Article type : Article

Size at Maturity, Shell Conditions, and Morphometric Relationships of Male and Female Jonah Crabs *Cancer borealis* in the Mid-Atlantic Bight

Noelle A. Olsen[1]* and Bradley G. Stevens[1]

[1]University of Maryland Eastern Shore, Department of Natural Sciences, 1 College Backbone Rd, Princess Anne, Maryland, 21853, USA

Email: bgstevens@umes.edu

*Corresponding author email: noelleaolsen@gmail.com

Short Title: Size at maturity for male Jonah crabs

Keywords: Jonah crabs, Crustacea, Decapoda, maturity, reproduction, Mid-Atlantic Bight

ABSTRACT

Jonah crabs *Cancer borealis* are a data-poor species with an unknown stock status and were historically caught as bycatch in American lobster *Homarus americanus* traps. The decline of the Southern New England lobster stock since 1990 helped stimulate a targeted fishery and a 6-fold increase in both the landings and ex-vessel value of Jonah crab. Current knowledge on Jonah crab growth and reproduction is scarce and dated. Therefore, this research focused on updating fundamental biological information for Jonah crabs in the Mid-Atlantic Bight. Morphometric analyses determined that male crabs reach size at 50% sexual maturity (SM_{50}) at 98.31 ± 1.4 mm carapace width (CW), and female crabs reach SM_{50} at 88.2 mm CW. These values are below the current minimum legal size. An increase in the proportion of female crabs in a new-shell condition during the spring and summer months suggests a seasonal mating period. Expanding available information will substantiate accurate appointment of minimum legal sizes, minimize discard mortality, and increase understanding of stock dynamics, thus improving management and long-term sustainability for the Jonah crab fishery.

INTRODUCTION

Jonah crab *Cancer borealis* have been landed historically as bycatch in the fishery for American lobster *Homarus americanus*, and a steep decline in the Southern New England (SNE) lobster stock in the late 1990s helped stimulate a targeted fishery and growing market for Jonah crab. Increased sea temperatures and poor stock recruitment are associated with the decline of the SNE lobster stock (Bell 2010). Over the past two decades, both the landings and ex-vessel value of the Jonah crab fishery have increased 6-fold (ACCSP 2018). Jonah crabs are found along the eastern coast of North America from Newfoundland to Florida, but the majority of landings come from Massachusetts (~70%) and Rhode Island (~24%) (Lewis and Ayers 2014, ASMFC 2015). In addition to a whole-crab fishery, there is a small, historic claw fishery in New Jersey, Delaware, Maryland, and Virginia which accounts for only about 1% of the fishery (ASMFC 2015). In 2018, about 10,076 t of Jonah crabs were landed with a total ex-vessel value of $18.5 million USD (ACCSP 2018). From 2010–2015, about 75 t of Jonah crab claws were harvested, although this is likely an underestimate due to underreporting (ASMFC 2017). In comparison, about 9,335 t of Dungeness crabs *Cancer magister* were landed in the 2018–2019 season in Oregon with a total ex-vessel value of $66.7 million USD (OR DFW 2019). From 2010 to 2015, about 7,431 t of stone crab (*spp. Menippe*) claws, a claw-only fishery, were harvested in Florida (FL FWC).

The Jonah crab fishery is managed as a mixed crustacean fishery in conjunction with the lobster fishery so as not to impact the number of vertical lines and traps in state and federal waters, as recommended by the American Lobster Board of the Atlantic States Marine Fishery

Commission (ASMFC). The ASMFC implemented an Interstate Fishery Management Plan (FMP) for Jonah crab in June 2016 (ASMFC 2015). There is a minimum legal size (MLS) of 4.75” or 120.65 mm carapace width (CW), a minimum chela length of 2.75 in (69.85 mm) if more than five gallons of claws are harvested, and a prohibition on retaining ovigerous female crabs (ASMFC 2015, 2016, 2017). NOAA Fisheries adopted similar management regulations for federal waters in December 2019 (NMFS 2019). In fishery management, minimum legal size limits are typically based on size at maturity to give individuals an opportunity to reproduce before being harvested but are sometimes an artifact of market preference (Goshima et al. 2000, Worton et al. 2010).

Crustacean sexual maturity can be defined by a variety of physical, physiological, and behavioral indicators. The size at 50% maturity (SM_{50}) refers to the size at which at least 50% of the population is considered mature and may differ based on the indicator(s) of interest (Mente 2008). While physiological maturity (e.g. the development of reproductive organs) is often reached at smaller sizes than morphometric maturity (e.g. the development of secondary sexual characters), morphometric techniques have an advantage in that measuring a crab in the field (and during fishing operations) can be done quickly and without sacrificing the animals (Goshima et al. 2000, Mente 2008). Morphometry has been used to determine the SM_{50} in a wide variety of decapod crustaceans: male stone crab *Hapalogaster dentate* from Hakodate Bay, Japan (Goshima et al. 2000); male and female spider crab *Maja brachydactyla* from the Ría da Coruña estuary in Galicia, Spain (Corgos and Freire 2006); and, male and female red king crab *Paralithodes camtschaticus* and male tanner crab *Chionoecetes bairdi* from the eastern Bering Sea (Somerton 1980).

There have been relatively few studies conducted on morphometric maturity of Jonah crabs. The SM_{50} of male Jonah crabs from the Scotian Shelf was estimated to be 127.6 mm CW by comparing the allometric relationship between CW and chela propodus height (ChH) (Moriyasu et al. 2002). Some male crabs with a carapace width greater than 150 mm CW exhibited a blackened scar on their chelae caused by copulation, although this scar may not appear in recently molted crabs (Moriyasu et al. 2002). In a lab experiment using Jonah crabs collected from Grand Manan, Bay of Fundy, various types of lengthy embraces were exhibited throughout the copulation process in which the male Jonah crab used its chelipeds and anterior walking legs to cover and carry the female crab (Elner et al. 1985). Carpenter (1978) collected

Jonah crabs from the Norfolk Canyon and noted a gradual increase in the relative size of the abdomen width (AW) to CW in female crabs < 59 mm CW, found an accelerated increase in relative size of AW to CW in female crabs ≥ 60 mm CW, and concluded that a fully functional female abdomen was achieved by 90 mm CW. Rather than a large increase in the size of the abdomen relative to the body, Carpenter (1978) found a gradual increase in the allometric relationship between carapace length (CL) and CW, suggesting that female crabs did not undergo a pubertal molt.

The overall goal of this research was to estimate the size at 50% sexual maturity of male and female Jonah crabs in the Mid-Atlantic Bight using morphological techniques. In addition to an individual's maturity status, its stage in its molt cycle is an important factor that regulates its ability to copulate (Hartnoll 1969). Thus, the shell condition of each crab was scored to indicate relative time since last molt. Copulation is often restricted to when female crabs have softer shells post-ecdysis, so female shell condition may indicate when mating cycles occur (Hartnoll 1969). Morphometric relationships are useful for predicting the size of body parts, and would be helpful for determining the size of declawed crabs from their landed chelae. Carapace width is commonly used as a measure of size for crabs, but can be quite variable, especially if the measurement includes lateral spines that can wear down or break. Carapace length, however, is a more accurate measurement, as are width measurements taken anterior to the spines (Stevens and Guida, 2016). For example, Stevens and Guida (2016) used CL to define the SM_{50} for red deep-sea crabs because it is a more consistent measurement than CW used by other studies; similarly, our definition of CW (see Methods) is more accurate than width between spine tips (herein defined as SW) due to spine erosion over time. Thus, a complete cross reference of morphometric relationships for exploited crab species is highly useful for management and other purposes.

METHODS

Sampling

From December 2015 to September 2017, 1,473 Jonah crabs were collected from the Mid-Atlantic Bight (MAB) using a variety of methods. Crabs were predominantly caught as bycatch in lobster and black sea bass pots from commercial fishing vessels operating out of West Ocean City, Maryland and Bethany Beach, Delaware. The general area fished included the following geographic boundaries: 37.7249 – 38.71028˚ N; 74.34333 – 74.97732˚ W (Fig. 1). Lobster and black sea bass traps used were constructed of 2.5 cm (1 in) plastic-coated wire mesh and followed federal regulations for American Lobster Management Area 5. In general, twenty traps were attached to each fishing rig and soaked for two weeks. Additional Jonah crabs were targeted directly using 0.057 m^3 (2 ft^3) ventless crab traps with 2.5 cm wire mesh within the same region of the MAB in 2017. Because a majority of the sampling occurred under normal commercial fishing operations, typically, the first 50 or so Jonah crabs were kept for processing and were roughly equal in terms of sex ratio. Selective sampling techniques were used to target both male and female Jonah crabs within specific carapace width size ranges in order to have representation from all size classes possible. Four, two, and three baited ventless traps were used on June 13, 2017, August 14, 2017, and September 15, 2017, respectively. Crabs were kept on ice until processed.

During May 5 – 28, 2016, 174 Jonah crabs were caught as bycatch in the Virginia Institute of Marine Science (VIMS) Mid-Atlantic sea scallop dredge survey. In 2017, 74 additional Jonah crabs were collected by the same survey. All bycaught Jonah crabs from the VIMS survey were kept, but only crabs collected below 39° N. latitude were included in the analyses, in order to maintain geographic consistency with those caught in traps (Fig. 1). Crabs were kept frozen until processed. Dredge survey implementation and methodology can be found in Rudders and Roman (2016).

