



## Morphometric and physiological maturity of male Jonah crab, *Cancer borealis* Stimpson, 1859 (Decapoda: Brachyura: Cancridae), in southern New England, USA

Amanda Lawrence<sup>1</sup>, Bradley G. Stevens<sup>2,✉</sup>, Burton Shank<sup>3</sup> and J. Sook Chung<sup>1,✉</sup>

<sup>1</sup>Institute of Marine and Environmental Technology, University of Maryland Center for Environmental Science, Columbus Center, 701 E. Pratt Street, Baltimore, MD 21202, USA;

<sup>2</sup>University of Maryland Eastern Shore, University of Maryland Center for Environmental Science, 11868 College Backbone Rd, Princess Anne, MD 21853, USA; and

<sup>3</sup>Northeast Fisheries Science Center, National Oceanic and Atmospheric Administration, 166 Water St, Woods Hole, MA 02543, USA

Correspondence: J.S. Chung; e-mail: [chung@umces.edu](mailto:chung@umces.edu)

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### ABSTRACT

Fisheries management requires a thorough understanding of the processes involved in reproduction, including the ability to distinguish sexually mature individuals. The Jonah crab, *Cancer borealis* Stimpson, 1859, occurs from Newfoundland to Florida, but the fishery is concentrated in New England. The crab contributes to a significant and growing male-driven fishery; however, little is known about its life history. We investigated the relationship between morphometrics and physiological maturity, and the size at which these life changes occur in the southern New England stock. The size at 50% sexual maturity ( $SM_{50}$ ) in male *C. borealis* was estimated morphometrically to be 105.9 mm carapace width (CW). This size is larger than the estimate of 98.3 mm CW for the species in the Mid-Atlantic Bight but lower than the estimate of 127.6 on the Scotian Shelf, consistent with a poleward gradient in size at maturity. The gonadosomatic index differs significantly between CW size groups, maturity status, and season whereas spermatophore size was not related to CW. Fisheries management should include multiple measures of sexual maturity and consider factors including geographical distribution when establishing and assessing guidelines for this economically important species.

**Key Words:** crustacean fisheries, gonadosomatic index, life history, natural resource management, reproduction, sexual maturity, spermatophores

### INTRODUCTION

Understanding the life history of a species is critical for the management of natural resources. In fisheries that target mature individuals, knowledge of size at sexual maturity is critical for establishing suitable minimum size limits (MSL) for harvest. Most crustacean species harvested in the US waters, including the snow crab (*Chionoecetes opilio* (Fabricius, 1788)), Tanner crab (*C. bairdi* Rathbun, 1924), and red king crab (*Paralithodes camtschaticus* (Tilesius, 1815)) support male-driven fisheries that are managed based on the presumptive size at sexual maturity (Pinfold, 2006; NPFMC, 2011). Among crustaceans, however, sexual maturity can be defined by at least three different sets of criteria, including morphometric, functional, or physiological (gonadal) maturity. A fourth criterium is that of behavioral sexual maturity; however, with few studies establishing this criterium due to the efforts required by observational studies, we focus on the first three criteria for the purpose of our study.

Indicators for all three definitions of maturity are based on the ability of an individual to be reproductively successful. These indicators, however, do not always occur at the same life stage, presenting a challenge in the distinction of mature and immature individuals. Physiological maturity refers to the gonadal capability of producing viable and mature gametes; functional maturity as the ability for an individual to participate in mating activities successfully, and morphometric maturity depends on morphological changes throughout ontogeny (Gerhart & Bert, 2008; Zhang *et al.*, 2017). Behavioral maturity can also be inferred via observations of mating behavior or by other indicators such as the presence of sperm plugs in females (Tallack, 2007; Ungfors, 2007; Öndes *et al.*, 2017).

