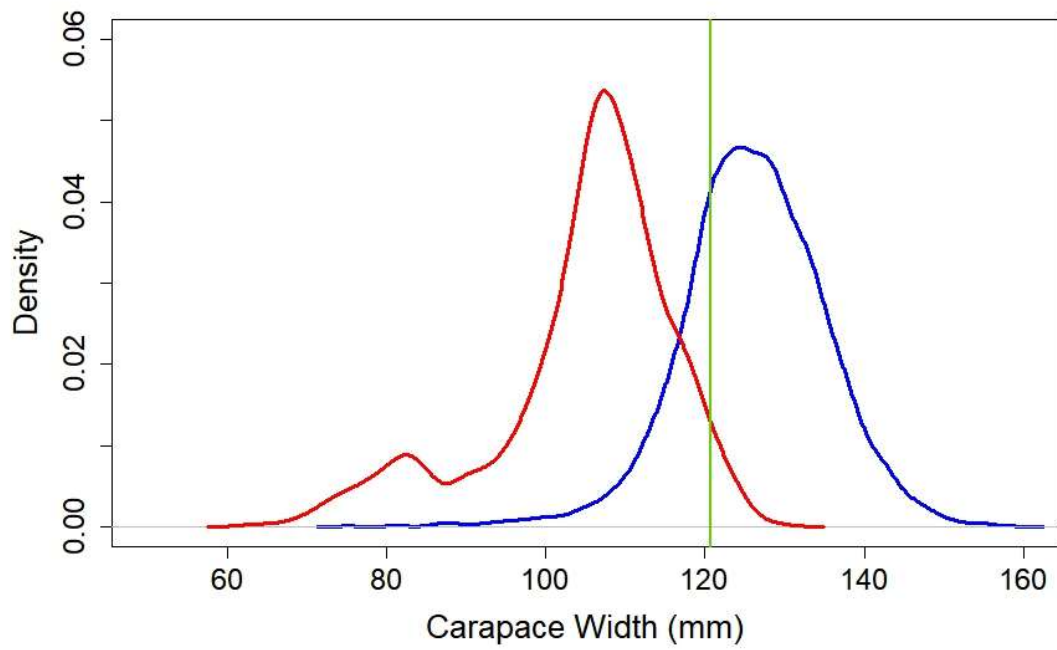


Figure 6. Carapace width density plot of commercially-caught male (blue) and female (red) Jonah crabs in study area. Green line represents legal minimum size for commercial fishery.