Morphometrics, Shell Condition, and Size at 50% Maturity (SM_{50})

Each crab was sexed and the shell condition of their carapace was classified into 4 standard categories, defined by NOAA Fisheries for brachyuran crabs, indicating relative time since molting (Jadamec et al. 1999). We have adapted these categories (as described by Stevens and Guida, 2016) as new, hard, old, or very-old. New-shell crabs have no sign of dark coloration or abrasions on their carapace or sternum with pointy spines on their carapace (Fig. 2A, Stevens and Guida 2016); paper-shell crabs were also classified as a new-shell crab. Hard-shell crabs begin to show some discoloration on the carapace and sternum (Fig. 2B); old-shell crabs have many more areas with discoloration and abrasions with dull carapace spines (Fig. 2C); and, very old-shell crabs' carapaces and sternums are almost entirely discolored with many abrasions and typically have epibiota (Fig. 2D). Wet weights of crabs were measured to the nearest gram using an A&D SK-2000WP[1] balance, except for some small crabs (carapace width less than 46 mm) which were weighed to the nearest 0.1 mg using a Mettler Toledo® MS104S analytical balance. Morphometric measurements were made to the nearest 0.01 mm using Mitutoyo ABSOLUTE IP67 (500-764-10)[1] electronic calipers and include:

1. Carapace length (CL)—the distance from the right eye socket to the center of the posterior edge of the carapace.
2. Carapace width (CW)—the distance between indentations anterior to the lateral spines of the carapace.
3. Spine width (SW)—the distance between the outer tips of the lateral spines of the carapace.
4. Abdomen width (AW)—the widest part of segment six of the female abdomen.
5. Chela length—the length measured horizontally along the base of the proprodus of the right chela (RChL) and left chela (LChL) (Fig. 3).
6. Chela height—the greatest propodus height excluding spines of the right chela (RChH) and left chela (LChH) (Fig. 3).
7. Chelae weight (ChW)—the combined wet weight of the right and left chelae, separated along the basi-ischium plane.

Statistical Analyses

Relationships between CL, CW, SW, RChL, RChH (male crabs), AW (female crabs), LChL, LChH, and ChW were calculated using geometric mean (GM) functional regression. GM functional regressions are used when both the predictor and response variables are random continuous numbers rather than predetermined values and variability is mainly natural rather than being due to measurement error (Ricker 1973, 1975). GM functional regression has the additional advantage that it can be used to predict either variable from the other, because variance is equal in both directions. All predictor and response variables were transformed to natural logs (ln). Analyses of covariance (ANCOVA) were performed to determine if there were significant differences in the slopes (B_1) of the linear regressions between the sexes for each combination of predictor and response variable tested except for male RChH and female AW. Regression analyses were performed separately for each sex if significant differences were found

---

[1] Mention of trade names does not imply endorsement by the University of Maryland Eastern Shore.

between their B_1 terms. The slope of a GM functional regression (B_{1F}) is calculated from the slope (B_1) of a simple linear regression using the following formula:

$$B_{1F} = B_1 \cdot R^{-1}$$

Where R, the correlation coefficient, is calculated as

$$R = \rho(x, y) = \mathrm{cov}(x, y) \cdot (\sqrt{\mathrm{var}(x) \cdot \mathrm{var}(y)}\ )^{-1}$$

The intercept or B_0 term (B_{0F}) is calculated by the following formula:

$$B_{0F} = \bar{y} - B_{1F} \cdot \bar{x}$$

A Pearson's Chi-squared test for independence (X^2) was performed to see whether shell condition (paper or new, hard, old, very old) is independent from both season (e.g. spring, summer, fall, winter) and maturity status (e.g. immature or mature). Male and female crabs were analyzed separately. A significance level of 0.05 was used.

The SM_{50} was calculated separately for male and female crabs using two different R (R Core Team, 2019) applications called "Crab Maturity". "Crab Maturity" was developed by Bradley Stevens and based on Somerton's (1980) methods of determining size at sexual maturity in male and female *P. camtschatica* and male *C. bairdi*. Somerton (1980) used the relationship between ChH and CL for *P. camtschatica* and the relationship between ChH and CW for *C. bairdi*. The program used for male Jonah crabs in this study has three major steps and is based on the relationship between ChH and CW. To account for missing chelae or male crabs with one regenerated chela, the chela with the largest ChH was used in the SM_{50} analysis because Jonah crabs have symmetrical chelae. In the first step, crabs were assigned to known immature, known mature, or unknown groups based on a visual assessment of the data, assuming that the smallest crabs were immature, and the largest crabs were mature. The upper and lower boundaries of CW for the unknown crabs were varied to find the values which produce the best fit, based on whichever boundaries produce the highest *F*-ratio value. In this analysis, we tested a combination of lower boundaries in the range 60 – 90 mm and upper boundaries in the range 110 – 120 mm in 5 mm intervals, totaling 21 combinations. In the second step, natural log transformed (ln) ChH was regressed against ln(CW) separately for the known immature crabs, and for the known mature crabs. The crabs that fell within the unknown boundaries were then assigned to either the known immature or known mature regression lines based on proximity. This was repeated until no points changed lines and all crabs were assigned a maturity status.

In the third step, crab maturity status was logistically regressed against CW using a generalized linear model (GLM) with a binomial link. This method uses a logit model, in which linear regression is used to predict the logit, defined as the log of the odds (P/(1-P)):

$$\text{Log}\left(\frac{p(X)}{1-p(X)}\right) = C_0 + C_1 X$$

This model differs from that used by Somerton (1980); we also use C_0 and C_1 to label the intercept and coefficient parameters in order to distinguish them from B_0 and B_1 used in the GM model above. The inflexion point of the GLM curve is defined as SM_{50}, or the CW at which at least 50% of the male crabs are classified as mature, and is calculated by the following formula:

$$SM_{50} = -C_0 \cdot C_1^{-1}$$

The Standard error (SE) of SM_{50} was estimated by a bootstrap technique which resampled the data with replacement and calculated the mean estimate of SM_{50} 1000 times (n = 552). The confidence interval around the mean SM_{50} was calculated as 1.96 · SE.

Female SM_{50} was calculated using a broken-stick regression version of "Crab Maturity". Both AW and CW were natural log transformed. Similar to the process used to estimate SM_{50} for male crabs, CW boundaries were selected to assign crabs to one of three categories: known immature, known mature, and unknown. Boundaries for unknown crabs that were tested ranged from 60 to 90 for the low end and 110 to 120 at the upper end. Initially, AW was regressed against CW using all data points using a linear equation. Two separate regression lines were then created, with the first breakpoint being the data point with the smallest CW and an unknown maturity status. The R application then iteratively re-assigned the breakpoint to the remaining data points that fell within the selected unknown range while re-estimating the parameters of the two regression lines with each new breakpoint. The program ran until all data points within the unknown ranges were tested and selected the breakpoint that created the smallest pooled residual sums of squares (RSS) for the two regression lines, which is defined as SM_{50} for female crabs. The two-line solution was then compared to the single-line solution using a comparison F-value, calculated as the ratio of the difference mean square ($MS_{diff} = (RSS_{single}$ –

RSS_{pool})/2) to the pooled mean square ($F = MS_{diff}/MS_{pool}$), and, if significant, the two-line solution is considered a better choice than the single-line RSS.

RESULTS

Morphometrics and Shell Condition

A total of 564 male and 798 female Jonah crabs were caught in 2016 and 2017 from the Mid-Atlantic Bight. Male crabs reached larger sizes than female crabs (Fig. 4). The mean width of male crabs was 97.38 ± 26.03 mm CW (mean ± SD) with a range of 19.14 – 159.74 mm CW, whereas the mean width of female crabs was 90.53 ± 15.78 mm CW with a range of 25.22 – 122.32 mm CW. About 22% of male crabs and 1% of female crabs caught were larger than the minimum legal size limit of 120.65 mm CW (n = 123, n = 10, respectively). The minimum legal claw length is 69.85 mm RChL (or LChL) when at-sea claw harvests exceed five gallons. About 12% (n = 68) of male crabs had at least one claw that exceeded the MLS, and no female claws exceeded the minimum size limit. On average, claws make up about 27% of the overall body weight for male crabs and about 19% for female crabs. Using the MLS of 120.65 mm CW, the predicted mean chela lengths are 66.0 mm RChL (or LChL) for male crabs and 55.6 mm RChL (or LChL) for female crabs. Mean CW predicted from the minimum claw length is 126.3 mm CW for male crabs and 150.3 mm CW for female crabs.

Sexual dimorphism was evident in the majority of morphometric comparisons. Sex was found to be a significant factor in the ANCOVA analyses ($p < 0.0001$) for each combination of predictor and response variables except for the following cases: LChH vs. LChL, LChH vs ChW, RChL vs. ChW, and RChL vs. LChL (Table 1). For these relationships, a combined GM regression equation was calculated for both sexes.

There was a significant relationship between shell condition and season for both male and female Jonah crabs. Chi-squared analyses were performed separately for male crabs ($X^2 = 86.47$, df = 9, $p < 0.0001$) and female crabs ($X^2 = 117.35$, df = 9, $p < 0.0001$). For female crabs, the proportion of new-shell crabs remained almost constant throughout the spring and summer but decreased during the fall (Fig. 5). One post-molt, softshell (i.e. "paper shell") female crab was collected via trap on June 22, 2017 and was given a score of 1. The proportion of new-shell crabs increased throughout the spring to the fall for male crabs, which suggests varying molting cycles between the two sexes (Fig. 5). Neither sex had new-shell crabs present throughout the winter (Fig. 5).