Morphometric maturity in brachyuran crabs is indicated by a change in allometric growth and is related to the development of secondary sexual characteristics that are associated explicitly with mature life stages (Hartnoll, 1978; Zhang *et al.*, 2017). Secondary

sex characteristics of brachyuran crabs, including changes in the shape and/or relative size of chelipeds, can also be used to determine the onset of sexual maturity (Hartnoll, 1974; Williner *et al.*, 2014; Zhang *et al.*, 2017). The transition from juvenile to adult in decapod crustaceans occurs at the pubertal molt and is often distinguished by significant changes in the allometric growth rate of certain body structures (Hartnoll, 1978; Bueno, 2009). Secondary sexual characters of male crabs may include differentiation of the chelipeds, which can also be used as a tool to set size limits.

Identifying the size at which a transition in allometry occurs can provide one indicator of size at maturity. Morphometric maturity that may coincide with gonadal maturity (Brown & Powell, 1972) is typically defined as the size at which 50% of the population is mature ( $SM_{50}$ ) based on the allometric relationship of two body parts (Ennis *et al.*, 1990; Goshima *et al.*, 2000). Identifying the  $SM_{50}$  is a widely used tool for management of crustacean fisheries because it is non-invasive and non-labor-intensive (Somerton, 1980; Paul, 1992; Williner *et al.*, 2014; Zhang *et al.*, 2017). The  $SM_{50}$  does not always occur at the same size as other types of maturity (Goshima *et al.*, 2000; Moriyasu *et al.*, 2002; Tallack, 2007).

The Jonah crab, *C. borealis*, is distributed between Newfoundland, Canada and Florida, USA (Haefner, 1977) at depths > 750 m but primarily between 50–300 m, and temperatures of 8–14 °C (Robichaud, 2000; Moriyasu *et al.*, 2002). Caught initially as a bycatch species along with the American lobster, *Homarus americanus* H. Milne Edwards, 1837, *C. borealis* has transitioned from being exclusively a bycatch species to becoming a highly desirable and increasingly valued target species for many fishing vessels in New England. Landings (primarily male crabs > 120.65 mm carapace width (CW)) have steadily increased by 650% since early 2000 (ASMFC, 2008) from ~ 3 million lbs in 1994 to over 17 million lbs in 2017; the ex-vessel price per pound across all states has nearly doubled in the same time frame from just under \$0.40 in the early 1990s, to over \$0.70 by 2012 (FIP, 2014; NOAA, 2019).

Informed management policies are required for sustainable management. The Jonah crab, however, is a data-poor species due to a lack of information on life history, reproduction, age, growth, maturity, or stock status (ASMFC, 2015). The current minimum size limit of 120.65 mm CW is based on studies conducted off the Scotian shelf and Virginia, and the fishery is male driven since females tend to be smaller in size than males (Robichaud & Frail, 2006). The size at 50% morphometric maturity of male *C. borealis* in the Scotian shelf has been estimated at 128 mm CW and gonadal maturity is estimated to occur at 68.5 mm CW (Moriyasu *et al.*, 2002). In contrast, the  $SM_{50}$  for male *C. borealis* in the Mid-Atlantic Bight is estimated at 98.3 mm CW (Olsen & Stevens, 2020).

We aimed to investigate the allometric growth and physiological development of *C. borealis* from the North Atlantic region of southern New England, where the greatest harvest of crabs occurs as bycatch in the American lobster fishery. To this end, the size at maturity ( $SM_{50}$ ) of male crabs was estimated, and spermatophores were measured to determine if they were related to body size.

## MATERIALS AND METHODS

### Collection

Male individuals of *C. borealis* were collected in federally managed waters between Martha's Vineyard and Block Island, Rhode Island, USA (40°52'N to 41°16'N and 70°20'W to 71°60'W). Crabs were collected by commercial fishers using modified (ventless) lobster pots, 1.9 cm (0.75 in) mesh size, re-designed to catch and keep small crabs. Samples included crabs of all sizes and were representative of the catch landed over a two-year period from September 2018 through November 2019. Crabs

were collected during four seasons, defined as winter (December–February), spring (March–May), Summer (June–August), and Fall (September–November).

