ABSTRACT

Title of Thesis:	EFFECTS OF ENVIRONMENTAL VARIABLES AND CHANGES IN SEASONAL PATTERNS ON SPATIAL DISTRIBUTIONS OF JONAH CRABS (*CANCER BOREALIS*) AND ATLANTIC ROCK CRABS (*CANCER IRRORATUS*) IN GEORGES BANK AND THE MID-ATLANTIC BIGHT, USA Kaitlynn Jean Wade, Master of Science, 2023
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The economic and commercial importance of Jonah crabs (*Cancer borealis*) and Atlantic rock crabs (*Cancer irroratus*) has increased greatly in the USA. The objectives of my research were to determine spatial distributions, habitat preferences, and potential seasonal movements of both species. Data were obtained from the offshore Northeast Fishery Science Center bottom trawl surveys. Analyses included kernel density estimates, generalized additive models, empirical cumulative distribution functions, and ANOVAs. The spatial distributions of Jonah and Atlantic rock crabs changed over time during the 1970s – 2000s. Compared to Atlantic rock crabs, Jonah crabs preferred slightly warmer temperatures, deeper depths, and muddier sediments. Seasonally, Jonah crabs were found farther offshore in the winter and closer to shore in the fall and spring. Atlantic rock crabs were found closer inshore in the winter and spring and more offshore in the fall. Both species were found to have different seasonal patterns in the Mid-Atlantic Bight.

EFFECTS OF ENVIRONMENTAL VARIABLES AND CHANGES IN SEASONAL PATTERNS ON SPATIAL DISTRIBUTIONS OF JONAH CRABS (*CANCER BOREALIS*) AND ATLANTIC ROCK CRABS (*CANCER IRRORATUS*) IN GEORGES BANK AND THE MID-ATLANTIC BIGHT, USA

by

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Dedication

I would like to dedicate this work to my late advisor Dr. Daniel Cullen. His passion for fisheries science and work was a true inspiration. I am thankful to have been mentored by him for the first year of my degree, and I will never forget the lessons he taught me.

I would also like to dedicate this work to my late grandmothers who taught me the true meaning of working hard and never giving up.

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Table of Contents

List of Tables

List of Figures

Chapter 1 : The influence of environmental variables on distributions of Jonah and Atlantic rock crabs

1.1. Abstract

Jonah crabs (*Cancer borealis*) and Atlantic rock crabs (*Cancer irroratus*) were traditionally considered a bycatch species in the American lobster (*Homarus americanus*) fishery until around the 1990s. As popular crustaceans experienced declines, Jonah and Atlantic rock crabs became more commercially important. However, there is currently limited data for these two species to guide the management in creating a sustainable fishery. Therefore, this research determines the spatial distributions of Jonah and Atlantic rock crabs over time with binomial kernel density estimates (KDEs). Environmental preferences such as temperature (°C), depth (m), and grain size (ϕ) for these two species were also analyzed using generalized additive models (GAMs), and the habitat usage between the two crabs were compared using cumulative distribution functions. Data were obtained from the Northeast Fisheries Science Center (NEFSC) offshore spring bottom trawl surveys from 1968 – 2021 in Georges Bank (GB) and the Mid-Atlantic Bight (MAB). The spatial distributions of Jonah and Atlantic rock crabs are changing over time. Grain size was the most important environmental variable when determining the presence of Jonah crabs, and depth was the most important variable for determining Atlantic rock crab presences. The GAM with the lowest Akaike Information Criterion for both crabs included all environmental, spatial, and temporal variables. Overall, Jonah crabs preferred slightly warmer temperatures, deeper depths, and muddier sediments compared to Atlantic rock crabs. This work will provide information on spatial distributions and habitat preferences that will elucidate how Jonah and Atlantic rock crabs may respond to environmental changes.

1.2. Introduction

Understanding population distribution and habitat usage is crucial for effective fisheries management. Specifically, patterns of how a species' habitat use responds to its environment provides insights into its behavior and changes in time and space (Denis et al., 2002; Heinänen et al., 2008; Hofmann & Powell, 1998; Sagarese et al., 2014). When population dynamics are not properly understood, declines in populations can go undetected, which can cause species to be overexploited. Additionally, critical habitats such as spawning and nursery areas might not be protected from degradation and the fishery. Current approaches for stock assessments often include assumptions that the environment and hence spatial distribution of a stock is relatively stable over time. However, environmental variability affects populations through changes in distributions and abundances (Hofmann & Powell, 1998; Perry & Smith, 1994; Tseng et al., 2013; Windle et al., 2012). Responses of populations to changes in the environment is important for future management actions and overall conservation efforts (Hofmann & Powell, 1998). Environmental variables have a significant effect on the distribution of many species like black sea bass (*Centropristis striata*), scup (*Stenotomus chrysops*) (Cullen & Guida, 2021), squid (*Loliginid spp.*) (Denis et al., 2002), cod (*Gadus morhua*), and haddock (*Melanogrammus aeglefinus*) (Hofmann & Powell, 1998). Examining how populations respond to changes in important environmental factors can improve fisheries management (Melle et al., 2014).

Climate change and the threat of declining biodiversity have caused an increasing focus on studies to understand how changes in habitat affect populations (Morley et al., 2018; Nye et al., 2009). Environmental variables such as temperature, depth, and sediment can affect the distribution and abundance of crustaceans and demersal organisms (Bell, 2010; Jacob et al., 1998; Reiss et al., 2011; Windle et al., 2012; Young et al., 2006). Temperature influences crustacean behaviors and activity levels (McLeese & Wilder, 1958; Young et al., 2006), and rising temperatures due to climate change have been attributed to the decline of the economically important American lobster (*Homarus americanus*) population in New England (Bell, 2010). Other crustaceans such as snow crabs (*Chinoecetes opilio*), Tanner crabs (*Chionoecetes bairdi*), and Bristol Bay red king crabs (*Paralithodes camtschaticus*) have also been influenced by climate change, and their distributions and productivity are projected to change in the future (Szuwalski et al., 2021). The distributions and survival of crabs and lobsters also can be influenced by depth (Tremblay et al., 2009; Windle et al., 2012). For example, depth was the most important variable when modeling snow crab abundance on the Newfoundland-Labrador Shelf (Windle et al., 2012), and demersal fish assemblages in southern New Zealand (Jacob et al., 1998) are also influenced by temperature and depth. The presence and absence of crustaceans in their distribution range at least in part of their life cycles also seems to be heavily impacted by sediment (Dionne et al., 2003; Tremblay et al., 2009). Understanding how these environmental variables influence growing Jonah crabs (*Cancer borealis*) and Atlantic rock crabs (*Cancer irroratus*) is important for stock assessment and management because environmental variables such as temperature are changing within their distribution ranges (Wallace et al., 2018).

Both of these crabs are distributed along the western North Atlantic Ocean. Jonah crabs are found in coastal waters from Newfoundland to Florida as well as in the Bermudas (ASMFC, 2021; Haefner, 1977; Pezzack et al., 2010). Atlantic rock crabs are distributed in coastal waters from Labrador to South Carolina (Haefner, 1976; Rebach, 1985). Atlantic rock crabs have also recently been reported in Icelandic waters in the eastern North Atlantic (Gíslason et al., 2014). Traditionally considered bycatch in the American lobster fishery, Jonah crabs became commercially important around the 1990s when more popular crabs such as blue crabs

(*Callinectes sapidus*) and American lobster populations started experiencing declines (Gulf of Maine Research Institute & University of Maine, 2013; Lewis & Ayers, 2014; Pezzack et al., 2010; Robichaud & Frail, 2006). Today, a mixed crustacean fishery exists for Jonah crabs and American lobsters in which fishers seasonally adjust their fishing strategies between the two species through modifications in trap vents, bait type, and fishing locations (ASMFC, 2015; Gulf of Maine Research Institute & University of Maine, 2013; Robichaud & Frail, 2006). This fishery predominately takes place offshore in southern New England with about 57.4% of the landings occurring in Massachusetts and 21.4% of the landings occurring in Rhode Island (ASMFC, 2021; Gulf of Maine Research Institute & University of Maine, 2013).

Jonah crab catch has increased since the 1980s as they became more popular and actively targeted by fishers (ASMFC, 2021; Goldstein & Carloni, 2021; Truesdale et al., 2019). Abundance of Jonah crabs also appears to have changed over time. In fall groundfish surveys, Jonah crabs went from averaging 1.0 per tow between 1973 – 1999 to averaging about 4.5 per tow in 2001 (Leland, 2002). The landings of the Jonah crab fishery has also increased 669% from 2000 – 2017 with a total catch in 2019 of 17.7 million pounds and an ex-vessel value exceeding $13 million USD (ASMFC, 2019, 2021). With the increasing popularity and catch, there is a need to understand more about this data limited species along with Atlantic rock crabs that are often grouped or confused with Jonah crabs.

The increase in fishing pressure and economic value for Jonah crabs has raised concerns from stakeholders on the long-term health and management of this fishery (ASMFC, 2015; Bradt et al., 2016; Goldstein & Carloni, 2021; Truesdale et al., 2019). This concern led to the first Interstate Fishery Management Plan (FMP) for Jonah crabs by the Atlantic States Marine Fisheries Commission (ASMFC) in 2015 (ASMFC, 2015). The first Jonah crab stock assessment was recently conducted but was unable to provide advice on stock status as data are still limited (ASMFC, 2023). Therefore, this species has the potential of being over-exploited or under-exploited without more data. Areas in the United States and Canada may have already experienced declines and recoveries of Jonah crab populations (Gulf of Maine Research Institute & University of Maine, 2013). There is also limited evidence that Jonah crabs may be increasing due to a decline in predation by groundfish (Frank et al., 2005; Myers & Worm, 2003). High abundance of Jonah crabs could decrease the survival of juvenile lobsters as well as modify the distribution of prey such as green sea urchins (Leland, 2002; Lewis & Ayers, 2014; McKay & Heck, 2008). Atlantic rock crabs on the other hand are not as commercially important, but their catch may increase over time to offset declines in other crustacean populations (Krouse, 1972).

Despite the increasing importance of the Jonah crab fishery, there is still limited information on their habitat use and how environmental variables such as temperature, depth, and sediment impact their distribution (ASMFC, 2021). Information on habitat use is also lacking for Atlantic rock crabs. Therefore, my goal is to evaluate potential spatial-temporal trends in Jonah and Atlantic rock crab distributions and the relationships between crab presence and environmental variables using data from the Northeastern Fishery Science Center (NEFSC) spring bottom trawl surveys during 1968 – 2021. The first objective was to describe Jonah and Atlantic rock crab distributions over time using kernel density estimates (KDEs), and the second objective was to analyze their species – habitat relationships using generalized additive models (GAMs). The third objective was to compare Jonah and Atlantic rock crab habitat use using empirical cumulative distribution functions (eCDFs).

1.3. Methods

1.3.1 Study Area

The study area encompasses the Mid-Atlantic Bight (MAB) and Georges Bank (GB) along the northwest Atlantic coast (Figure 1.1) where the majority of the fishery catch occurs. These regions support high biological productivity and fisheries due to nutrient rich and well mixed waters (Townsend et al., 2006). The MAB portion of the continental shelf is approximately 110,000 km^2 and is about 850 km long; the northern portion of the MAB is about 100 km wide, and the southern portion is approximately 30 km. The MAB is fairly shallow with depths of about 100 m in the northern MAB and depths of about 40 m in the southern MAB (Lentz, 2008; Wallace et al., 2018). The MAB also interacts with waters of the Gulf Stream and the Slope Sea (Wallace et al., 2018).

GB is an offshore submarine plateau located at the southern end of the Gulf of Maine. It is about 62 miles offshore and encompasses an area of approximately 30,000 km^2 (Townsend et al., 2006; Wallace et al., 2018). GB is bounded by the Northeast Channel and the Great South Channel, which separates it from the Scotian Shelf and the MAB (Wallace et al., 2018). It receives an inflow of water from the Gulf of Maine and upwelling around its borders. Generally, the water column in GB stays well mixed throughout the year due to tides (Townsend et al., 2006). GB is also fairly shallow with a depth range of about 20 – 100 m, which affects water circulation and causes increased productivity in the area. Overall, the coastal currents in GB and MAB are part of a larger coastal circulatory system where the water originates in the subarctic seas and is transported to the temperate shelf (Wallace et al., 2018). The bottom sediment in both of these areas is predominately dominated by sand with a few deeper areas that have a higher concentration of mud and silt sediments. There are also a few areas closer to the shore with a more rockier and mixed substrate (Townsend et al., 2006; Uchupi, 1968). A study from 1977 – 2016 also found that temperatures in these areas have warmed (Wallace et al., 2018).