There was also a significant relationship between shell condition and maturity status, as defined by the estimated SM_{50} values, for both male and female Jonah crabs (Table 2). Immature male crabs had all four shell types similarly represented, but mature male crabs included very few new-shell crabs and the highest proportion of very-old-shell crabs (Table 2). Immature female crabs were predominately new- and hard-shell crabs, and, similar to male crabs, the smallest proportion of mature female crabs were new-shell crabs (Table 2). In general, the highest proportion of new-shell crabs occurred among the smaller size classes for both male and female crabs (Fig. 6). Likewise, the highest proportions of old- and very old-shell crabs occurred among the larger size classes for both sexes (Fig. 6). It is unknown whether Jonah crabs undergo a terminal molt, but the largest male and female new-shell crabs were 152.44 mm CW and 112.66 mm CW, respectively. The largest male and female very old-shell crabs were 156.13 mm CW and 122.32 mm CW, respectively. The smallest male and female very-old-shell crabs were 70.24 mm CW and 78.62 mm CW, respectively.

Size at 50% Maturity (SM_{50})

The lower and upper boundaries for an unknown maturity status for male Jonah crabs which produced the highest F-value were (log-transformed) 60 mm and 120 mm CW, respectively. "Unknown" crabs within that range were assigned to the closest regression line. The residual sums of squares (RSS) for the single-regression line analysis was 82.71, whereas the RSS for the two-regression line solution was 1.809. The comparison F-value was 219 ($p < 0.0001$), supporting the conclusion that two lines were superior to a single line (Fig. 7). Smaller, regenerated chelae created some outliers seen in Figure 7. The coefficients estimated by the generalized linear model were $C_0 = -19.87$ and $C_1 = 0.2021$, and the bootstrap procedure produced an estimated SM_{50} for male Jonah crabs of 98.31 ± 1.4 mm CW (Fig. 8).

A broken-stick regression was fit to natural log-transformed AW and CW of female crabs (Fig. 9). The lower and upper boundaries that produced the lowest F-value were (log-transformed) 70 mm and 110 mm CW, respectively. The residual sums of squares (RSS) for the single-regression line analysis was 1.538, whereas the RSS for the two-regression line solution was 1.415. The comparison F-value was 34.3 ($p < 0.0001$), so the two-line solution was considered the better choice. The SM_{50} for female Jonah crabs estimated by the breakpoint of this regression occurred at 88.2 mm CW (Fig. 9).

DISCUSSION

The results suggest that, within the Mid-Atlantic Bight, 50% of male crabs reach sexual maturity nearly 20 mm below the MLS of 120.65 mm CW and 50% of female crabs reach maturity about 30 mm below the MLS (ASMFC 2015). The male SM_{50} estimate is similar to Carpenter's (1978) maturity range of 90 – 100 mm CW which coincided with the development and presence of spermatophores in the vas deferens. The female SM_{50} estimate is consistent with a previous female maturity range of 80 – 90 mm CW, based on the relationship between CL and SW in the Chesapeake Bight (Carpenter 1978). Currently, there is no female SM_{50} estimate from a northern region like Nova Scotia; however, Hines (1991) collected 11 ovigerous females in lobster traps in Boothbay Harbor, ME in July 1984, and the mean size of the females was 120 mm CW (range 105–139 mm CW, n = 11) which is just below the minimum legal size. For male crabs, however, Moriyasu et al. (2002) estimated SM_{50} to be 127.6 mm CW in the Scotian Shelf using methods similar to "Crab Maturity", by finding a conspicuous change in allometry between chela length and CW. This suggests there is latitudinal variation in Jonah crab size and size at maturity throughout its range.

Such geographic variation in female size at sexual maturity has been documented in brachyuran families including Lithodidae, Cancridae, Grapsidae, Majidae, Portunidae, and Oregoniidae (Mente 2008, Orensanz et al. 2007, Webb 2014). Variation in molt frequency and/or the number of molts required to reach maturity can manifest into variation in size at maturity (Orensanz et al. 2007, Hines 1989). Multiple factors influencing size at maturity in crustaceans have been suggested, including: phenotypic plasticity related to age and development (Orensanz et al. 2007); temperature and temperature-photoperiod interactions, predation levels, discontinuities in currents that affect thermal regimes and larval dispersal, and food availability (Hines 1989); and, population density and the availability of mates (Annala et al. 1980).

The correlation between body size and latitude exhibited by many species is known as Bergmann's or James's Rule, and is generally assumed to represent an inverse relationship between size and temperature (Blackburn et al. 1999). In contrast, some species, particularly arthropods, exhibit smaller body mass with increasing latitude (or decreasing temperature), a phenomenon known as inverse-Bergman/James's rule (Blanckenhorn and Demont 2004). An inverse James's cline, i.e. positive correlation between size and temperature, has been reported for mean size at maturity of female snow crabs *C. opilio* in Alaska (Somerton 1981), and for both male and female snow crabs in eastern Canada (Sainte-Marie and Gilbert 1998), median CW for both sexes of snow crab in western Greenland (Burmeister and Sainte-Marie 2010), mean size of ovigerous females in red and blue king crabs (*Paralithodes camtschaticus* and *P. platypus*) as well as golden king crab *Lithodes aequispinus* (Webb 2014), and both mean size (Stevens and Guida 2016) and size at maturity (Martínez-Rivera et al. 2020) of red deep-sea crab *Chaceon quinquedens*. Burmeister and Sainte-Marie (2010) hypothesized that the increased size at maturity with temperature in *C. opilio* was due to more frequent molting, the onset of maturity at a specific age, and constant relative growth increment, allowing crabs to reaching a higher instar number in a limited time period. In this regard, Jonah crab is an unusual example of a crustacean exhibiting James's cline in size at maturity.

Differences in age and size at maturity along a geographic gradient could have substantial implications for the reproductive output for Jonah crabs which, in turn, could influence stock structure and management practices (Smith and Addison 2003). If management does not account for latitudinal differences in size at sexual maturity, the effects on stock structure could become exacerbated because of the disparity in fishing effort among the Atlantic states.

Both Carpenter (1978) and Moriyasu et al. (2002) used carapace width measured across the widest spine tips as their measure of crab size. We have found, however, that spine-to-spine measurements, which we renamed spine width (SW), can be quite variable among both crabs and observers, and that width measured across the widest part of the carapace anterior to the largest spines (our carapace width) is a more reliable measure. Even more reliable, however, is carapace length, as described herein. Different measures of chela size are also used by different authors, so we have provided measures of both chela height and length. Because Jonah crab are occasionally declawed and discarded, the relationships between body size or weight and chela size or weight can be useful for back-calculation of landed crab size. In addition, chela-carapace relationships are typically based on a single claw, but regeneration of chelipeds can make these highly variable. Thus it is useful to know the relationship of both claws, so that they can be substituted.

The proportion of types of shell conditions varied seasonally for both male and female Jonah crabs (Fig. 5). Molting and reproduction are two inextricably linked and cyclical processes for crustaceans (Shields 1991). The proportion of recently molted female crabs, indicated by a new-shell condition, was greatest during spring and summer months, which may indicate a spike in mating (Fig. 5). Jonah crabs are known to mate while the female crab is in a new-shell condition, and a decrease in the proportion of new-shell females throughout the fall and winter help support the hypothesis that the end of summer is the peak mating season (Elner et al. 1985, Fig. 5). The proportions of male shell conditions exhibited a slightly different pattern than that of female crabs. There was an increase in the proportion of new-shell male crabs from spring to fall which may be dependent on the maturity status of the crab. The proportion of shell types also varied by maturity status for both male and female Jonah crabs, as defined by their estimated SM_{50} values (Table 2). A conspicuous change in morphometric relationships and relative growth rates occurs between immature and mature crabs (Mente 2008). Thus, the frequency at which crabs molt will differ at different stages in their lives (e.g. immature vs. mature). In general, immature crabs exhibited a higher proportion of new-shell crabs, likely because they are molting more often, and this was more apparent in male crabs (Table 2). In contrast, mature crabs should molt less often and have the highest proportion of very old-shell crabs. This was more apparent in female crabs (Table 2). An investigation in physiological or gonadal maturity indicators of both sexes would complement the information provided by the changing proportions of shell condition throughout the year.

The results from this study have the potential to help inform management regulations for the Jonah crab fishery. The estimated morphometric SM_{50} values for both male and female Jonah crabs in the Mid-Atlantic are below the MLS which increases the probability that Jonah crabs are able to reproduce at least once before being removed from the fishery. However, the physiological and functional maturity of Jonah crabs should also be investigated to better understand the reproductive potential of crabs at various sizes (Goshima et al. 2000). Male crabs are disproportionately targeted over female crabs by both the whole-crab and claw-only fisheries as an artifact of their larger sizes and larger chelae. Furthermore, legal-sized female crabs removed by the fishery are nearing their maximum CW limits and are considered the most fecund individuals in the population (Mente 2008). Without a formal stock assessment, it is unclear how these factors will affect the population structure and the sustainability of the fishery.

Future studies should incorporate randomized sampling and environmental data to understand the distribution of Jonah crabs within the Mid-Atlantic Bight. The results from a tagging or ageing study could provide estimates of growth rates, natural mortality rates, and size-at-age (Wilson 2017). Given that about 95% of commercial Jonah crab landings occur in New England, SM_{50} should be determined at varying latitudes to sufficiently manage and provide long-term sustainability for the Jonah crab throughout its entire range.