Crabs were shipped overnight to the Institute of Marine and Environmental Technology (IMET, Baltimore, MD, USA), and acclimated for 1 to 2 weeks in a dark, cold room. Aquarium tanks (57–76 l) holding approximately 38 l of ~3,032 ppt artificial seawater housed 6–10 individuals at a time at 10 °C with constant aeration. Crabs were measured to the nearest 0.1 mm using an electronic caliper (Mitutoyo, Kawasaki, Japan). Carapace width (CW) was recorded by measuring the distance between notches anterior to both lateral spines. Chela height (ChH) was measured as the greatest propodus height excluding the spines of the right chela (Paul & Paul, 1996).

### $SM_{50}$

A set of R codes called “crab maturity” based on Somerton (1980) and developed by BS (Olsen and Stevens, 2020; [https://github.com/Crabman52/Crustacean\\_Sensation](https://github.com/Crabman52/Crustacean_Sensation)) as used to estimate an  $SM_{50}$  for the male population in which the samples were collected. The code operates in three main steps. In the first step, the independent (CW) and dependent (ChH) variables are selected and natural log-transformed, and a single regression line through all the data is calculated. In the second step, the user selects a range of values for the lower and upper boundaries encompassing the unknown maturity region of the data, assuming points to the left of the lower bound are immature and points to the right of the upper bound are mature. The program iteratively varies the boundaries in 5 mm increments and finds the closest boundaries where differences between the two regression lines are greatest, based on the combined F-value. Therefore, the exact location of the initial bounds is not critical as long as they include the majority of unknown points, and do not overlap.

Two separate regression lines were then estimated: one line for an immature cluster of crabs (represented by the solid line) and a second line for a mature cluster of crabs (represented by the dotted line) (Fig. 1). Each point falling within the unknown maturity group was then assigned to either the immature or mature cluster based on the closest corresponding line, and the regression lines were recalculated. This process was repeated until no points changed lines, which usually required 4–10 iterations. The pooled residual sum of squares (RSS) for the two-line model was then compared to the RSS for the single regression line to determine the best model for the data.

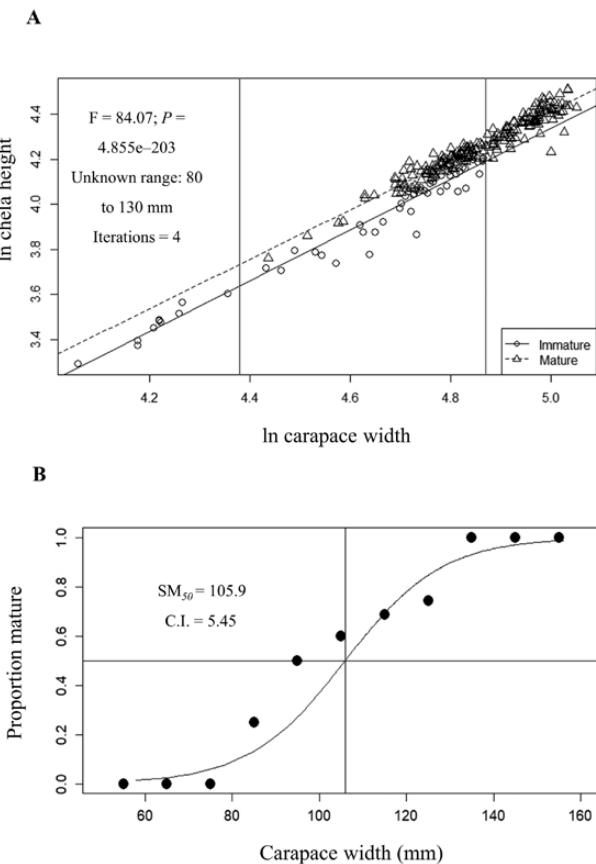
In the third and final step, logistic regression of assigned maturity *versus* CW was conducted using a generalized linear model (GLM) with a binomial link. The  $SM_{50}$  was defined as the inflection point of the curve, where 50% of the individuals were classified as mature, and was calculated from the regression coefficients as:

$$SM_{50} = B_0 + B_1^{-1}$$

The standard error of the maturity estimate was calculated via bootstrapping by resampling the data (with replacement) and recalculating the  $SM_{50}$  1,000 times. The confidence interval (CI) around the estimate was calculated as  $SE \times 1.96$ .