1.3.2 Data

Presence and absence of Jonah and Atlantic rock crabs from the Northeast Fishery Science Center (NEFSC) spring bottom trawl surveys during 1968 – 2021 were used to estimate habitat use (https://www.fisheries.noaa.gov/inport/item/22561). Annual NEFSC spring bottom trawl surveys used were conducted on the northeastern continental shelf of the United States from Cape Cod, Massachusetts to Cape Hatteras, North Carolina. The NEFSC spring trawl survey incorporated a stratified random sampling design where strata were defined mainly by depth and latitude with the number of stations sampled within each stratum being proportional to stratum size each year. Approximately 300 to 600 stations were sampled in each survey (Figure 1.1; Johnston & Sosebee, 2014; Politis et al., 2014). Environmental variables considered included grain size (ϕ), bottom temperature (°C), and average depth (m), bottom salinity (ppt), and rugosity (log m). Spring surveys were used because their timing was more consistent than fall surveys, and only tows in offshore strata were analyzed due to inshore strata not being sampled in the NEFSC trawl survey after 2009. The total number of tows was 8,918, with a sample size of 1,729 Atlantic rock crab presences and 1,284 Jonah crab presences.

Several vessels were used to conduct the NEFSC spring bottom trawl surveys. During 1968 – 2008, the R/V *Albatross IV* conducted surveys using a standard #36 Yankee trawl with rollers and codend liner with a stretch mesh of 11.4 cm towed at about 3.5 to 3.8 knots for 30 min in depths of approximately 5 – 365 m. The R/V *Delaware II* also conducted surveys using the same gear and trawling methods as the R/V *Albatross IV* for about fourteen years during 1973 – 2003 when the R/V *Albatross IV* was unable to survey. The R/V *Henry B. Bigelow* was the main research vessel for 2009 – 2021. The R/V *Henry B. Bigelow* used a 400 x 12 cm, 3-bridle, 4-seam trawl with codend with a stretch mesh of 12 cm to conduct the surveys. Jonah and Atlantic rock crabs have catchability differences among the three vessels as the R/V *Delaware II* and R/V *Henry B. Bigelow* had higher mean catch per tow compared to the R/V *Albatross IV* (Byrne & Fogarty, 1985; Miller et al., 2010; Politis et al., 2014).

Through the late 1980s, bottom temperature (°C) and average depth (m) were measured using an Expendable Bathythermograph (XBT) during the NEFSC bottom trawl surveys. After the late 1980s, these environmental variables and salinity were measured using SeaBirdTM conductivity, temperature, and depth (CTD) profilers (Reid et al., 1999; Politis et al., 2014). Grain size (ϕ) was calculated using data from the *trawlData* package including the Continental Margin Mapping Program (CONMAP) and the US East Coast Sediment Texture databases during 1997 – 2014 with more information found in Morley et al. (2018) (https://github.com/rBatt/trawlData). Grain size values were measured on the Wentworth Phi (ϕ) scale (Wentworth, 1922) based on estimates of the percentage of gravel, sand, and mud within a sample. In general, the value for gravel is -2.7, sand is 1.7, and mud is 7.5, which means larger grain size values represent finer sediments (µm) and smaller values represent rockier sediments (mm) (Morley et al., 2018; Wentworth, 1922). Rugosity was measured by comparing the mean depth of a cell with the mean depths of neighboring cells (Cullen & Guida, 2021).

1.3.3 Statistical Analysis

To describe the spatial and temporal distribution of Jonah and Atlantic rock crab presences and absences, a first order property of a point process analysis was evaluated for their intensity using a bivariate kernel density estimate (KDE). KDE is a powerful tool for visualization as it describes a smooth empirical probability density function (i.e., intensity) over time and space (Węglarczyk, 2018). I assumed independence among the presence observations with absences representing a control. The intensity was estimated by calculating the average number of presences within a given area. I estimated the bandwidth using the *bw.scott* function (Scott, 1992). I developed a KDE for each decade during 1970s – 2010s with the sample sizes found in Table 1.1. The 1960s and 2020s were excluded from this analysis due to an insufficient number of years sampled in the trawl survey. I then evaluated the KDEs using 1,000 Monte Carlo permutations to estimate how the intensity of Jonah or Atlantic rock crabs changed over time. Data sets for the Monte Carlo analyses were conducted using the function *relrisk.mc* using point process datasets with the absences used as a control (Kelsall & Diggle, 1995).

The presences of both crab species were also mapped using ArcGIS Pro (version 2.7.0). Temperature, depth, and grain size were mapped using inverse distance weighting (IDW, smoothing power, p = 2) to interpolate the values spatially. I also used empirical cumulative distribution functions (eCDFs; Perry & Smith 1994) to describe the distributions of the environmental variables and habitat usage by the two species in R. I used Kolmogorov – Smirnov tests to describe the significance of the differences in the eCDFs.

I used generalized additive models (GAMs) to estimate the relationships among Jonah and Atlantic rock crab presence – absence and the environmental variables and selected the best model using cross validation. GAMs were implemented using the *mgcv* package. The data included all presences of both species and a reduced number of absences in order for each year to have an equal number of presences and absences for each crab species. Absences were randomly selected without replacement in each year until the target number was reached. Data sets for cross validation were developed by splitting the data set into a training set (75.1 – 77.6%) and testing set (22.4 – 24.9%) (Table 1.2). The testing sets for both crab species included every 4th year of the time series (total of 13 years).

Before implementing the different GAMs, I examined correlation coefficients for multicollinearity due to environmental variables not being independent from one another. For pairs of parameters with correlation coefficients greater than 0.8 and a p-value of less than 0.05, one of the pair was excluded from the GAMs. Parameters with correlation coefficients greater than 0.5 were analyzed further with concurvity coefficients. Concurvity describes non-independence among variables that might influence the outcomes and significance of nonlinear relationships. In other words, it can be thought of as the non-linear form of multicollinearity (Kovács, 2022). The estimate was found by analyzing two smooth functions in the same model to see how much variation was explained (Wood, 2017). I examined the concurvity coefficients greater than 0.5 using the *concurvity* function further with GAM effect plots and degrees of freedom (df) to make certain a variable was not introducing errors within the models (Kovács, 2022; Wood, 2017). Rugosity was excluded from the analyses based on it being highly correlated with depth, and salinity was removed from the analyses due to it being highly correlated with temperature.

The binomial family was chosen for all GAMs due to the two species being evaluated by their presences and absences. Spline functions were used for all continuous variables, and the number of knots were determined by balancing the simplicity of the model against the explanatory power using the minimized generalized cross-validation (GCV) score in the *mgcv* package (Wood, 2017). I used tensor product splines to represent an interaction of spatial and temporal variables, which includes year, latitude, and longitude. Each marginal term penalizes the average flexibility of a tensor product (Pedersen et al., 2019; Wood, 2006). The tensor product spline selected the best number of knots across five dimensions. Vessel changes were included as a factor in each model to account for potential catchability differences among the three vessels.

I used the training data set for each species to estimate the GAMs, and the GAMs were used to predict the testing set values. The predicted and actual testing set values were then compared using confusion matrices with a threshold of 0.5. A confusion matrix is a table that analyzes the number of actual presences and absences against the predicted number of presences and absences for each GAM model. The sensitivity of a confusion matrix represents the ability of the model to predict presences, and the specificity represents the ability of the model to predict absences. Other diagnostics that were analyzed for choosing the best model with the best predicted power included root mean square error (RMSE) and mean absolute error (MAE). I also calculated the area under the curve (AUC) for the best model to show the accuracy of the model in predicting the presence and absence of the two crab species separately using the *auc* function from the *pROC* package (Robin et al., 2011). The importance of depth, grain size, and temperature variables in the best GAMs was also analyzed using the *biomod2* package (Filla et al., 2021; Thuiller et al., 2023). I used a simpler GAM that did not include temporal or spatial variables for each species when estimating the importance of selected explanatory variables.

1.4. Results

Jonah crabs had a high intensity of presences in the northern MAB area near Massachusetts and Rhode Island (Figure 1.2). Atlantic rock crabs consistently also had a high intensity of presences in the southern MAB near North Carolina during the study period. The most recent decades (2000s – 2010s) also showed a growing intensity of presences in GB compared to earlier years, especially more inshore. Atlantic rock crabs increased in intensity on

GB starting in the 1990s (Figure 1.3). The results of the KDE plots for Jonah crabs (Figure A1.1) and Atlantic rock crabs (Figure A1.2) by decade from the Monte Carlo permutations indicated substantial changes of the intensity of presences over time. The intensity of Jonah crabs started more along the outer continental shelf of the northern MAB region in the earlier decades, but the intensity shifted to be closer to shore in the most recent decades. Atlantic rock crabs consistently had a high intensity in the southern MAB region, but they have grown in intensity in the northern MAB and GB regions in the most recent decades.

Jonah crabs were abundant in the northern MAB and GB areas with depths over 100 m and fine sediments (Figures 1.4A & C, and 1.5). Jonah crabs tended to be located along the outer continental shelf at deeper depths (Figure 1.4A), and Jonah crabs aggregated in areas with finer sediments (Figure 1.4C) than Atlantic rock crabs. Atlantic rock crabs were found in shallower areas more inshore (Figure 1.4B & 1.5) and at grain size values around 2, which represents sandy sediments (Figure 1.4D & 1.5). Maps of the average temperature over the study area for each decade can be found in the appendix with Jonah and Atlantic rock crab presences (Figures A1.3 & A1.4).

The majority of the MAB and GB have depths less than 100 m, but a substantial portion of Jonah crab presences were found in areas with depths greater than 100 m (Figure 1.5A). Atlantic rock crabs were found in lower temperature habitat than Jonah crabs, on average (Figure 1.5C). Kolmogorov – Smirnov tests comparing both crabs with one another and all the data with each crab had p-values less than 0.05 for all three environmental variables. The eCDFs and Kolmogorov – Smirnov tests showed that Jonah and Atlantic rock crabs were not randomly distributed and were observed at specific depth and grain size values. Figures that show the density distribution of Jonah and Atlantic rock crab presences compared to the overall study area can be found in the appendix (Figures A1.5 – A1.6).

The best GAM model for both Jonah and Atlantic rock crabs included temperature, depth, grain size, and an interaction between year and location (latitude and longitude) (Tables 1.3 and 1.4). The significance of each variable and interaction between variables that were included in the best GAM for both crab species is in Table 1.5. While these GAMs are the most complex of those estimated, and they had high concurvity among independent variables, cross validation indicated that they were more accurate than simpler models. The most complex model also had the lowest AIC and the highest explained deviance of 16.1% for Jonah crabs. The best model for Atlantic rock crabs also had the highest sensitivity value of 0.72 and a specificity of 0.72. Several models had equal or slightly higher specificity values, but the chosen model had a lower AIC, higher AUC of 0.77, and higher explained deviance of 20.7%. The residuals diagnostics for the binomial GAMs did not indicate major violations of model assumptions for either species (Figures A1.7 & A1.8).

Jonah crab presences increased with increasing depth (Figure 1.6A). Jonah crab presences also increased as grain size values increased, and the majority of crabs were found in sandy and muddier sediments (grain size > 2; Figures 1.6B). For temperature, Jonah crabs preferred an intermediate temperature range between approximately 4 – 14°C (Figure 1.6C). The GAM effect plots for the spatial and temporal variables as well as changes in vessel were included in the appendix (Figures A1.9 & A1.10). There was not a significant difference of crab presence per year, but the spatial variables were highly significant, especially when looking at the interaction of spatial-temporal variables as a tensor product with crab presences.

Unlike Jonah crabs, the depth GAM effect plot for Atlantic rock crabs showed that they preferred depths less than 100 m or depths greater than 250 m deep (Figure 1.7A). For grain size values, Atlantic rock crabs were found mostly inhabiting sandy areas with a grain size value around 2 (Figure 1.7B). Similar to Jonah crabs, Atlantic rock crabs also had an intermediate temperature range preference between approximately 3 – 14°C (Figure 1.7C). The results for the GAM effect plots for the spatial, temporal, and changing vessel as a factor is included in the appendix, and they had similar results to Jonah crab GAM effect plots (Figures A1.11 & A1.12).

The GAM effects plots for the models that were used to understand the importance of environmental variables were similar to the best models for both Jonah crabs (Figure A1.13) and Atlantic rock crabs (Figure A1.14). The simpler model results for both species are found in the appendix (Table A1.1). Temperature, depth, and grain size values were all significant with p-values less than 0.05. For Jonah crabs, grain size was the most important variable, describing over 40% of habitat selection. Temperature had an importance of about 10% (Figure 1.8). For Atlantic rock crabs, depth had the highest importance value (> 60%), and temperature had the lowest value (< 10%; Figure 1.9). The factor for changing vessel had the lowest importance for both species. Carapace width of Jonah crabs was positively correlated with depth (Figure A1.15), but carapace width for Atlantic rock crabs was not positively correlated with depth (Figure A1.16).