ACKNOWLEDGEMENTS

Funding for this research was provided by the NOAA Educational Partnership Program and the NOAA Living Marine Resources Cooperative Science Center at the University of Maryland Eastern Shore (Grant NA11SEC4810002). We thank Wes and Chet Townsend for allowing us to sample during their fishing trips and for providing additional Jonah crabs when we couldn't join them at sea. We thank Sally Roman, Dr. David Rudders, and their at-sea crew from the Virginia Institute of Marine Science (VIMS) for providing the Jonah crabs from the VIMS Mid-Atlantic sea scallop dredge survey. Special thanks to Edwin Sánchez, Melati Tarrant, and Rebecca Peters for their assistance and support.

REFERENCES

Annala, J.H., J.L. McKoy, J. D. Booth, and R. B. Pike. 1980. Size at the onset of sexual maturity in female *Jasus edwardsii* (Decapoda: Palinuridae) in New Zealand. New Zealand Journal of Marine and Freshwater Research 14:217–227.

Atlantic Coastal Cooperative Statistics Program (ACCSP). 2018. Non-confidential Commercial Landings: Annual Summary for 2018, US Atlantic Coast, CRAB, JONAH; generated using Public Data Warehouse [online application], Arlington, VA: Available at https://www.accsp.org (accessed May 12, 2020).

Atlantic States Marine Fisheries Commission (ASMFC). 2015. Interstate Fishery Management Plan for Jonah Crab. Atlantic States Marine Fisheries Commission, Arlington, VA. 73p.

Atlantic States Marine Fisheries Commission (ASMFC). 2016. Addendum I to the Interstate Fishery Management Plan for Jonah Crab. Atlantic States Marine Fisheries Commission, Arlington, VA. 5p.

Atlantic States Marine Fisheries Commission (ASMFC). 2017. Addendum II to the Interstate Fishery Management Plan for Jonah Crab. Atlantic States Marine Fisheries Commission, Arlington, VA. 12p.

Bell, M.C. 2010. Recruitment Failure in the Southern New England Lobster Stock. External Independent Peer Review, Center for Independent Experts for the ASMFC Lobster Technical Committee. 32 pp.

Blackburn, T. M., K. J. Gaston, and N. Loder. 1999. Geographic gradients in body size: a clarification of Bergmann's rule. Diversity and Distributions 5:165-174.

Blanckenhorn, W. U., and M. Demont. 2004. Bergmann and Converse Bergmann Latitudinal Clines in Arthropods: Two Ends of a Continuum? Integrative and Comparative Biology 44:413-424.

Burmeister, A., and B. Sainte-Marie. 2010. Pattern and causes of a temperature-dependent gradient of size at terminal moult in snow crab (*Chionoecetes opilio*) along West Greenland. Polar Biology 33:775-788.

Carpenter, R. K. 1978. Aspects of growth, reproduction, distribution and abundance of the Jonah crab (*C. borealis*) Stimpson in Norfolk Canyon and the adjacent slope. University of Virginia, Charlottesville, Virginia. 69 pp.

Elner, R. W., C. A. Gass, and A. Campbell, 1985. Mating behavior of the Jonah crab, Cancer borealis Stimpson (Decapoda, Brachyura). Crustaceana 48:34–39.

Florida Fish and Wildlife Conservation Commission (FL FWC). Commercial Fisheries Landings Summaries: Annual Summary for 2010–2015, CRAB, STONE, CLAWS (All grades); generated using Public Fisheries-Dependent Monitoring [online application], Tallahassee, FL: Available at https://public.myfwc.com/FWRI/PFDM/ (accessed May 12, 2020).

Goshima, S., M. Kanazawa, K. Yoshino, and S. Wada. 2000. Maturity in male stone crab *Hapalogaster dentata* (Anomura: Lithodidae) and its application for fishery management. Journal of Crustacean Biology 20:641–646.

Hines, A.H. 1989. Geographic variation in size at maturity in Brachyuran crabs. Bulletin of Marine Science 45:356–368.

Hines, A. H. 1991. Fecundity and Reproductive Output in 9 Species of Cancer Crabs (Crustacea, Brachyura, Cancridae). Canadian Journal of Fisheries and Aquatic Sciences 48:267–275.

Jadamec, L. S., W. E. Donaldson, and P. Cullenberg. 1999. Biological field techniques for *Chionoecetes* crabs. University of Alaska Sea Grant Program, Anchorage, AK. 80 pp.

James, F. C. 1970. Geographic Size Variation in Birds and Its Relationship to Climate. Ecology 51:365-390.

Lewis, L. and J. Ayers. 2014. Temperature preference and acclimation in the Jonah Crab, *Cancer borealis*. Journal of Experimental Marine Biology and Ecology 455:7–13.

Martínez-Rivera, S., W. C. Long, and B. G. Stevens. 2020. Physiological and behavioral sexual maturity of female red deep-sea crabs *Chaceon quinquedens* (Smith, 1879) (Decapoda: Brachyura: Geryonidae) in the Mid-Atlantic Bight. Journal of Crustacean Biology 40:330-340.

Mente, E. 2008. Reproductive biology of crustaceans: case studies of decapod crustaceans. Science Publishers, New Hampshire.

Moriyasu, M., K. Benhalima, D. Duggan, P. Lawton, and D. Robichaud. 2002. Reproductive biology of male Jonah crab, *Cancer borealis* Stimpson, 1859 (Decapoda, Cancridae) on the Scotian Shelf, Northwestern Atlantic. Crustaceana 75:891–913.

National Marine Fisheries Service (NMFS). 2019. Fisheries of the Northeastern United States; Jonah Crab Fishery; Interstate Fishery Management Plan for Jonah Crab. Federal Register 84:219(13 November 2019):61569–61579.

Oregon Department of Fish and Wildlife (OR DFW). 2019. 11th Annual Oregon Department of Fish and Wildlife Marine Resources Program Dungeness Crab Fishery Newsletter, November 2019. 8pp.

Orensanz, J.M.L., B. Ernst, and D.A. Armstrong. 2007. Variation of female size and stage at maturity in snow crab (*Chionoecetes Opilio*) (Brachyura: Majidae) from the Eastern Bering Sea. Journal of Crustacean Biology 27:576–591.

R Core Team 2019. R: A language and environment for statistical computing. R Foundation for statistical Computing, Vienna, Austria. URL http://www.R-project.org/.

Ricker, W. 1975. Computation and Interpretation of Biological Statistics of Fish Populations. Bulletin of the Fisheries Research Board of Canada, Vol. 191. Dept. of the Environment, Fisheries and Marine Service, Ottawa, CA. 382 pp.

Ricker, W. 1973. Linear Regressions in Fishery Research. Journal of the Fisheries Research Board of Canada, 30:409–434.

Rudders, D., and S. Roman. 2016. Results for the 2015 VIMS/Industry Cooperative Survey of the Mid-Atlantic Sea Scallop Resource Area. Marine Resource Report No. 2016-3. Virginia Institute of Marine Science, William & Mary. 28 pp.

Sainte-Marie, B., and D. Gilbert. 1998. Possible effects of changes in CIL temperature and thickness on population dynamics of snow crab, *Chionoecetes opilio*, in the Gulf of Saint Lawrence. Fisheries and Oceans.

Shields, J.D. 1991. The reproductive ecology and fecundity of *Cancer* crabs. *Crustacean Egg Production*, pp.193–213.

Smith, M.T., and J.T. Addison. 2003. Methods for stock assessment of crustacean fisheries. Fisheries Research 65:231–256.

Somerton, D. A. 1980. A computer technique for estimating the size of sexual maturity in crabs. Canadian Journal of Fisheries and Aquatic Sciences 37:1488–1494.

Somerton, D. A. 1981. Regional variation in the size and maturity of two species of tanner crab (*Chionoecetes bairdi*, and *C. opilio*) in the eastern Bering Sea, and its use in defining management subareas. Canadian Journal of Fisheries and Aquatic Sciences 38:163-174.

Stevens, B.G., and V. Guida. 2016. Depth and temperature distribution, morphometrics, and sex ratios of red deepsea crab (*Chaceon quinquedens*) at 4 sampling sites in the Mid-Atlantic Bight. Fishery Bulletin 114:343–359.

Webb, J. 2014. Reproductive ecology of commercially important Lithodid crabs. Pages 285-314 *in* B. G. Stevens, editor. King Crabs of the World: Biology and Fisheries Management. CRC Press (Taylor and Francis), Boca Raton, FL.

Wilson, J. 2017. Age determination of red deep-sea crabs (*Chaceon quinquedens*) by growth ring analysis. MS Thesis, University of Maryland Eastern Shore. 57 pp.

Worton, C.L., D. Urban, K.M. Swiney, Z. Grauvogel, and S. Byersdorfer. 2010. Size at Physiological Maturity and Minimum Size at Functional Maturity for Male Dungeness Crabs in Alaska Waters. Biology and Management of Exploited Crab Populations under Climate Change. Alaska Sea Grant, University of Alaska Fairbanks. 22 pp.

TABLES

Table 1. Geometric mean relationships for male and female Jonah crabs (*C. borealis*). All intercept and slope values in this table were significant ($p < 0.0001$). All male-female comparisons were significant ($p < 0.0001$) except where noted as Both. Predictor and response

variables include carapace length (CL), weight, carapace width (CW), spine width (SW), right chela length (RChL), right chela height (RChH), abdomen width (AW), left chela length (LChL), left chela height (LChH), and the combined weight of the chelae (ChW). Other abbreviations include adjusted R^2 (Adj. R^2), and degrees of freedom (DF).