### Gonadosomatic index (GSI) and sperm content

The male reproductive system of decapod crustaceans includes a pair of testes, vas deferens, and ejaculatory ducts. The three structures were removed from one side of each of 58 male crabs and weighed as “gonad” to the nearest 0.1 g. The total gonad weight per individual was multiplied by two. The gonadosomatic index (GSI) was then calculated following Anderson & Gutreuter (1983):



**Figure 1.** Relationship between natural log-transformed chela height (ChH) to carapace width (CW) of male Jonah crabs (*C. borealis*) ( $N = 273$ ). The red vertical lines indicate the upper boundary of  $\ln(130)$  mm CW, and lower boundary of  $\ln(80)$  mm CW for males assigned an unknown maturity status (A). Relationship of natural log chela height and natural log carapace width of male Jonah crabs for mature and immature regression lines ( $N = 274$ ). Males with unknown maturity status ( $80 \text{ mm} < \text{CW} < 130 \text{ mm}$ ) were iteratively assigned based on proximity to either mature or immature regression lines (B). Logistic regression of proportion maturity to carapace width.  $\text{SM}_{50}$  for male crabs is estimated at the point of inflection of the curve to be  $105.9 \pm 5.5 \text{ mm CW}$  ( $N = 273$ ). The black circles indicate the average proportion of mature individuals in intervals of 10 mm CW.

$$\text{GSI} = \frac{\text{Gonad wet weight}}{\text{Total body wet weight}} \times 100$$

We measured the surface area ( $\mu\text{m}^2$ ) of spermatophores of 16 males across a wide range of sizes (110.08–140.64 mm CW). All individuals were collected during the fall of 2019. We prepared the samples by first taking two smears of the distal portion of the vas and diluting them seven times with crustacean saline solution. Approximately two or three drops of each spermatophore solution per individual was then transferred to two separate slides, and two photographs were taken in different areas of each slide (10 $\times$  magnification with an Echo Revolve 12.0 microscope 12.0 (Echo, San Diego, CA, USA). The area of every spermatophore fully within the image frame was measured ( $\mu\text{m}^2$ ) using ImageJ (Schneider *et al.*, 2012). We disregarded spermatophores that were partially out of view.

#### Physiology data and statistical analyses

Prior to analysis, the normality of GSI in individuals ranging 67.3–148.9 mm CW (mean  $\pm$  SE,  $116.7 \pm 2.2 \text{ mm CW}$ ) was

tested using a q-q plot and Shapiro test, and both indicated that GSI was normally distributed (Shapiro  $W = 0.983$ ,  $P = 0.555$ ). We used analysis of covariance (ANCOVA) to determine the relationship between GSI, CW, and maturity status as assigned by the Mature program ([https://github.com/Crabman52/Crustacean\\_Sensation](https://github.com/Crabman52/Crustacean_Sensation)), based on the CW:ChH relationship. We used analysis of variance to determine the effect of Season on Maturity. Season is a factor with four categories, including winter, spring, summer and fall. Post-hoc comparisons of GSI between seasons were made by pairwise t-tests with the Bonferroni correction (Zar, 1984), and statistical significance was accepted at  $P < 0.05$ .

We analyzed the relationship between spermatophore area and CW with regression models after eliminating the smallest crab (65.1 mm CW); all remaining crabs were in the size range of 110–140 mm CW ( $N = 16$ ). Spermatophore areas were non-normally distributed (Shapiro  $W = 0.987$ ,  $P < 0.001$ ), so further analysis was conducted using transformed data, which had symmetrical residual distributions. A simple regression model (Model R:  $Y = a + bX$ ) was created by regressing Area (Y) on CW (X) using the gls command from the nlme package in R. A repeated measures model (Model RM) was created by regressing Area on CW, with observations repeated within each crab, i.e., crab (ID) was treated as a random variable:  $Y = a + bX | ID$ , using the lme command. A null version of model RM (Model 0:  $Y = a$ ) was created with only the intercept and no slope. All three models were compared using the ANOVA command in R, and the model with the lowest AIC value was selected as the best model. All analyses were conducted using R version 3.6.1 (R Core Team, 2019).