1.5. Discussion

The distribution of Jonah and Atlantic rock crabs appears to be changing over time. Jonah crabs were found to be shifting more inshore in GB, and Atlantic rock crabs were found to increase their intensity in GB and the northern MAB in the spring. Both crabs preferred different habitats that are not based solely on the environmental variables evaluated. Jonah crabs were mostly found on the outer continental shelf at deeper depths and areas with sandy to muddy sediments, while Atlantic rock crabs were closer inshore and in the southern MAB at shallower depths and sandy sediments. However, none of the habitat variables considered in my analysis appeared to strongly predict presence or changes in the distribution of crabs. Grain size was the most important variable in predicting Jonah crab presences, and depth was the most important in predicting Atlantic rock crab presences in the GAMs. Both crabs had similar temperature ranges that did not appear to be driving their distributions.

1.5.1 Spatial and temporal changes

Jonah and Atlantic rock crabs in my KDE analyses and GAMs appeared to be expanding their range particularly in inshore areas. Jonah crabs had a shift in their intensity from the outer continental shelf of GB to more inshore with a growing intensity in recent years. Atlantic rock crabs, in contrast, had a growing intensity in GB and northern MAB in the most recent decades. Including spatial and temporal components in the GAMs helped account for changes over time in the distribution of the two species. There are several reasons that their spatial distributions may have changed during 1970 – 2020 including changes in exploitation, changes in predators, and climate change. The Jonah crab fishery did not start until around the 1990s, and catch is primarily concentrated in waters surrounding Massachusetts and Rhode Island. It is observed from the Jonah crab KDE (Figure 1.2) that the intensity in the northern MAB, which is where the majority of their fishery takes place, has declined and shifted more inshore starting after their fishery became more popular. However, the majority of the study area shows an expansion of Jonah and Atlantic rock crabs, especially within the GB. This expansion in GB is supported by observed increases in Jonah and Atlantic rock crabs in Narragansett Bay during 1959 – 2006 (Collie et al., 2008). Atlantic rock crabs also do not have a high catch rate in this fishery and are also not targeted because of their lower value and smaller size compared to Jonah crabs. Therefore, their range shift is likely not caused by fishing.

Jonah and Atlantic rock crabs may be indirectly affected by fishing on other species, which could cause a release from predation (Collie et al., 2008; Myers & Worm, 2003). Because many important predators like groundfish have experienced declines in the MAB and GB, it may have allowed Jonah and Atlantic rock crabs to expand their range. While both Jonah and Atlantic rock crabs have been found to feed on a broad range of organisms including bivalves, snails, isopods, sea urchins, small fish, crustaceans, etc., it is unclear that these organisms are being heavily impacted by potential abundance increases in these crab species (Donahue et al., 2009; Hanson et al., 2014; McKay & Heck, 2008). One laboratory study did find that Jonah crabs have the ability to significantly decrease green sea urchin populations, which in turn could reduce kelp consumption (McKay & Heck, 2008). Atlantic rock crabs have also been recently documented in Iceland, hypothesized to have come from the transfer of their larvae in ballast water, such that it is now one the most abundant crustaceans in southwest Iceland (Gíslason et al., 2014). Another anthropogenic activity that could have produced a change in Jonah and Atlantic rock crab distributions over time is climate change. Hare et al. (2016) scored these two species together as moderate in vulnerability and biological sensitivity to climate change. For example, suitable habitat of American lobster has changed regionally as their stocks have declined in southern New England and increased in the Gulf of Maine (ASMFC, 2020; Mazur et al., 2020). There is also evidence that spawning American lobster female’s distributions have changed from shallow inshore areas to deeper offshore areas (Bell, 2010). These distribution changes for American lobsters have been estimated to be primarily due to changes in the environment that are caused by warming temperatures in the northeast Atlantic (ASMFC, 2020). While temperature did not explain a substantial amount of the changing distributions of the two species in my study, other changing environmental variables that are caused by climate change that were not incorporated into my research, such as changes in their prey, could be causing Jonah and Atlantic rock crabs to shift. My study area also incorporated the middle of the distribution range of Jonah and Atlantic rock crabs where the species might not be encountering high temperatures that they are unable to tolerate.

1.5.2 Depth range of Jonah and Atlantic rock crabs

Jonah crabs have been found at depths from the intertidal to 750 m (Haefner, 1977; Lewis & Ayers, 2014; Stehlik et al., 1991). While my study only covers depths from 13 – 470 m, it was found that Jonah crabs preferred depths greater than 100 m and were found mostly on the outer continental shelf (Figure 1.6A). Other studies have also found that Jonah crabs prefer deeper, offshore waters, especially in the southern end of their range (Jeffries, 1966; Krouse, 1980). Depth was the second most important variable for predicting Jonah crab presence in my study (Figure 1.8). It was also found that the carapace width of Jonah crabs was positively correlated with depth, which likely means that larger crabs will be found at deeper depths compared to smaller crabs (Figure A1.15).

Atlantic rock crabs are found in a narrower depth range than Jonah crabs, intertidal – 450 m deep (Stehlik et al., 1991), and depth was the most important variable for predicting their presence in an area in my analyses (Figure 1.9). Atlantic rock crabs showed an unusual response to depth in which most were caught in depths less than 100 m, but they also appeared to prefer depths greater than 300 m (Figure 1.7A). However, there was a higher amount of uncertainty in the presence of Atlantic rock crabs at deeper depths. Haefner (1976) found that depth and size of the crab were positively correlated, and that the majority of Atlantic rock crabs were found to be in depths of 40 – 60 m. However, my results found that Atlantic rock crabs were not positively correlated with depth, but I did find that they were mostly found in depths less than 100 m (Figure A1.16).

1.5.3 Grain size range of Jonah and Atlantic rock crabs

Jonah crabs were found mainly in sandy to muddy sediments with a higher grain size value with a mean of 2.9, especially where the majority of their fishery is located in Massachusetts and Rhode Island (Figure 1.6B). Other trawl surveys and interviews with commercial fishers in southern New England indicated that the highest abundance of Jonah crabs was in silty sand and muddy sediments (Truesdale et al., 2019). However, other studies mostly with SCUBA, trapping, and video surveys indicated that Jonah crabs were found mostly in rockier substrates, which would have a smaller grain size value (Jeffries, 1966; Krouse, 1980; Rebach & Wowor, 1997; Richards & Cobb, 1986). Many of these studies indicated Jonah crabs preferred rockier habitat compared to what my study found were conducted in the Gulf of Maine and farther north. Jonah crabs in different regions may prefer different habitats due to variability in available habitat and competition with other crustaceans (Richards & Cobb, 1986). Additionally, rockier substrates may be harder to survey with trawls compared to other methods. It is also thought that when protecting themselves, crabs would opt for either a muddy habitat to bury themselves, or a rockier substrate in order to hide in the crevices. Therefore, even though my study found that grain size was the most important in predicting the presence of Jonah crabs, these crabs can be found in several different sediment types from mud to rocks (Figure 1.8; ASMFC, 2021).

Atlantic rock crabs preferentially inhabited sediments with sandier and larger grain sizes compared to Jonah crabs in my study. Other studies along the Atlantic coast also found that

Atlantic rock crabs preferred sandy to soft mud habitats; however, they were still found in other sediment types such as gravel and mixed rocky sediments (Jeffries, 1966; Krouse, 1972; Palma et al., 1999; Rebach & Wowor, 1997; Robichaud & Frail, 2006; Scarratt & Lowe, 1972). According to the eCDFs and the importance plot analyses, grain size was not a strong predictor of Atlantic rock crab presence (Figure 1.5B & Figure 1.9). This result indicates that Atlantic rock crabs may have stronger preferences to other environmental variables that were not included in my study, and variables such as depth and grain size were not good indicators of Atlantic rock crab presence.

1.5.4 Temperature preferences for Jonah and Atlantic rock crabs

Several studies have evaluated the effect of temperature on Jonah and Atlantic rock crabs, and my results were similar to previous findings. I found that Jonah crabs were most abundant in a temperature range of 4 – 14 °C in the spring (Figure 1.6C). A study using trawl and dredge surveys from Nova Scotia to Cape Hatteras, NC found that the highest abundance of Jonah crabs occurred in 8 – 12 °C water temperatures in the spring (Stehlik et al., 1991). Another study in the MAB also found Jonah crabs concentrated in a temperature range of 6 – 16 °C in March (Haefner, 1977). Other studies that took place around Nova Scotia and Gulf of Maine found similar temperature preferences for Jonah crabs, approximately 5 – 15 °C (Krouse, 1980; Pezzack et al., 2010). However, a laboratory study found that Jonah crabs from Massachusetts have a preferred temperature around 15.4 °C and adjusted their direction and movements to find their preferred temperature range (Lewis & Ayers, 2014). This latter temperature is warmer than the range found in my research. My results found a larger range of temperatures that the crabs preferred that were mostly cooler than Lewis & Ayers (2014), which indicates that Jonah crab distributions might not be dependent on temperature. Catchability of crabs in the NEFSC spring trawl survey could be temperature – dependent because Jonah crabs have reduced movements when they are below their ideal temperature (Lewis & Ayers, 2014). My results also indicated that Jonah crabs may not be strongly selecting for temperature, because temperature had the lowest importance compared to depth and grain size (Figure 1.8).

Even though Jonah crabs can inhabit a broad range of temperatures, their range is narrower than Atlantic rock crabs (Krouse, 1980). Atlantic rock crabs were mostly found in temperatures 4 – 7 °C in the spring (Stehlik et al., 1991), while other studies found a broader range of temperatures (0 – 14 °C; Haefner, 1976; Musick & McEachran, 1972). Similarly, my study found that the majority of Atlantic rock crabs were found within a range of 3 – 14 °C in the spring (Figure 1.7C). While Atlantic rock crabs have a large thermal range, they prefer cooler temperatures and are negatively correlated with temperature (Stehlik et al., 1991). Temperature was the least important environmental variables in my GAMs for Atlantic rock crabs (Figure 1.9).

1.5.5 Comparison of Jonah and Atlantic rock crabs

Jonah and Atlantic rock crabs appear to prefer different habitats. Jonah crabs were found in deeper waters along the outer continental shelf and in the northern MAB and GB area and in soft and silty sediments. Atlantic rock crabs, by contrast, were more evenly distributed along the continental shelf, were particularly concentrated in the southern MAB area, and were closer to inshore areas that are less than 100 m deep than Jonah crabs. Atlantic rock crabs also seemed to prefer sandy sediments. In Narragansett Bay, Rhode Island, Jonah and Atlantic rock crabs did not inhabit the same areas (Jeffries, 1966), and these two species were not significantly associated together in the Chesapeake Bight (Musick & McEachran, 1972). Jonah crabs tend to be more abundant in deeper waters along the shelf edge and in GB compared to Atlantic rock crabs that are more widespread across the continental shelf (Krouse, 1980; Musick & McEachran, 1972; Stehlik et al., 1991). Comparison studies between the two species also found that Atlantic rock crabs more often inhabit sandy sediments, but Jonah crabs preferred rocky and gravel substrates (Krouse, 1980; Jeffries, 1966; Musick & McEachran, 1972). While my results indicated that Atlantic rock crabs were more present in sandy substrates, I also found that Jonah crabs preferred substrates that were soft and muddy (Figure 1.5B). These differences could be due to the lack of rocky substrates sampled by my study and regional differences in Jonah crab's presences. My study also found that in the spring, both crab species inhabited a similar temperature range, but other studies that occurred at different times of the year found that Atlantic rock crabs are more eurythermal than Jonah crabs (Figure 1.5C; Jeffries, 1966; Musick & McEachran, 1972). The general distribution and environmental variable differences found between these two crabs mean that they probably respond to stressors such as climate change and other changes to their environment differently.