Predictor (X)	Response (Y)	Sex	Intercept	Slope	Adj. R^2	DF
SW	RChL	Male	-1.663	1.211	0.948	535
		Female	-1.106	1.063	0.931	763
	CL	Male	-0.292	0.955	0.997	560
		Female	-0.427	0.991	0.995	792
	Weight	Male	-8.977	3.040	0.981	544
		Female	-8.762	2.989	0.976	792
	CW	Male	-0.047	1.003	0.999	560
		Female	-0.069	1.009	0.999	796
	RChH	Male	-2.740	1.315	0.931	536
	AW	Female	-3.528	1.473	0.978	795
	LChL	Male	-1.625	1.203	0.963	402
		Female	-1.204	1.083	0.921	647
	LChH	Male	-2.587	1.282	0.949	400
		Female	-2.085	1.139	0.921	680
	ChW	Male	-13.03	3.651	0.972	385
		Female	-11.55	3.241	0.956	619
CL	RChL	Male	-1.291	1.268	0.948	537
		Female	-0.651	1.073	0.926	759
	CW	Male	0.260	1.051	0.997	560
		Female	0.365	1.017	0.995	792
	RChH	Male	-2.339	1.378	0.931	538
	AW	Female	-2.889	1.484	0.982	791
	LChL	Male	-1.261	1.261	0.963	403
		Female	-0.754	1.097	0.921	645
	LChH	Male	-2.200	1.345	0.950	401

		Female	-1.607	1.152	0.922	678
	ChW	Male	-11.90	3.821	0.973	385
		Female	-10.14	3.266	0.956	617
	Weight	Male	-8.027	3.180	0.981	556
		Female	-7.424	3.002	0.977	788
RChL	LChL	Both	-0.029	1.006	0.930	992
	Weight	Male	-4.633	2.471	0.949	526
		Female	-5. 449	2.758	0.906	746
	ChW	Both	-7.992	3.001	0.960	986
	RChH	Male	-0.939	1.087	0.993	532
	AW	Female	-1.997	1.385	0.910	749
	CW	Male	1.336	0.827	0.947	530
		Female	0.982	0.948	0.929	750
CW	Weight	Male	-8.847	3.034	0.981	549
		Female	-8.561	2.964	0.977	779
	RChH	Male	-2.693	1.314	0.930	531
	AW	Female	-3.428	1.460	0.980	782
	LChL	Male	-1.577	1.201	0.962	397
		Female	-1.137	1.076	0.924	634
	LChH	Male	-2.536	1.281	0.949	395
		Female	-2.011	1.131	0.922	667
	ChW	Male	-12.89	3.647	0.973	380
		Female	-11.36	3.221	0.957	606
Weight	RChH	Male	1.099	0.440	0.937	527
	AW	Female	0.797	0.497	0.960	778
	LChL	Male	1.892	0.399	0.965	394
		Female	1.973	0.361	0.908	630
	LChH	Male	1.165	0.426	0.953	392
		Female	1.229	0.386	0.907	663
	ChW	Male	-2.257	1.192	0.985	380
		Female	-2.070	1.085	0.961	606

ChW	RChH	Male	1.934	0.366	0.970	385
	AW	Female	1.723	0.454	0.936	619
	LChL	Male	2.644	0.336	0.970	381
		Female	2.660	0.332	0.922	616
	LChH	Both	1.961	0.358	0.958	998
LChH	RChH	Male	-0.060	1.018	0.923	387
	AW	Female	-0.835	1.293	0.908	680
	LChL	Both	0.818	0.936	0.982	1044
LChL	RChH	Male	-0.936	1.087	0.927	389
	AW	Female	-1.899	1.362	0.910	647

Table 2. Proportion of shell conditions of male and female Jonah crabs (*C. borealis*) caught in the Mid-Atlantic Bight in 2015-2017. Maturity status is defined by their estimated SM_{50} values. Mature male crabs are those ≥ 98.31 mm CW and mature female crabs are those ≥ 88.2 mm CW.

		New	Hard	Old	Very Old	X^2	df	p-value
Males	Immature	0.30796	0.23529	0.21107	0.24567			
	Mature	0.02952	0.22878	0.30996	0.43173	82.33	3	9.73E-18
Females	Immature	0.39749	0.43515	0.12971	0.03766			
	Mature	0.11449	0.25939	0.32916	0.29696	159.92	3	1.91E-34

FIGURES

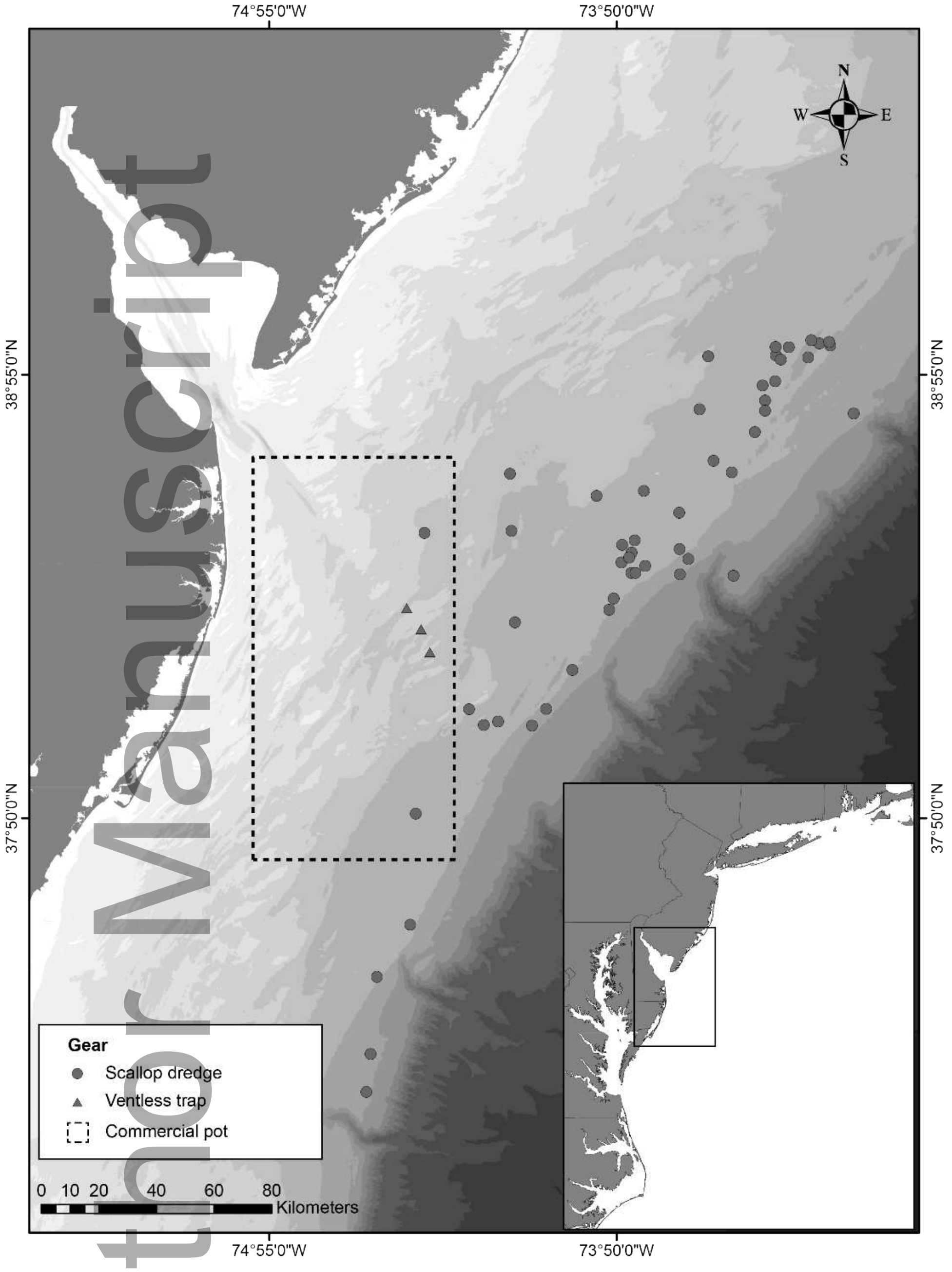

Figure 1. Sampling locations throughout the Mid-Atlantic Bight. Circles represent locations of VIMS Sea Scallop Dredge Survey dredges where Jonah crabs (*C. borealis*) were collected. Triangles represent locations where ventless lobster pots were used. The dashed-line rectangle represents the area fished by commercial black sea bass and lobster pots.