## RESULTS

### $\text{SM}_{50}$

A total of 273 male *C. borealis* ranging 65.2–153.4 mm CW ( $125.1 \pm 1.1 \text{ mm CW}$ ) were caught between September 2018 and November 2019 off the coast of Rhode Island. The lower and upper bounds of carapace width selected for crabs of unknown maturity status were  $\ln$  of 80 mm and  $\ln$  of 130 mm, respectively. Crabs within the unknown range were assigned to the closest fitting regression line (Fig. 1A). The pooled RSS for the two-line model was significantly less than the RSS of the single regression line ( $F = 84.1$ ,  $P < 0.001$ ), and was therefore accepted as the better model. The generalized linear model produced an  $\text{SM}_{50}$  of  $105.9 \pm 5.45 \text{ mm CW}$  (mean  $\pm$  CI) for male *C. borealis* (Fig. 1B).

### Gonadosomatic index and sperm content

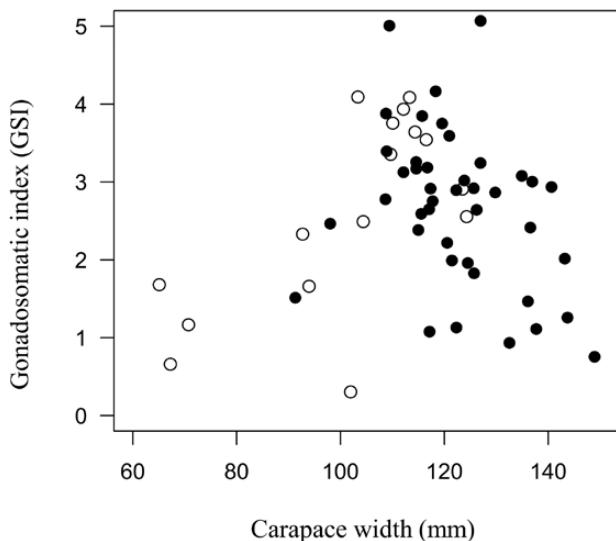
Gonadosomatic index (GSI) was not related to CW or Maturity (ANCOVA,  $F = 0.3$  and  $0.05$ ,  $P = 0.6$  and  $0.82$ , respectively) (Fig. 2). A separate ANOVA showed that GSI was affected by Season ( $F = 5.36$ ,  $P = 0.003$ ) but not Maturity ( $F = 0.01$ ,  $P = 0.9$ ) (Fig. 3). Pairwise comparisons showed that GSI was greatest in fall and differed significantly from spring and summer, but not from winter, whereas winter, spring, and summer were similar (Fig. 3A).

Spermatophores present in the distal vas deferens of the males varied in size (Fig. 4). Analysis with linear mixed-effects models showed that CW had no significant effect on the size of spermatophores ( $P = 0.0935$ ). The best model with the lowest AIC value was Model 0, i.e., the Null model (Table 1). The AIC value for Model Null was 170.8 less than that of Model R, and 1 point greater than Model RM, indicating that it differed from the latter only due to having one less variable (3 df *versus* 4) (Table 1). A difference of 1 between the AIC values of Model Null and Model RM is not significant, so that the Null model can be considered to be the best predictor of spermatophore size, and estimating a mean value of  $774.99 \pm 20.45 \mu\text{m}^2$  (mean  $\pm$  SE,  $N = 16$ ).

## DISCUSSION

Our results provide the first estimate of size at maturity for male Jonah crab in southern New England. We also demonstrated that GSI of male Jonah crabs is affected by season, but not by crab size or maturity, and that spermatophore size is not a useful indicator of maturity in this species.