1.5.6. Catchability differences

Catchability differences due to the changes in vessels that occurred from 1968 – 2021 in the NEFSC spring bottom trawl surveys were accounted for by adding a changing vessel factor for each GAM analyzed to understand environmental preferences for both Jonah and Atlantic rock crabs. However, calibration among the three vessels would better account for the differences in catchability that might be influencing the results of this research. Calibration studies between the R/V *Albatross IV* and R/V *Henry B. Bigelow* were conducted in 2008 through paired tows and a beta-binomial model for American lobsters. These studies were used in order to estimate calibration factors that were length based to convert American lobster landings from the R/V *Henry B. Bigelow* to the R/V *Albatross IV* for years after 2008. The study used length-based calibrations as differences in the size-selectivity and overall size composition when conforming catches from R/V *Henry B. Bigelow* and R/V *Albatross IV*. Overall, the calibration study found that the R/V *Henry B. Bigelow* landed 64% more American lobsters compared to R/V *Albatross IV* as well as more smaller lobsters (Jacobson & Miller, 2012). Since the bottom trawl surveys went from using a #36 Yankee trawl with the R/V *Albatross IV* to a 400 x 12cm, 3 bridle 4 seam trawl with the R/V *Henry B. Bigelow*, it would be important to incorporate calibration factors for Jonah and Atlantic rock crabs similarly to American lobsters in future studies (Politis et al., 2014). Comparison studies not only have found catchability differences for Jonah crabs and Atlantic rock crabs between the R/V *Albatross IV* and R/V *Henry B. Bigelow,* but also between R/V *Albatross IV* and R/V *Delaware II* (Byrne & Fogarty, 1985; Miller et al., 2010). Even though R/V *Albatross IV* and R/V *Delaware II* used the same gear, calibration factors are also needed between these two vessels to account for differences between the two vessels that could influence the catchability between the two crabs.

Typical of other crustacean species, Jonah and Atlantic rock crabs will often bury themselves, which can reduce their catchability to trawls in areas with soft and sandy sediments. For example, dredge surveys, which sample deeper in the sediment than bottom trawls, caught more female Atlantic rock crabs than males. This difference in sex ratio could be due to males being more active in the day and avoiding the dredge, and females may have been buried in the sediment more often than males and were not able to avoid the dredge surveys (Stehlik et al., 1991). Jefferies (1966) found that Atlantic rock crabs are more active in general compared to Jonah crabs in a lab experiment. Therefore, habitat – specific behaviors of these two species as well as differences between males and females may influence the accuracy of their estimated preferred areas.

During 2012 – 2019, 92.7% of Jonah crabs in the fishery were caught using traps, 6.1% of Jonah crabs were caught by unknown gear types, and only 0.2% Jonah crabs were from trawls and 0.1% from dredges (ASMFC, 2021). Trawl surveys can also have a lower catchability rate in rockier and unsuitable areas where Jonah and Atlantic rock crabs can be located, which can skew abundance and environmental preference estimates (Sagarese et al., 2014; Sheperd et al., 2002). However, the fishery – independent data from the NEFSC bottom trawl surveys used for this project covered the majority of the Jonah and Atlantic rock crabs' range in the United States. The potential differences in catchability among the three research vessels used for these trawl surveys during 1968 – 2021 were relatively small according to the GAMs.

1.5.7 Conclusion

Understanding the spatial distribution and changes over time in Jonah and Atlantic rock crab populations, particularly where their fishery occurs, will help in creating a sustainable fishery and stock assessment for them. The commercial value and popularity of Jonah crabs has greatly increased since the start of their directed fishery, and it is expected to continue to grow as other crustacean species experience declines. Calibrations for the catch of Jonah and Atlantic rock crabs between vessels in the NEFSC bottom trawl surveys are important in order to accurately understand their population. The popularity and importance of Atlantic rock crabs might also increase as their population expands and has the potential to support struggling groundfish and lobster fisheries as an alternative market. This research helps provide fishery – independent analysis of the spatial distribution of Jonah and Atlantic rock crabs over time that can help in the general management and creation of a stock assessment for these species. Understanding the changes in their distribution can also help provide information for forecasting future changes in these populations. Another aspect that will help guide the management and predicting future changes of this fishery is using the results of how different environmental variables influence Jonah and Atlantic rock crabs. My results indicate that Jonah and Atlantic rock crabs can inhabit a broad range of temperatures, which means they may not be as heavily impacted by climate change as other crustaceans and organisms in this area. This research also illustrates that, while these two crabs resemble one another and are often grouped together, these species are different in their distributions and environmental preferences in the spring.

Even though the Jonah crab fishery is still fairly new, this research has an important application to other crustacean and marine species, especially as ecosystem – based fishery management (EBFM) becomes increasingly more important. Not only does temperature, depth, and grain size influence crustacean movements, growth rates, survivability, metabolism, activity levels, etc., but also other environmental variables that were not analyzed in this study such as dissolved oxygen, pH, photoperiod, and stratification (ASMFC, 2020; Hawkins, 1996). For instance, one of the most valuable fisheries in the United States is American lobsters. American lobsters have been found to be heavily influenced by raising temperatures along the Atlantic coast, which has caused their center of biomass to experience a northeast shift (Pinsky & Fogarty, 2012). Environmental changes in the Bering Sea have also been found to influence several crustacean species such as snow crabs, Tanner crabs, and Bristol Bay red king crabs. Similar to lobsters, these species are shifting poleward or to deeper waters (Szuwalski et al., 2021). Therefore, applying this research to other crustacean populations can help understand environmental preferences and potential changes in spatial distributions to help create sustainable fisheries that are resilient to climate change and other anthropogenic activities.

1.6. Tables

Table 1.1: Number of presence and absence observations of Jonah and Atlantic rock (Rock) crabs for the kernel density estimate analysis (KDE) by decade during 1970 – 2010s.

Decade	Jonah presence	Jonah absence	Rock presence	Rock absence
1970s	375	1,580	333	1,622
1980s	194	1,087	175	1,106
1990s	74	1,350	139	1,285
2000s	224	1,576	365	1,435
2010s	376	1,501	653	1,224

Table 1.2: Cross validation sample sizes for Jonah and Atlantic rock crabs for generalized additive models. Sample sizes include an equal number of presences and absences for each year from 1968 – 2021.

	Jonah crab	Atlantic rock crab
Training set	1,992	2,596
Testing set	576	862

Table 1.3: Binomial generalized additive models for Jonah crabs ordered by their Akaike information criterion (AIC; lowest is the best). Columns include the model degrees of freedom (df), specificity (spec), sensitivity (sen), area under the curve (AUC), root mean square error (RMSE), mean absolute error (MAE), cover between the actual and predicted testing set values, and explained deviance (exp dev) (%). The environmental variables include temperature (temp), depth, grain size (grain), latitude (lat), longitude (long), and year. The "s" represents a smoothing spline for continuous variables, and the "te" represents a tensor product spline to represent the interaction between spatial and temporal variables.

Model	df	AIC	spec	sen	AUC	RMSE	MAE	cover	exp dev %
temp + depth+ grain+ year+ lat,lon+ lat,lon, year	68.9	2454.15	0.62	0.72	0.74	0.58	0.33	0.67	16.10
temp, year+ depth+ grain+ lat,lon	46.5	2502.35	0.66	0.69	0.73	0.57	0.32	0.68	12.80
temp + depth+ grain+ lat,lon	38.5	2530.72	0.62	0.74	0.72	0.57	0.33	0.68	11.10
temp + depth+ grain+ lat,lon +year	41.0	2531.74	0.64	0.70	0.72	0.58	0.33	0.67	11.30
temp + depth+ grain, year+ lat,lon	40.8	2531.94	0.64	0.71	0.72	0.57	0.33	0.68	11.30
temp, year + depth+ grain+ lat	33.4	2562.74	0.67	0.66	0.70	0.58	0.34	0.66	9.62
temp, year + depth+ grain	21.6	2575.44	0.63	0.59	0.68	0.63	0.39	0.61	8.30
temp + depth, year+ grain	28.7	2581.14	0.62	0.59	0.68	0.63	0.39	0.61	8.61

temp + depth+ grain+ lat+ year+ lat, year	31.7	2591.95	0.57	0.66	0.69	0.62	0.38	0.62	8.44
temp+ deph+ grain+ lat	28.2	2602.92	0.55	0.74	0.69	0.60	0.36	0.64	7.79
temp+ depth+ grain+ lat+ year	25.9	2604.92	0.55	0.66	0.68	0.63	0.40	0.60	7.54
temp + depth+ grain+ year	27.7	2609.78	0.60	0.63	0.67	0.62	0.38	0.62	7.50
temp + depth+ grain	16.9	2620.85	0.55	0.71	0.69	0.61	0.37	0.63	6.32
temp + depth+ grain, year + lat	23.3	2626.66	0.52	0.68	0.67	0.63	0.40	0.60	6.57
temp + depth+ grain, year	22.3	2626.99	0.55	0.67	0.67	0.63	0.39	0.61	6.49
depth+ grain	12.7	2628.91	0.50	0.74	0.68	0.62	0.38	0.62	5.72
temp+ grain	14.1	2641.43	0.50	0.75	0.66	0.61	0.38	0.63	5.37
grain	5.4	2659.35	0.39	0.83	0.66	0.62	0.40	0.61	4.09
temp + depth	12.2	2679.87	0.54	0.65	0.65	0.64	0.41	0.59	3.84
depth	8.5	2683.01	0.54	0.67	0.65	0.63	0.40	0.60	3.46
temp	7.1	2739.62	0.56	0.58	0.60	0.66	0.44	0.56	1.31

Table 1.4: Binomial generalized additive models for Atlantic rock crabs ordered by their Akaike information criterion (AIC; lowest is the best). Columns include the model degrees of freedom (df), specificity (spec), sensitivity (sen), area under the curve (AUC), root mean square error (RMSE), mean absolute error (MAE), coverage between the actual and predicted testing set values, and explained deviance (exp dev) (%). The environmental variables include temperature (temp), depth, and grain size (grain), latitude (lat), longitude (long), and year. The "s" represents a smoothing spline for continuous variables, and the "te" represents a tensor product spline to represent the interaction between spatial and temporal variables.

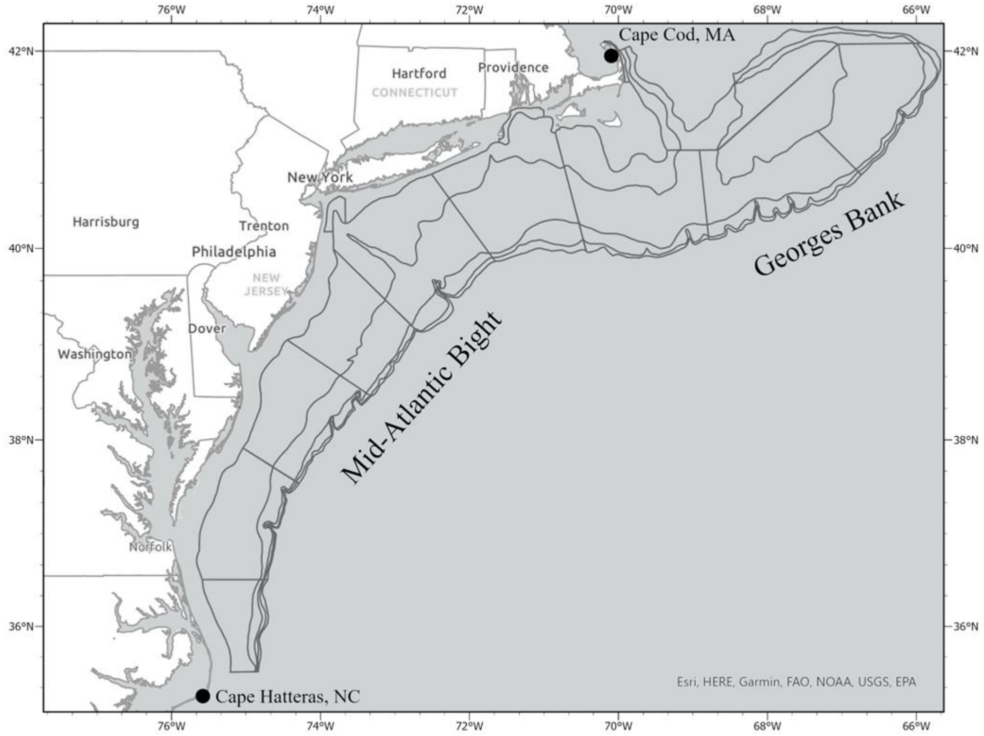
Model	df	AIC	spec	sen	AUC	RMSE	MAE	cover	exp dev %
temp + depth + grain+ year+ lat,lon+ lat,lon, year	81.2	3014.53	0.72	0.72	0.78	0.53	0.28	0.72	20.70
temp, year+ depth+ grain+ lat,lon	44.1	3081.93	0.76	0.66	0.78	0.54	0.29	0.71	16.80
temp+ depth+ grain+ lat+year +lat,year	43.6	3085.44	0.67	0.70	0.75	0.56	0.32	0.68	16.70
temp+ depth+ grain+ lat,lon	34.5	3104.30	0.71	0.67	0.76	0.56	0.31	0.69	15.70
temp+ depth+ grain, year + lat,lon	41.3	3104.78	0.72	0.65	0.76	0.56	0.31	0.69	16
temp+ depth+ grain+ year+ lat,lon	35.6	3106.26	0.71	0.67	0.76	0.56	0.31	0.69	15.70
temp, year+ depth+ grain+ lat	33.9	3129.97	0.69	0.65	0.75	0.57	0.33	0.67	14.90
temp+ depth+ grain+	24.7	3161.72	0.68	0.67	0.74	0.57	0.33	0.67	13.50