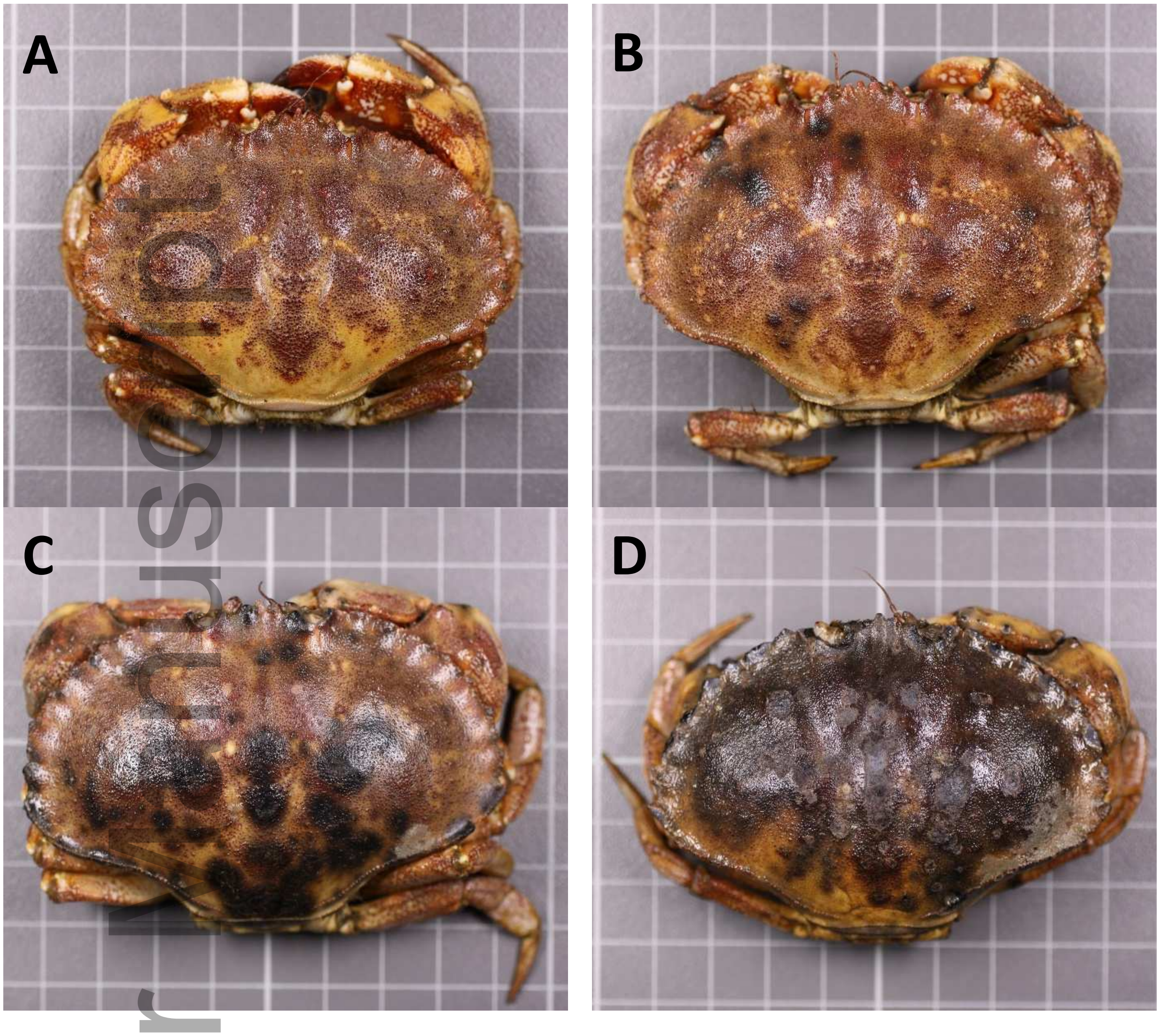

Figure 2. Shell conditions of Jonah crabs (*C. borealis*) based on Jadamec et al. (1999) and Stevens and Guida (2016). Shell condition is categorized as (A) new-shell, (B) hard-shell, (C) old-shell, and (D) very-old shell. Each grid cell represents 1 cm^2.

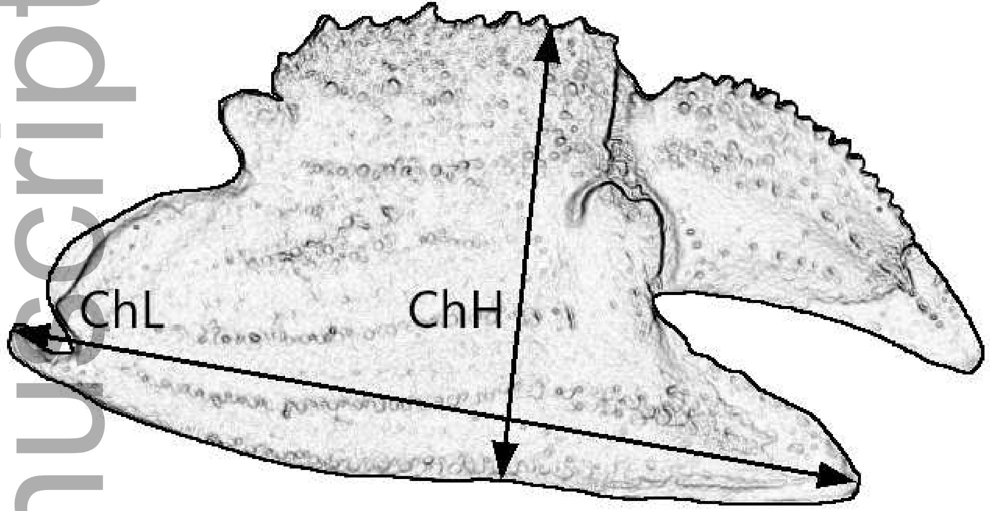

Figure 3: Lateral view of the right chela of a male Jonah crab (*C. borealis*) showing the measurements for chela length (ChL) and chela height (ChH).

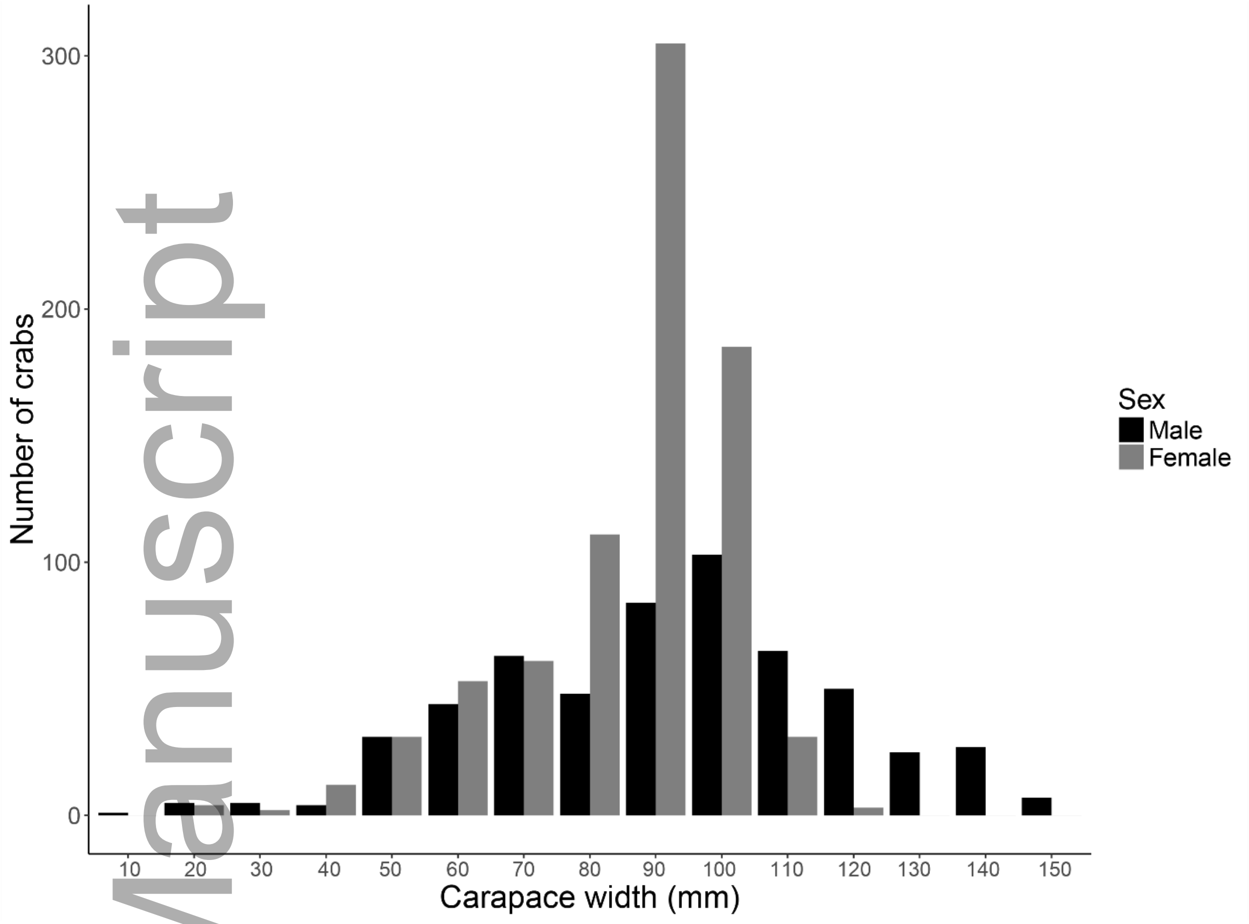

Figure 4. Carapace width frequency of male (n = 562) and female (n = 798) Jonah crabs (*C. borealis*) caught in the Mid-Atlantic Bight during 2015-2017.