Our estimate of morphometric size at maturity (105.9 mm CW) for males at 40.5°N in southern New England is 7 mm greater than the estimate of 98.3 mm CW made for the species at 38.5°N in the Mid-Atlantic Bight (Olsen & Stevens, 2020), but 22 mm less than the estimate of 127.6 mm CW at 45°N on the Scotian Shelf (Moriyasu *et al.*, 2002). The difference between these estimates is proportional to the difference in latitude between these three sites. Olsen & Stevens (2020) suggested that the  $SM_{50}$  for *C. borealis* exhibits a pattern consistent with James's cline. The slope of the ChH:CW relationship for both mature and immature regression lines increase with decreasing latitude. Immature slope values progress from 1.217, 1.269 to 1.1274 off the Scotian Shelf (Moriyasu *et al.*, 2002), southern New England, and in the Mid-Atlantic Bight



**Figure 2.** Plot of gonadosomatic index against carapace width (mm). Black circles indicate mature individuals, the empty circles immature individuals.

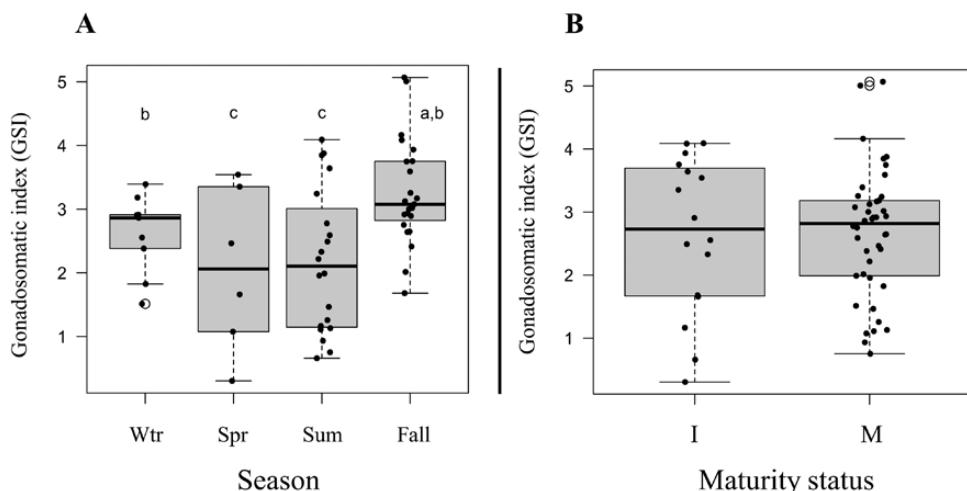
(Olsen & Stevens, 2020) respectively, and mature slope values progress from 1.078, 1.098, and 1.146. These values indicate a poleward trend of increasing size at maturity with latitude, consistent with the James's cline, and should be considered when setting appropriate size limits for harvesting in different locations.

The timing of the spawning season for *C. borealis* is also thought to progress latitudinally from south to north along the eastern coast of the US. Spawning is reported to take place from late winter to early spring in the Mid-Atlantic Bight, but beginning in mid-July in Rhode Island, and in late summer from August through September off the eastern portion of George's Bank, MA (FOC, 2009; Anonymous, 2013).