lat								
temp+ depth+ grain+ year+lat	25.7	3163.67	0.68	0.67	0.74	0.57	0.33	0.68	13.50
temp+ depth+ grain, year+lat	25.4	3164.11	0.68	0.65	0.74	0.58	0.33	0.67	13.50
temp+ depth, year+ grain	34.8	3197.95	0.66	0.68	0.73	0.58	0.33	0.67	13.10
temp, year+ depth+ grain	30.9	3215.78	0.68	0.66	0.73	0.57	0.33	0.67	12.40
temp+ depth+ grain	18.5	3247.76	0.67	0.66	0.71	0.58	0.34	0.66	10.80
temp+ depth+ grain+ year	19.5	3249.76	0.67	0.65	0.71	0.58	0.34	0.66	10.80
temp+ depth+ grain, year	20.3	3254.91	0.66	0.65	0.71	0.59	0.35	0.66	10.70
temp+ depth	10.1	3259.56	0.66	0.67	0.72	0.58	0.33	0.67	9.99
depth+ grain	15.7	3263.45	0.67	0.66	0.71	0.58	0.34	0.67	10.20
depth	7.4	3275.67	0.67	0.64	0.71	0.59	0.34	0.66	9.39
temp+ grain	15.0	3410.58	0.75	0.53	0.65	0.60	0.36	0.64	6.06
grain	11.7	3473.64	0.79	0.43	0.63	0.63	0.39	0.61	4.13
temp	6.9	3497.37	0.74	0.45	0.60	0.64	0.41	0.59	3.20

Table 1.5: The estimated degrees of freedom and p-values (in parentheses) for each variable in the best generalized additive models for both Jonah and Atlantic rock crabs. Vessels include R/V Delaware II (DE), R/V Henery B. Bigelow (HB), and R/V Albatross IV (AL).

Variables	Jonah crab	Atlantic rock crab
Temperature	2.14 (0.28)	2.42 (0.076)
Depth	6.83 (6.94e-05)	4.56 (0.0028)
Grain size	1.43 (0.018)	1.00 (0.48)
Year	1.00 (0.57)	1.00 (0.57)
Latitude, Longitude	23.77 (< 2e-16)	23.85 (0.00029)
Latitude, Longitude, Year	30.73 (< 2e-16)	45.32 (6.78e-07)
Vessel: DE	(0.024)	(0.93)
Vessel: HB	(0.35)	(0.59)
Intercept: AL	(0.90)	(0.42)

1.7. Figures



Esri, HERE, Garmin, FAO, NOAA, USGS, EPA

Figure 1.1: The sample area of the Northeast Fishery Science Center spring bottom trawl survey's offshore strata for the Mid-Atlantic Bight and Georges Bank. The dark gray lines show the strata used in the analyses.

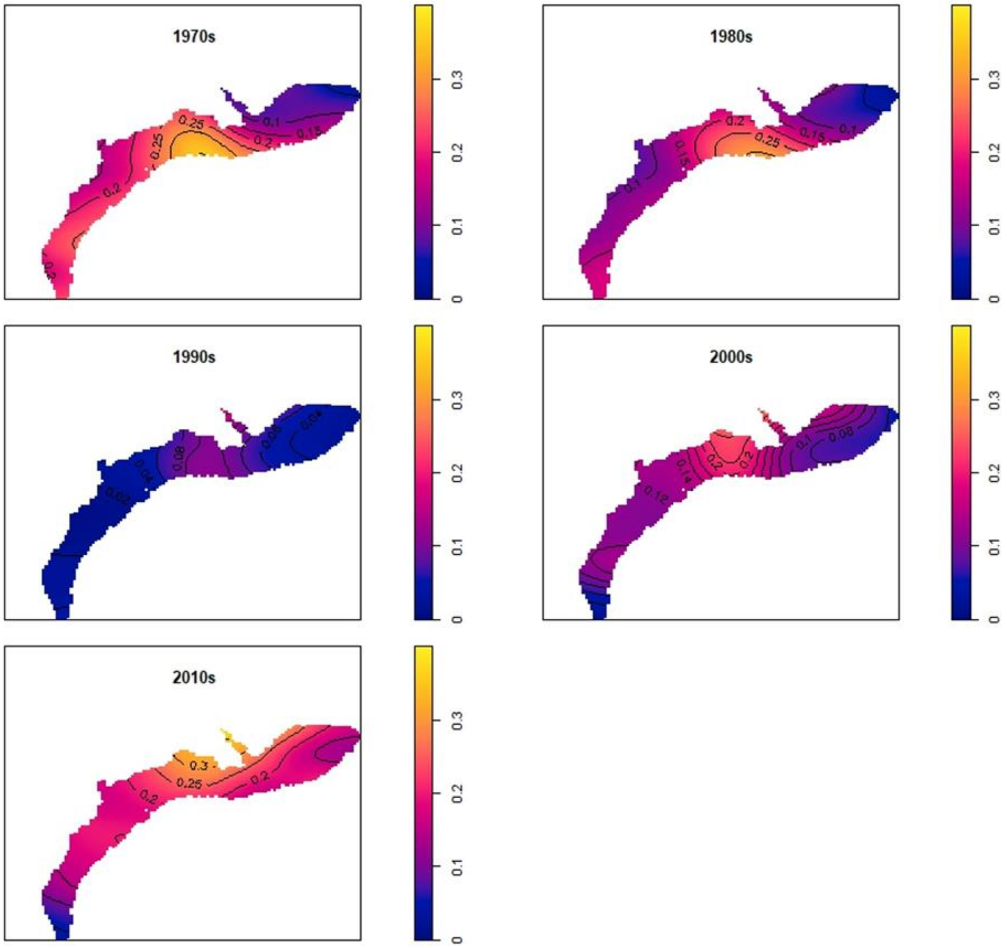


Figure 1.2: The kernel density estimates of Jonah crab presences with absences used as a control by decade. The cooler colors (blue) represent low intensities or probability of crab presences and warmer colors (yellow) represent high intensities of crab presences.

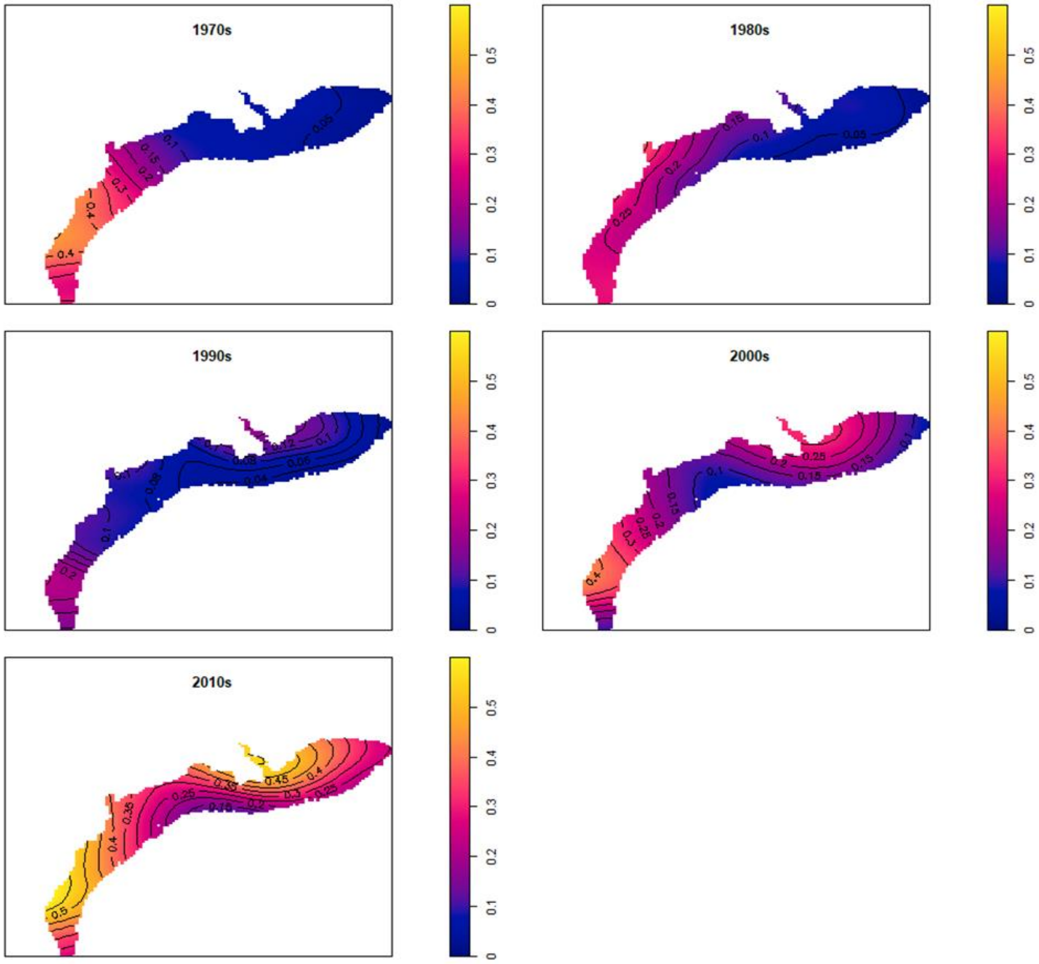


Figure 1.3: Kernel density estimates of Atlantic rock crab presences with absences used as a control by decade. The cooler colors (blue) represent low intensities or probabilities of crab presences and warmer colors (yellow) represent high intensities of crab presences.

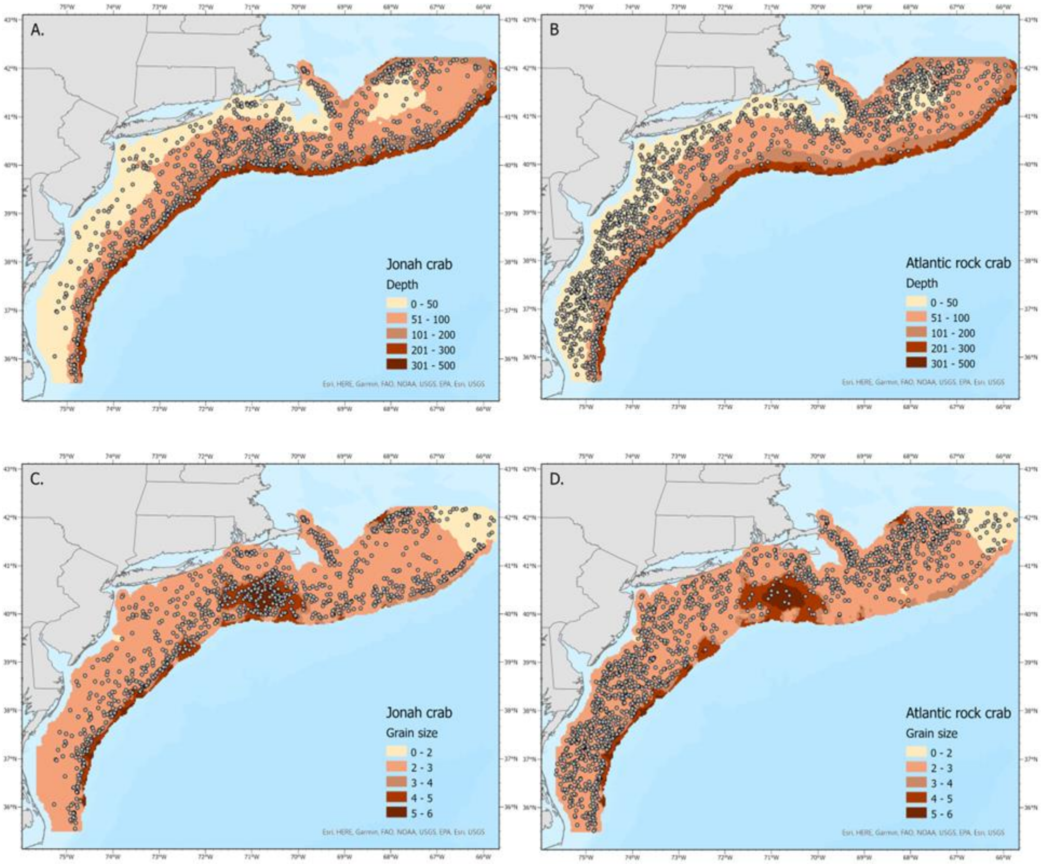


Figure 1.4: The presences of Jonah crabs with A) Depth and C) Grain size, and Atlantic rock crabs with B) Depth and D) Grain size during 1968 – 2021. Depth (m) and grain size values (ϕ) were calculated with inverse distance weighting.