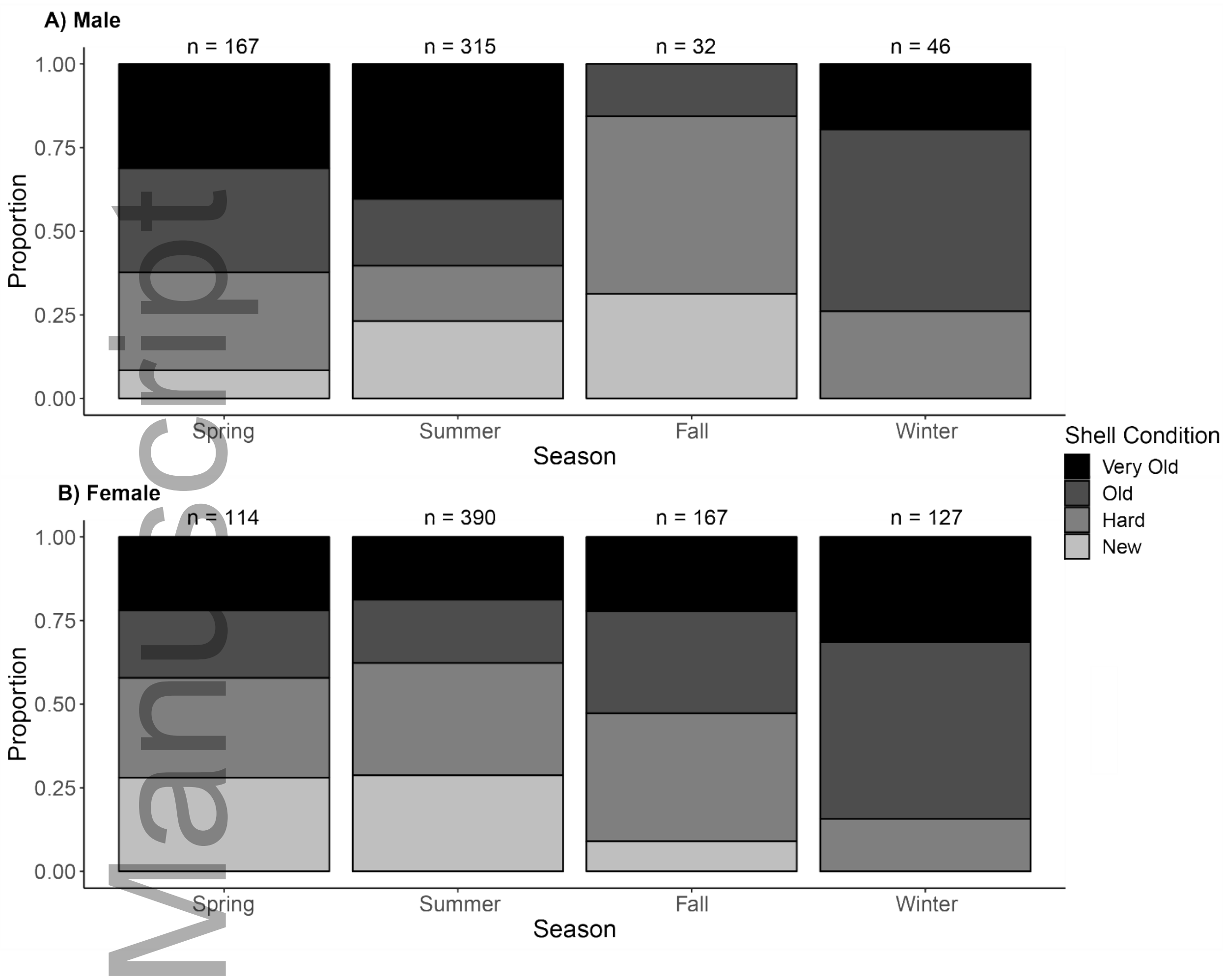

Figure 5. Proportions of seasonal shell conditions of (A) male and (B) female Jonah crabs (*C. borealis*) caught in the Mid-Atlantic Bight in 2015-2017. Seasons are defined as: spring (March, April, and May); summer (June, July, and August); fall (September, October, and November); and winter (December, January, and February). No crabs were collected during January or April.

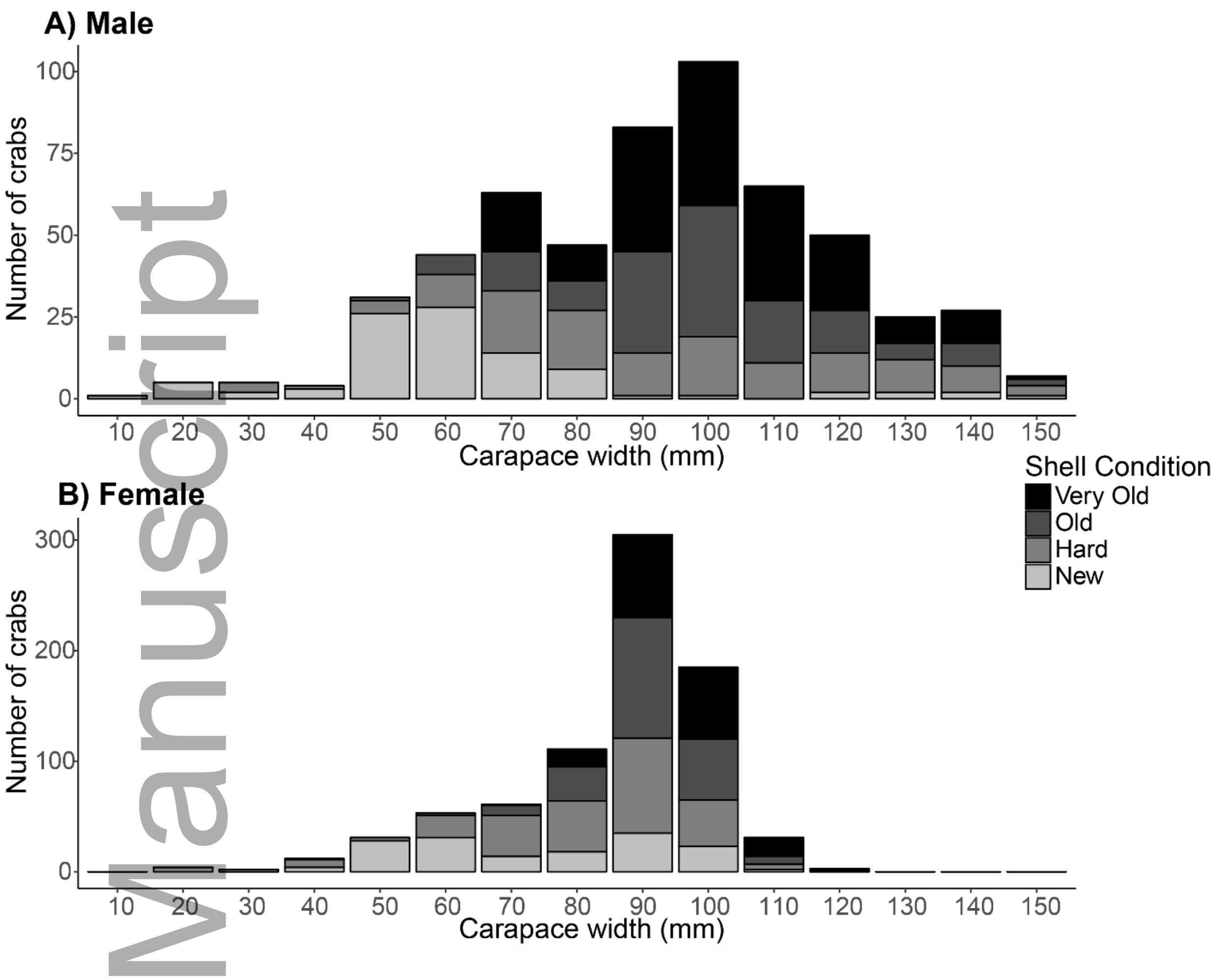

Figure 6. Width frequency distributions and shell conditions of (A) male and (B) female Jonah crabs (*C. borealis*) caught in the Mid-Atlantic Bight in 2015-2017. Note the different vertical scales between sexes.