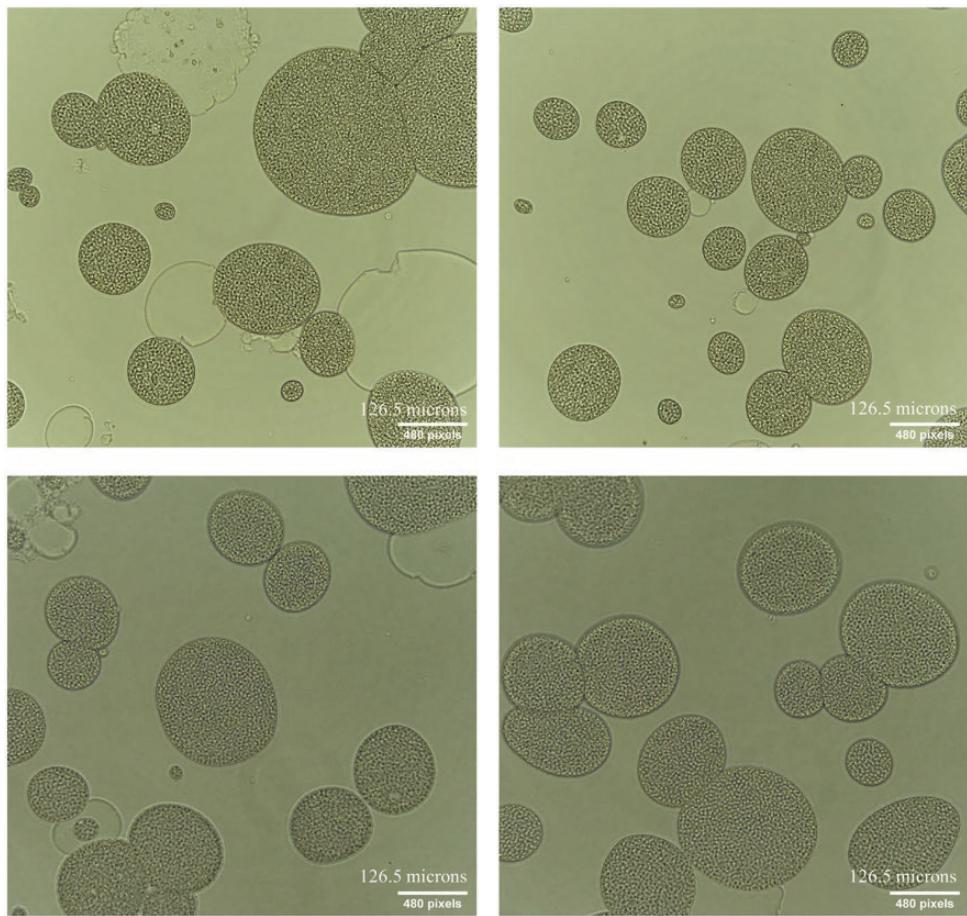
Differences between the size at onset of morphometric, gonadal, and functional maturity have been reported in many brachyuran species (Brown & Powell, 1972; Paul, 1992; Goshima *et al.*, 2000). Morphometric and functional maturity appear to occur at different sizes in the female edible crab (*Cancer pagurus* Linnaeus, 1758), making it hard to predict one maturity estimate based on the other, but in contrast, both types of maturity occur at the same size in male *C. pagurus* (Ungfors, 2007). Functional maturity has been assessed for male crabs of several species by observing precopulatory guarding behavior in the wild and in laboratory settings (Brown & Powell, 1972; Paul, 1992; Stevens *et al.*, 1993; Goshima *et al.* 2000). Few studies, however, have described precopulatory and copulatory behaviors in Jonah crabs (Elnér *et al.*, 1985). Due to these challenges, examining multiple indicators of maturity can allow for an improved understanding of sexual maturation.

Temperature and temperature-photoperiod interactions have been suggested as the factors affecting the geographical variation in size and onset of maturity and for latitudinal clines in metabolic rates, size, and growth (Giese, 1959; Kinne, 1970; Annala *et al.*, 1980; Stearns, 1976 Jones & Simons, 1983; McLay, 2015; McLay & Becker, 2015; Hartnoll, 2015). Such environmental conditions could lead to slower growth and delayed maturity at higher latitudes. Latitudinal effects on size at maturity of decapod crustaceans, in particular, seem to be inconsistent because some species of brachyuran crabs, including *Cancer irroratus* Say, 1817 and *Carcinus maenas* (Linnaeus, 1758), show latitudinal clines, but others do not (Hines, 1989; Bakke *et al.*, 2018).