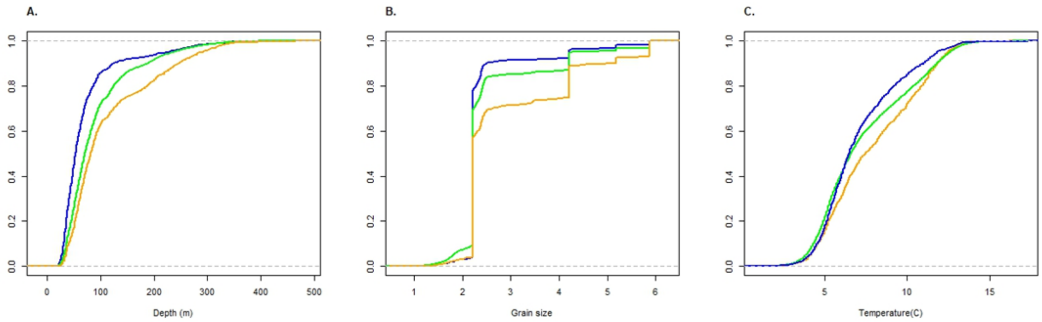


Figure 1.5: The empirical cumulative distribution functions show Atlantic rock crabs (blue), Jonah crabs (orange), and all data (green).The Kolmogorov – Smirnov test found p-values less than 0.05 for A) depth (m) between Jonah and Atlantic rock crabs (< 2.2e-16) and all data with both Jonah (8.78e-13) and Atlantic rock crabs (< 2.2e-16). , B) grain size (ϕ) between both crabs (< 2.2e-16) and all the data with both Jonah (< 2.2e-16)_and Atlantic rock crabs (5.03e-11), and C) temperature (°C) between both crabs (<2.2e-16) and all the data with both Jonah (< 2.2e-16) and Atlantic rock crabs (5.03e-11).

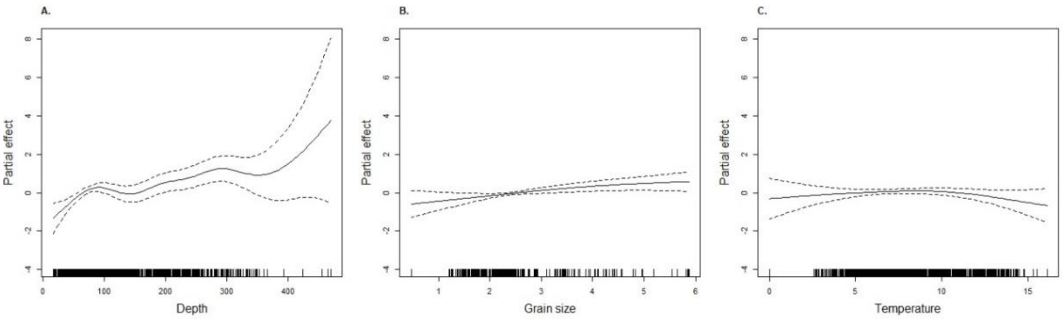


Figure 1.6: Jonah crab's generalized additive model effect plots from the best model with smoothing splines for A) depth (m), B) grain size (ϕ), and C) temperature (°C).

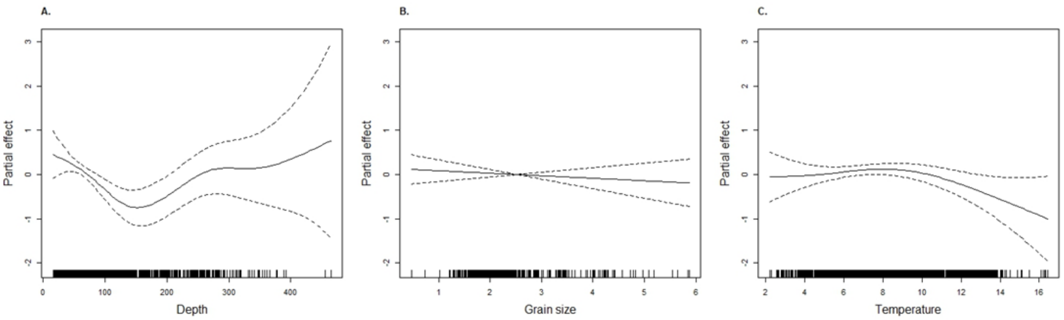


Figure 1.7: Atlantic rock crab's generalized additive model effect plots from the best model with smoothing splines for A) depth (m), B) grain size (ϕ), and C) temperature (°C).

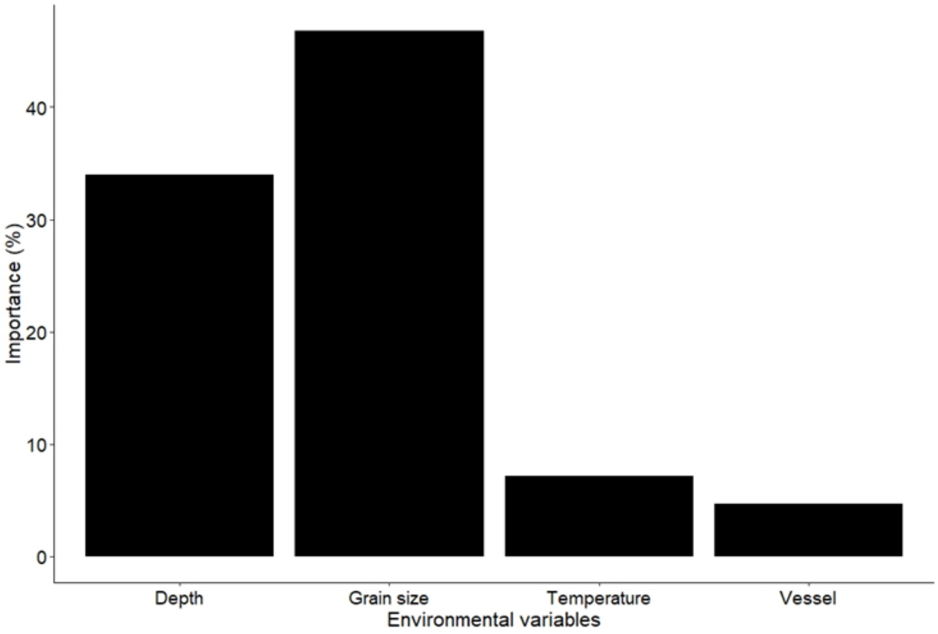


Figure 1.8: The estimated importance (%) of variables for Jonah crabs and the three environmental variables and the catchability differences among the three vessels.

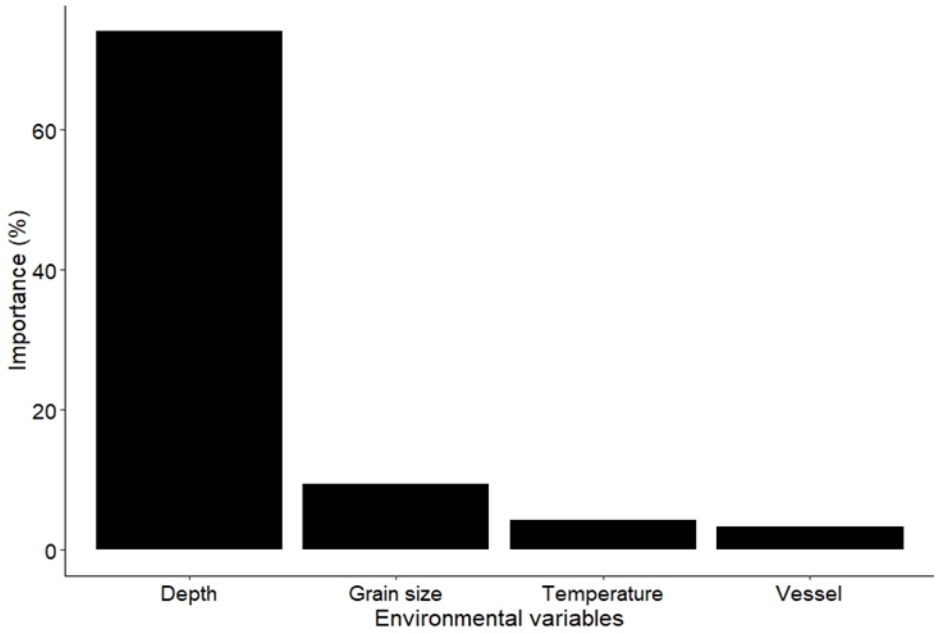


Figure 1.9: The estimated importance (%) of variables for Atlantic rock crabs and the three environmental variables and the catchability differences among the three vessels.

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Chapter 2 : Seasonal movement patterns of Jonah and Atlantic rock crabs along the U.S. Atlantic coast during 1992 - 2007

2.1. Abstract

Jonah crab (*Cancer borealis*) and Atlantic rock crab (*Cancer irroratus*) were traditionally bycatch species in the American lobster (*Homarus americanus*) fishery, but their economic importance has increased greatly in the U.S. since the 1980s. However, these species are data limited and potential differences in seasonal distributions are poorly understood. My objectives were to determine the seasonal distributions for both crab species and determine whether distributions differed by sex and maturity to improve understanding of habitat use and movement patterns. Data were obtained from offshore spring, fall, and winter bottom trawl surveys conducted by the Northeast Fisheries Science Center during 1992 – 2007. I conducted ANOVAs, empirical cumulative distribution functions, centroids of mass, and kernel density estimates to estimate differences in average depth (m) and distance to shore (km) among sex and maturity categories for Jonah and Atlantic rock crabs within Georges Bank and the Mid-Atlantic Bight regions. Jonah crabs were typically found closer to shore and at shallower depths in the fall and spring and moved farther from shore and to deeper depths in the winter. Atlantic rock crabs across all sex and maturity categories were observed farther offshore at deeper depths in the fall and closer to shore at shallower depths in the winter and spring. Sex and maturity also influenced seasonal distributions for both species. This work provides a better understanding of potential migration patterns of Jonah and Atlantic rock crabs that could help in developing quantitative stock assessments for these two species.

2.2. Introduction

Many marine species exhibit ontogenetic or seasonal migration including marine mammals (Horton et al., 2020), fish (Coetzee et al., 2010; Polovina, 1996), and crustaceans (Groeneveld & Branch, 2002). Migration is the movement of individuals together for specific motivations (Secor, 2015). These motivations that can cause migratory behavior include food variability, favorable reproductive conditions, and environmental changes (Visser et al., 2020). Partial migration is one form of migration when there are more than two life histories in the same species where some individuals perform migrations and other individuals do not (Secor, 2015). Particularly, some crustacean species have been found to have this complex migration pattern such as American lobsters (*Homarus americanus*). A portion of American lobsters undergo seasonal migrations where they inhabit shallow coastal waters in the spring and summer and deeper waters in the fall and winter in New England, but some lobsters do not migrate (Cooper & Uzmann, 1971; Haakonsen & Anoruo, 1994). Dungeness crabs (*Cancer magister*) have also been observed to have possible seasonal migrations based on sex and maturity (Taggart et al., 2004). Other species have differential migration where only part of the population will migrate based on their life stage, sex, or other defining characteristic (Secor, 2015). For example, only female blue crabs (*Callinectes sapidus*) will migrate to spawning areas around the summer and fall (Turner et al. 2003). Some crustaceans along the Atlantic coast such as blue crabs and northern lady crabs (*Ovalipes ocellatus*) are also suspected to be inactive and buried in the winter months, which might influence their catchability (Glandon et al., 2019; Stehlik et al., 1991). Current environmental changes that are occurring outside normal seasonal variability such as climate change and other anthropogenic activities have caused more species to change their distributions such as moving poleward, farther offshore, and into deeper waters (Hastings et al., 2020; Kortsch et al., 2015; Szuwalski et al., 2021). Understanding a species life history and migration patterns is the first step to identify the impact climate change might have on their populations and distributions (ASMFC, 2015).