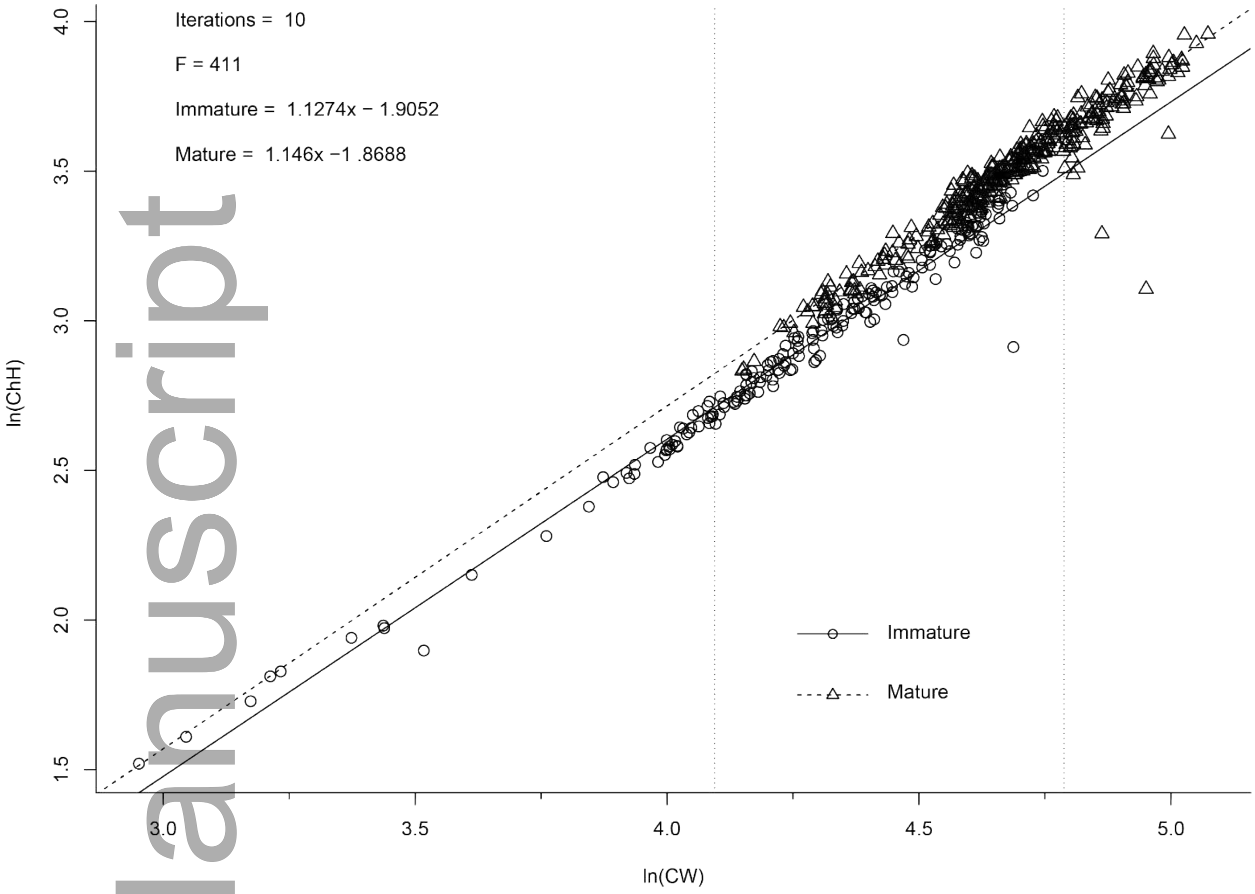

Figure 7. Relationship of natural log chela height (ChH, mm) to natural log carapace width (CW, mm) of male Jonah crabs (*C. borealis*) from the Mid-Atlantic Bight (*n* = 552). Crabs within the vertical dotted lines were initially labeled as "unknown" maturity status and then iteratively assigned to either the immature or mature regression lines based on proximity.

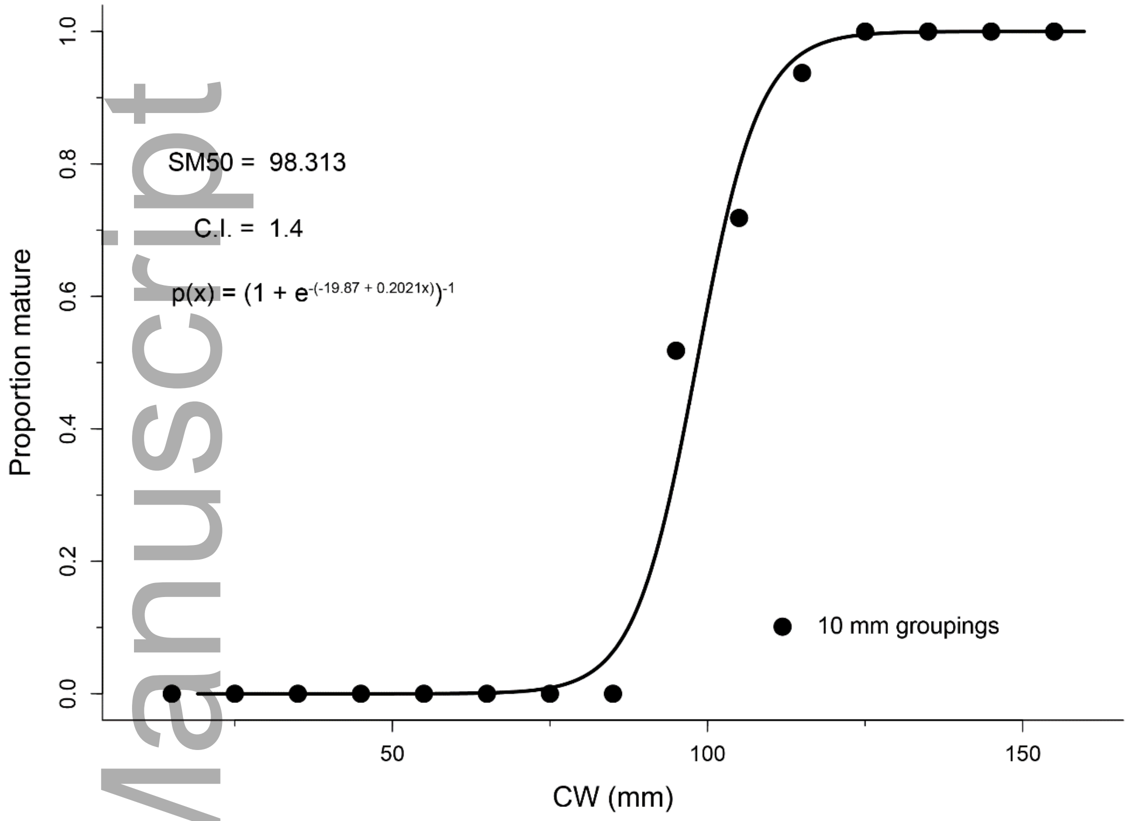

Figure 8. Logistic regression of proportion maturity to carapace width. SM_{50} for male Jonah crabs (*C. borealis*) from the Mid-Atlantic Bight is estimated at the inflection point of the curve at 98.31 ± 1.4 mm CW (*n* = 552). Black circles show average proportion of mature male crabs in 10 mm CW intervals.

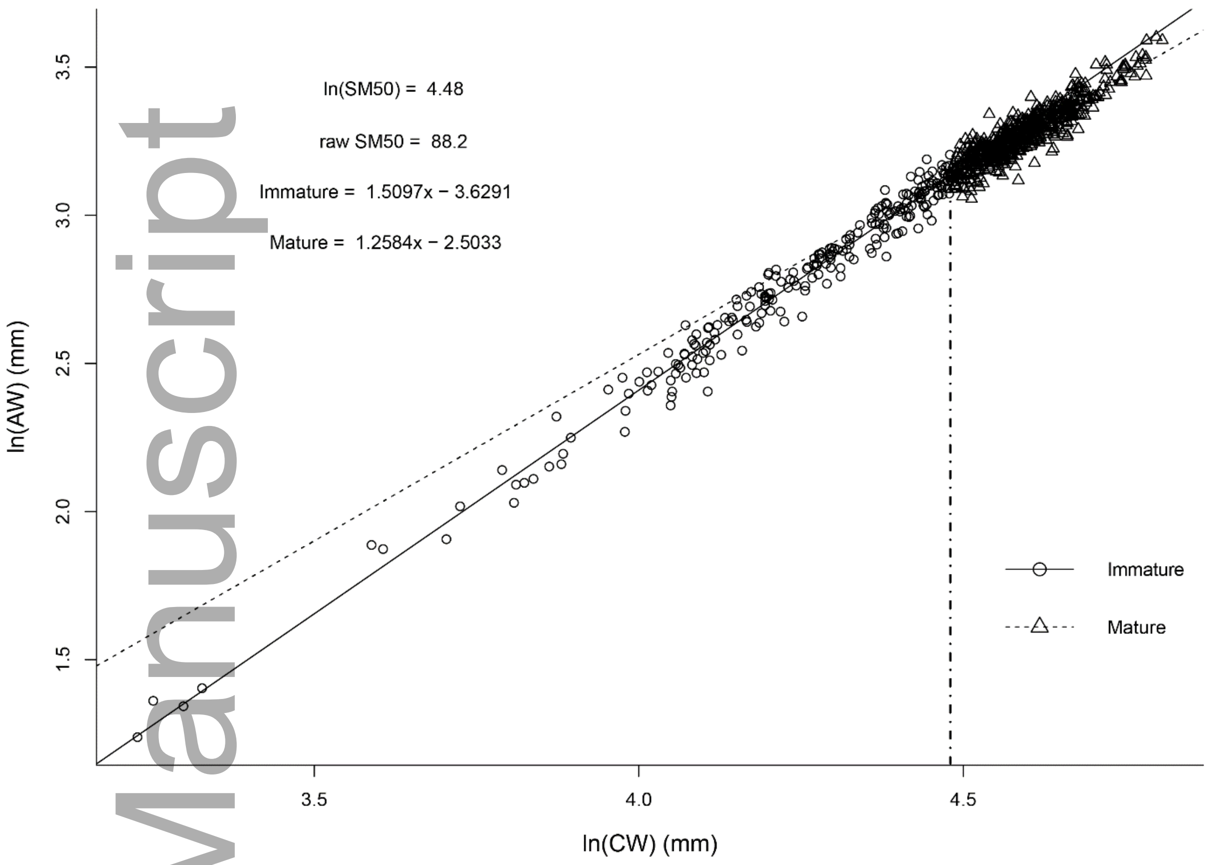

Figure 9. A broken-stick regression of natural log-transformed abdomen width (AW) against carapace width (CW) for female Jonah crabs (*C. borealis*) collected from the Mid-Atlantic Bight in 2016 and 2017 (*n* = 797). Estimated SM_{50} for female Jonah crabs occurs at the regression breaking point, indicated by the double-dashed line (SM_{50} = 88.2 mm CW).