Many species of terrestrial animals exhibit increasing body mass with latitude (or decreasing temperature), a phenomenon known as Bergmann's or James's rules (Blackburn *et al.*, 1999), whereas others, particularly arthropods, exhibit the inverse relationship of decreasing body mass with latitude (or increasing



**Figure 3.** Boxplot of gonadosomatic index of male *C. borealis* ( $N = 58$ ) across seasons (Wtr, winter; Spr, spring; Sum, summer; Fall, fall) (A). Boxplot of gonadosomatic index in males ( $N = 58$ ) larger than the estimated  $SM_{50}$  (M, mature) and males smaller than the estimated  $SM_{50}$  (I, immature) (B).



**Figure 4.** Spermatophores taken from the same individual of *C. borealis* (200 $\times$ magnification).

**Table 1.** Summary of regression models for spermatophore area. Dependent variable for all models was  $\log_{10}(\text{Area})$ . We examined four models to determine the best fit, including a simple regression model with CW (Model R), a repeated measures model with CW, and CrabID as a random variable (CW | ID; Model RM1); a version of model RM1 with CW and Maturity (Mat) (Model RM2); and a null version of model RM1 (Null Model). AIC, Akaike Information Criterion;  $\delta\text{AIC}$ , difference in AIC from best model;  $P$ , probability value of comparison between each model and the one above it.

Model	Variables	AIC	$\delta\text{AIC}$	P
R	CW	2071.4	171.2	
RM2	CW*Mat IID	1902.2	2.1	<0.0001
Null	IID	1900.6	0.5	0.221
RM1	CW IID	1900.2	0.0	0.115

with temperature) (Blanckenhorn & Demont, 2004). An inverse James's cline in female size at sexual maturity (i.e., positive correlation with temperature), has been reported in the snow crab (*Chionoecetes opilio*) in Alaska (Somerton, 1981) and eastern Canada (Sainte-Marie & Gilbert, 1998), the red (*Paralithodes camtschaticus*) and blue king crab in the northern Pacific (*Paralithodes platypus* (Brandt, 1851)), and golden king (*Lithodes aequispinus* Benedict, 1895) crabs in Alaska (Webb, 2014), red deep-sea crab (*Chaceon quinquedens* (Smith, 1879)) (Martinez-Rivera *et al.*, 2020) in the Mid-Atlantic Bight, and blue crab (*Callinectes sapidus* Rathbun, 1896) in Texas (Fisher, 1999).

The gonadosomatic index varies seasonally in *C. borealis* males. The proportional size of the male gonads is greatest in fall,

immediately before mating and deposition of spermatophores into females, as ovigerous females are observed from March to June in southern New England and are believed to bear eggs for five to six months. This implies that the mating season probably occurs between October and January as previously estimated (Anonymous, 2013), and aligning with the time of year where the GSI values are highest.

Our results indicate that GSI is lowest for *C. borealis* during spring and summer consistent with previous observations of non-mating season in this region and indicating that a post-mating period occurs during the summer. The GSI varied little between winter, spring, and summer. This result may be partially due to sample size (58), and because the majority of crabs in our sample were relatively large. A larger sample, or more even distribution of crab sizes might have produced a different result. Males in some crustacean species experience seasonal spermatogenesis activity, whereas activity in other species appears continuously active throughout the year (Sastry, 1983).

We found that the mean spermatophore surface area was not related to crab size (CW). In contrast, a positive relationship between size and spermatophore area has been demonstrated in some crustaceans, including lobsters and crabs (Paul & Paul, 1996; Sato & Goshima, 2006; Butler *et al.*, 2011). Our results might be due to small sample size (18) or a narrow size range of crabs sampled. The presence of spermatophores in the vas deferens is often a good indicator of sexual maturity in male crabs; however, it does not always warrant that mating can successfully occur (Watson, 1970). This relationship needs further investigating to determine if sperm and/or spermatophore viability is relative to male size and if it could be used as an index of maturity. Further studies should also examine the reproductive cycle of both male and female

Jonah crabs and determine if there is an annual or biannual testicular or ovarian maturation cycle in the species.

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