Seasonal movement patterns of Jonah crabs (*Cancer borealis*) and Atlantic rock crabs (*Cancer irroratus*) are not well understood (ASMFC, 2015, 2021). Similar to some American lobster populations, Jonah crabs may have seasonal migrations. Within their known distribution, Newfoundland to Florida and Bermuda, Jonah crab populations might have migratory and non-migratory groups (ASMFC, 2021; Haefner, 1977; Leland, 2002; Pezzack et al., 2010). The migratory group has been suggested to move inshore in the spring and fall and offshore to deeper, warmer waters during the winter months in the Gulf of Maine, Georges Bank (GB), and the Mid-Atlantic Bight (MAB) (Krouse, 1980; Leland, 2002; Stehlik et al., 1991). Female Jonah crabs may also move farther inshore compared to males in the late spring and summer as indicated in changes in catch rates (Krouse, 1980). Improving understanding of potential seasonal migrations and aggregations of female Jonah crabs is important to inform management on stock boundaries (ASMFC, 2021). Seasonal surveys have suggested sex-specific movement patterns of Jonah crab with higher catches of males in spring and summer trawl surveys, and higher catches of females in late summer and fall surveys in the Gulf of Maine, the MAB, and along the Atlantic coast from Nova Scotia, Canada to Cape Hatteras, NC (Haefner, 1977; Krouse, 1980; Stehlik et al., 1991).

Atlantic rock crabs may exhibit seasonal migrations and may also have non-migratory and migratory populations that vary regionally. The migratory populations might be more concentrated in the southern portion of their range and Atlantic rock crabs in the northern part of their distribution are usually found year-round along the coast (Bigford, 1979). The distribution of Atlantic rock crabs is as far south as South Carolina, U.S. to Labrador, Canada (and recently reported in Iceland) (Gíslason et al., 2014; Haefner, 1976; Rebach, 1985). Atlantic rock crabs in the MAB might inhabit areas closer to the coast from late fall to early spring and move offshore into deeper water in the late spring and summer (Bigford, 1979; Haefner & Van Engel, 1975; Rebach, 1985; Shotton, 1973; Stehlik et al., 1991). Male and female Atlantic rock crabs may have different seasonal movements or catchability. The catch ratios between females and males change depending on the season and location as males were more abundant than females in some surveys (Krouse, 1980; Scarratt & Lowe, 1972), but females were found to have a slightly higher catches in the fall in some studies (Bigford, 1979; Krouse, 1980; Stehlik et al., 1991).

Jonah and Atlantic rock crabs were originally considered nuisance species in the American lobster fishery. As American lobsters experienced declines in southern New England due to overfishing and rising temperatures, Jonah and Atlantic rock crabs increased in economic importance. Jonah crabs became a mixed crustacean fishery with American lobsters in the 1990s (ASMFC, 2015; Gulf of Maine Research Institute & University of Maine, 2013). They are typically fished in the winter in Massachusetts and Rhode Island by fishers modifying lobster pots through different trap vents, bait type, and fishing locations (ASMFC, 2015, 2021; Gulf of Maine Research Institute & University of Maine, 2013; Robichaud & Frail, 2006). The landings of the fishery have increased 669% during 2000 – 2017, and this trend is expected to continue (ASMFC, 2019). In 2019, Jonah and Atlantic rock crabs had a combined dockside value of $13 million USD and a total catch of 17.7 million pounds (ASMFC, 2021). While Atlantic rock crabs are not as popular or valuable compared to Jonah crabs due to their smaller size, they historically have been caught and could rise in popularity to help offset some fishing pressures of other crustaceans (Haefner & Van Engel, 1975). However, the spatial distributions throughout the year for both species are not well understood, and neither species has a quantitative stock assessment that is able to provide advice on stock status (ASMFC, 2023).

With Jonah crab commercial fishery increasing, concerns have been raised about the sustainability of their fishery (ASMFC, 2015; Bradt et al., 2016; Gulf of Maine Research Institute & University of Maine, 2013). The first Interstate Fishery Management Plan (FMP) was developed for Jonah crabs by the Atlantic States Marine Fisheries Commission in 2015 (ASMFC, 2015) out of stakeholder concerns. Little is known about Jonah crab biology and life history, which is crucial for maintaining a sustainable fishery and understanding how the species might respond to environmental changes. For example, changes in temperature, which are occurring in the MAB and GB, can cause changes in the depth or displacement of a species (Haakonsen & Anoruo, 1994; Wallace et al., 2018). Potential long-term changes in habitat can also affect the resilience and sustainability of fisheries for a migratory species (Pezzack et al., 2010). Because the migratory patterns for Jonah and Atlantic rock crabs are still unclear across the Atlantic coast of the U.S., the biological effects of management actions and environmental stressors are not well understood (ASMFC, 2015). While seasonal movements for Jonah and Atlantic rock crabs have been suggested in the literature, the habitat usage and description of seasonal movements is extremely limited, particularly in the MAB and GB (ASMFC, 2015). Therefore, my goal was to identify potential seasonal movement patterns for Jonah and Atlantic rock crabs in GB and the MAB. My specific objectives were to determine the seasonal spatial distributions of Jonah and Atlantic rock crabs and determine whether distributions differed by sex and maturity using the Northeast Fisheries Science Center (NEFSC) winter, spring, and fall bottom trawl surveys.

2.3. Methods

2.3.1. Study Area

The study area included GB and the MAB on the northwest Atlantic continental shelf (Figure 2.1). GB is a submarine plateau offshore from Cape Cod, Massachusetts (Townsend et al., 2006). The MAB extends approximately 850 km between Cape Cod, Massachusetts and Cape Hatteras, North Carolina along the U.S. Atlantic coast (Wallace et al., 2018). The MAB encompasses a larger area of the continental shelf (110,000 km^2) than GB (approximately 30,000 km^2; Townsend et al., 2006; Wallace et al., 2018). Both areas are relatively shallow with GB having a depth range of about 20 – 100 m, and the MAB having an average depth of about 100 m in the northern MAB and approximately 40 m deep in the southern MAB (Lentz, 2008; Wallace et al., 2018). GB receives an inflow of water from the Gulf of Maine, and the MAB interacts with the Gulf Stream and the Slope Sea (Townsend et al., 2006; Wallace et al., 2018). Due to the nutrient rich and relatively well mixed waters throughout the year, these areas support high productivity (Townsend et al., 2006). Temperatures in these areas are increasing due to climate change (Wallace et al., 2018).

2.3.2. Data

Jonah and Atlantic rock crabs were collected by the Northeast Fisheries Science Center (NEFSC) winter (https://www.fisheries.noaa.gov/inport/item/22563), spring (https://www.fisheries.noaa.gov/inport/item/22561), and fall (https://www.fisheries.noaa.gov/inport/item/22560) bottom trawl surveys during 1992 – 2007. These years represent the period when all three of the bottom trawl surveys were conducted. The winter bottom trawl survey commenced in 1992 and ended in 2007. The winter surveys, conducted from January 30th – March 5th, and the spring surveys, conducted from February 28th – April 27th, have some overlap in the period the trawl surveys were conducted. The fall surveys were conducted during September 4th – November 9th and did not overlap temporally with the other two trawl surveys. All seasonal surveys used a stratified random sampling design with the number of stations proportional to the area of each stratum (Politis et al., 2014). About 300 to 600 stations were sampled in the winter, spring, and fall surveys for each year (Johnston & Sosebee, 2014; Politis et al., 2014). The vessels used to conduct the NEFSC bottom trawl surveys were the R/V *Albatross IV* and the R/V *Delaware II*. A comparison between the two vessels found catchability differences with the R/V *Delaware II* having a higher mean catch per tow for both Jonah and Atlantic rock crabs than the R/V *Albatross IV* (Byrne & Fogarty, 1985). The spring and fall surveys used a standard #36 Yankee trawl with rollers and codend liner with a stretch mesh of 11.4 cm towed at about 3.5 to 3.8 knots for 30 minutes in depths of about 5 – 365 m. The winter trawl survey is also known as the “winter flatfish survey” and used a #36 Yankee trawl with some modifications relative to the spring and fall surveys. Some of the main modifications included a 4.5-inch rubber disk covered chain sweep that replaced rollers and the addition of a 30 fathom ground cable in front of the net (Stauffer, 2004).

Jonah and Atlantic rock crabs were enumerated for each tow. Each crab was identified to species and their sex and carapace width (CW) were recorded. Depth (m) was measured using SeaBirdTM conductivity, temperature, and depth (CTD) profilers (Politis et al., 2014; Reid et al., 1999). Latitude and longitude were also recorded for each tow. Distance from shore (km) was calculated using the near tool in ArcGIS Pro as the shortest distance between the tow and the shoreline. Maturity was assigned for each crab as a function of CW and sex using average CWs at 50% maturity from previous studies. Maturity was incorporated in this study in order to understand if mature crabs have different seasonal patterns compared to immature crabs. Male Jonah crabs with CWs ≥110 mm were categorized as mature (Carpenter, 1978; Lawrence, 2020; Olsen & Stevens, 2020; Perry et al., 2017), and female Jonah crabs were considered mature with CWs ≥ 90 mm (Carpenter, 1978; Olsen & Stevens, 2020; Perry et al., 2017). Male Atlantic rock crabs with CWs ≥ 90 mm were categorized as mature (Haefner, 1976; Scarratt & Lowe, 1972), and female Atlantic rock crabs were considered mature with CWs ≥ 70 mm (Haefner, 1976; Krouse, 1972; Scarratt & Lowe, 1972). Even if the averages for maturity are incorrect, my results will estimate if there are differences based on size for Jonah and Atlantic rock crabs.

2.3.3. Statistical Analysis

To evaluate potential seasonal migrations for Jonah and Atlantic rock crabs, I used ANOVAs to compare the mean depth and distance from shore of different groups of crabs such as sex, maturity, season, and region. The full model is found in Eq. 1 with D representing either depth or distance from shore depending on the ANOVA model, and ϵ representing a normally distributed error term. Models with all possible combinations of variables and interactions were fitted using the dredge function from the *MuMIn* package (Bartoń, 2023). I determined the best ANOVA model using corrected Akaike information criterion (AICc). Model diagnostics for the best models were evaluated to determine if the ANOVA assumptions were met.

Eq. 1.

$$\begin{aligned} D = {} & region + season + maturity + sex + (region \times season) + (region \times maturity) \\ & + (region \times sex) + (season \times maturity) + (season \times sex) \\ & + (maturity \times sex) + (region \times season \times maturity) \\ & + (region \times season \times sex) + (region \times maturity \times sex) \\ & + (season \times maturity \times sex) + (region \times season \times maturity \times sex) + \epsilon \end{aligned}$$

To address whether Jonah or Atlantic rock crab distributions differed seasonally, I calculated centroid locations. Centroids of mass were calculated separately for the GB and the

MAB regions and seasonally in ArcGIS Pro. Eq. 2 shows the latitude (X_{lat}) and longitude (Y_{lon}) of the centroid of mass calculated as the sum of the latitudes (x_i) and longitudes (y_i) of the individual samples divided by the number of observations (n).

Eq. 2:

$$X_{lat} = \frac{\sum_i x_i}{n} \; ; \; Y_{lon} = \frac{\sum_i \; y_i}{n}$$

The MAB and GB regions were separated due to the differences in demographics of the regions as well as to account for potential differences in crab behaviors such as movement patterns and activity levels. Centroids were also calculated seasonally by sex and maturity to explore evidence of sex-single migrations or movement patterns based on life stage. I also used catch ratios of male:female crabs or immature:mature crabs to understand potential differences between the sex and maturity of Jonah and Atlantic rock crabs in the winter, spring, and fall.

I used binomial kernel density estimates (KDEs) for the period 1992 – 2007 to estimate spatial empirical probability density functions for Jonah and Atlantic rock crabs seasonally (Węglarczyk, 2018). The intensity was calculated by averaging the number of observations in a given area, and the tows that had no crabs were included as a control. The area over which the observations were smoothed was determined by the bandwidth parameter. The bandwidth was calculated using the *bw.scott* function in R for every KDE separately (Scott, 1992). The null hypothesis for these KDE tests was that the intensity differences are equal throughout the study area. I evaluated the significance of spatial patterns in the KDEs with 1,000 Monte Carlo permutations. The Monte Carlo analyses for point process datasets were conducted using the *relrisk.mc* function in R (Kelsall & Diggle, 1995).

I estimated the distribution of depth (m) and distance from shore (km) for Jonah and Atlantic rock crabs along the Atlantic coast in the winter, spring, and fall using empirical cumulative distribution functions (eCDFs; Perry & Smith, 1994). eCDFs were used to compare the distributions between sexes and maturities as well as compare among seasons. Observations of crabs were divided regionally by GB and the MAB due to the differences in distance from shore and depth range, which could influence the overall results in the catchability differences or movements of crabs per season. Separating the regions also allowed us to understand if the crabs appear to behave differently between the regions. Pairwise differences in the distributions of depth and distance from shore among seasons and between different groups from eCDFs were analyzed using Kolmogorov – Smirnov (KS) tests. I adjusted the critical p-values for the KS tests depending on the number of tests used for each conclusion using the Bonferroni correction. For example, the distributions of Jonah and Atlantic rock crabs were compared for depth and distance to shore among the three seasons, which meant there were three tests. Therefore, the critical p-value when comparing the three seasonal distribution ranges of Jonah and Atlantic rock crab observations by depth and distance from shore for the MAB and GB separately was 0.017. The critical p-value when comparing the three seasonal distributions of Jonah and Atlantic rock crabs for sex and maturity categories was 0.0042 (twelve tests for depth and distance to shore for the MAB and GB separately).

2.4. Results

2.4.1. Sample sizes

A total of 2,325 Jonah crabs were caught in NEFSC bottom trawl surveys during 1992 – 2007 (Table 2.1). The majority of Jonah crabs were caught in the winter survey and the lowest number of crabs were caught in the spring survey (Table 2.1). For both the winter and spring surveys, more male Jonah crabs were caught than females with sex ratios of 2.24:1 (male to female) in the winter and 1.59:1 in the spring (Table 2.2). In the fall, the sex ratio was about 1:1.

Mature Jonah crabs were more abundant in the catch in the winter with a catch ratio of 4:1 (mature:immature), but catches of immature Jonah crabs were higher than mature Jonah crabs in the spring with a catch ratio of 1:1.32 and fall with a catch ratio of 1:1.27 (Table 2.2).

The total number of Atlantic rock crabs caught in the NEFSC bottom trawl surveys was 2,669 crabs during 1992 – 2007 (Table 2.3). Similar to Jonah crab, the highest Atlantic rock crab catches occurred in the winter and the lowest catch occurred in the spring (Table 2.3). More male Atlantic rock crabs were caught than females with sex ratios of 2.02:1 in the winter, 1.18:1 in the spring, and 1.10:1 in the fall (Table 2.4). Immature Atlantic rock crabs also outnumbered mature ones with catch ratios of 1:1.09 (mature:immature) in the winter, 1:2.72 in the spring, and 1:3.13 in the fall (Table 2.4).

2.4.2. Jonah crab

The most important variables for explaining the Jonah crab depth and distance from shore included sex, maturity, season, and region as well as interactions between season and sex, maturity and season, and region and season (Tables 2.5 – 2.7). The AICc best model for depth also included interactions between sex and region, maturity and region, and a three-way interaction with maturity, region, and season (Tables 2.6 & 2.8). The distance to shore ANOVA for Jonah crabs had an interaction between sex and maturity as well as a three-way interaction among sex, maturity, and season in the AICc best model (Tables 2.7 & 2.9). The residual diagnostics from the AICc best ANOVAs for Jonah crab appeared to reasonably meet the assumptions (Figures A2.1 & A2.2), and the other models within two AICc units included similar variables (Tables A2.1 & A2.2).

The centroid of Jonah crabs on GB was offshore in the winter and more northerly in the spring and fall (Figure 2.2A). Mature female and male Jonah crabs were also found in deeper depths on average in the spring compared to the fall and winter (Table 2.8). The seasonal eCDFs and KS tests for distance to shore in GB indicated that Jonah crabs were distributed more broadly and could be found closer to shore in the fall compared to the winter (p-value = 0.016; Table A2.3; Figure 2.3). The eCDF and KS tests for depth showed that Jonah crabs were found at a significantly greater depth in the fall (p-value = 5.44e-06) and spring (p-value = 0.00072) compared to winter (Table A2.3; Figure 2.3). These results differed somewhat from the depth ANOVA that found greater differences between the fall and spring than winter and fall (Table 2.8). However, the eCDFs suggested that Jonah crabs in the spring were found at deeper depths compared to fall, even though these differences were not considered significant (Table A2.3; Figure 2.3). The depth and distance from shore averages from the best ANOVAs for GB are reported in the appendix (Figures A2.16 – A2.17).

In the MAB, Jonah crabs were found more offshore in the winter and farther north in the fall (Figure 2.2A). Similarly, mature female crabs in the winter were found to be at about 105.6 m deep compared to the spring at 75.3 m (Table 2.8). Mature females were also found to be farther offshore at an average of 102.9 km in the winter compared to 61.2 km in the spring and 89.4 km in the fall (Table 2.9). Mature male Jonah crabs were found at an average distance from shore of 98.4 km in the winter compared to the fall that had an average distance of 73.9 km (Table 2.9). Immature male Jonah crabs also were farther offshore in the winter compared to the spring (Table 2.9). Similar to mature female Jonah crabs in the ANOVA for distance from shore, the eCDFs and KS tests for distance from shore found that all three seasonal distributions were significantly different (Table A2.3; Figure 2.3). Jonah crabs in the winter had the deepest distribution (p-value = 1.19e-11 in fall; p-value = 6.22e-08 in spring). Jonah crabs were closer to shore, on average, in the spring compared to the fall (p-value = 0.0012; Table A2.3; Figure 2.3).

The eCDF and KS tests for depth indicated significantly different distributions (p-value < 0.017) among all three seasons (Table A2.3; Figure 2.3). The ANOVAs, by contrast, showed a significant difference in depth between the spring and winter for mature female crabs (Table 2.8). KDEs for the differences in intensity for Jonah crab seasonally are found in the appendix (Figure A2.3 – A2.4). The appendix further illustrates the results of the best depth and distance from shore ANOVAs for Jonah crabs in the MAB (Figures A2.18 – A2.22).

Jonah crabs also had different seasonal patterns based on ontogeny in the MAB, but the centroid locations on GB were similar between mature and immature Jonah crabs (Figure 2.2B). In the depth ANOVAs, mature male and female Jonah crabs were found at deeper average depths, 216 m and 176.9 m respectively, compared to immature males (91 m) and females (51.9 m) in the spring (Table 2.8). Similarly, the eCDF and KS test for mature and immature male Jonah crabs in the spring also showed that mature crabs had a different depth distribution compared to immature crabs (p-value = 1.03e-05; Table 2.10 & Figure 2.4). Similarly, mature female Jonah crabs were found farther from shore (198.8 km), on average, compared to immature female Jonah crabs (169.7 km) in the winter (Table 2.9). Mature Jonah crabs in the spring were found more inshore and immature crabs were more spread out in GB, but these results were not consistent across tests; the ANOVAs and eCDFs indicated mature male crabs were deeper and farther from shore compared to immature male crabs (Tables 2.8 – 2.10; Figure 2.4 – 2.5 & A2.5). For the most part, mature and immature Jonah crabs had similar spatial patterns of intensities seasonally in GB, which was reflected in the seasonal centroids (Figure 2.2).

In the MAB, mature Jonah crabs were farther north in all seasons, especially in the spring, compared to immature crabs in the same seasons (Figure 2.2B). Immature Jonah crabs had a slightly higher intensity in the southern MAB compared to mature Jonah crabs in the winter and spring, but the intensities in the fall were similar (Figures 2.5 & A2.5). In the winter, mature male Jonah crabs had an average depth of 121.5 m and 98.4 km distance from shore compared to immature male crabs (average depth of 108 m; 86.7 km distance from shore; Tables 2.8 – 2.9). These results were similar to the KS tests between immature and mature male crabs for depth, which indicated significantly different distributions for depth (p-value = 8.72e-06) and for distance to shore (p-value = 0.00059; Table 2.11). The eCDFs illustrated that mature male Jonah crabs were found at deeper depths and farther from shore, on average, compared to immature male Jonah crabs in the winter (Figure 2.4). Mature female Jonah crabs were also found farther from shore (102.9 km) compared to immature female Jonah crabs (73.8 km) in the winter (Table 2.9). In winter, mature female Jonah crabs were also distributed at deeper depths (p-value = 3.98e-08) and farther from shore (p-value of 7.29e-09) compared to immature female Jonah crabs (Table 2.11; Figure 2.4). A comparison between mature and immature Jonah crab depth and distance from shore ANOVA averages in the MAB are in the appendix (Figure A2.23).

Jonah crab patterns of depth and distance from shore in GB were similar between males and females. In GB, male and female Jonah crabs had similar centroids for each season, and the average depths and distances from shore between the two groups were also similar in the ANOVAs (Tables 2.8 – 2.9; Figure 2.2C). The eCDFs and KS tests also showed no significant seasonal differences between the two sexes. Seasonal KDEs showed similar distributions of male and female Jonah crabs in the winter and fall, but female Jonah crabs were found more inshore in GB compared to male crabs found more in the southern MAB in the spring (Figures 2.6 & A2.6). In the MAB, the centroids for female Jonah crabs were farther north compared to male Jonah crabs in the spring and fall (Figure 2.2C). Mature male Jonah crabs were found at a deeper average depth (115.3 m) and a farther average distance from shore (88.3 km) compared to mature female Jonah crabs (average depth 75.3 m; average distance from shore 61.2 km; Tables 8 – 9). Immature male Jonah crabs were also found deeper than immature female Jonah crabs in the spring (Table 2.8). In the winter, female and male Jonah crabs had similar centroids of mass (Figure 2.2C). However, mature male Jonah crabs were found at significantly deeper depths than mature female Jonah crabs (Table 2.8). The only significant p-value from KS tests in the winter was between mature male and female Jonah crabs as male Jonah crabs had a deeper depth distribution compared to female crabs (p-value = 0.0015; Table 2.11; Figure 2.4). Seasonal centroids of Jonah crabs that were not split by region are in the appendix (Figures A2.7 – A2.9). Mature male and female Jonah crab depth and distance from shore averages from the best ANOVAs are also found in Figure A2.24.

2.4.3. Atlantic rock crab

The best ANOVAs for depth and distance from shore included sex, maturity, region, and season as important variables and an interaction between region and season (Tables 2.12 – 2.14). The depth ANOVA also included interactions between sex and region as well as maturity and season (Tables 2.13 & 2.15). The distance from shore ANOVA had interactions between sex and maturity as well as maturity and region (Tables 2.14 & 2.16). The residuals of the best ANOVAs as well as other ANOVAs that are less than 2 AIC units from the chosen ANOVAs are found in the appendix (Tables A2.4 – A2.5; Figures A2.10 – A2.11).

The ANOVAs indicated that for at least one season Atlantic rock crabs have different patterns by maturity and sex. In GB, the centroids for each season were very similar to one another with the winter centroid of mass slightly more south compared to the spring and fall

(Figure 2.7A). However, none of the differences were significant for depth or distance from shore (Tables 2.15 – 2.16). The ANOVA depth and distance from shore averages in GB are in the appendix (Figure A2.25). The KS tests for depth indicated seasonal differences on GB (winter and fall p-value = 1.78e-15; winter and spring p-value < 2.2e-16; Table A2.6; Figure 2.8). Overall, Atlantic rock crabs were observed slightly deeper in the winter compared to the fall and spring (Figure 2.8).

Unlike GB, the MAB showed more differences seasonally as Atlantic rock crabs in the fall were found farthest south and crabs in the spring were farthest north (Figure 2.7A). The depth ANOVA also indicated significant differences seasonally for Atlantic rock crabs in the MAB (Tables 2.15; Figures A2.26 – A2.30). Immature male and female crabs were found at deeper depths in the fall compared to the spring and winter, and mature male and female crabs were found at shallower depths in the spring compared to the winter and fall (Table 2.15). The ANOVA for distance also found significant differences across all seasons in all Atlantic rock crab groups, except for mature female crabs (Tables 2.16; Figures A2.26 – A2.30). Mature female crabs had similar distances from shore in the winter and fall, but they were closer to shore in the spring (Table 2.16). The other groups of Atlantic rock crabs were also found closest to shore in the spring, farthest from shore in the fall, and an intermediate distance in the winter (Table 2.16). The KS tests indicated seasonal differences in the distributions of Atlantic rock crab in the MAB for distance from shore (p-value < 1.78e-15) and depth (p-value < 2.2e-16; Table A2.6; Figure 2.8). Similar to the other results, Atlantic rock crabs were found farthest from shore and at their deepest depths in the fall and closest to shore and at their shallowest depths in the spring (Figure 2.8). Seasonal KDEs that do not group Atlantic rock crabs by sex and maturity can be found in the appendix (Figures A2.12 – A2.13).

Atlantic rock crabs also had seasonal differences in distance from shore and average depth by maturity. However, in GB, the seasonal centroids were similar, and differences among groups of Atlantic rock crabs for the average depths and distances from shore were relatively small (Figure 2.7B; Tables 2.15 – 2.16). The distributions of depth and distances from shore were also similar among groups, and the intensities of mature and immature crabs were similar in the KDEs in GB (Table 2.17; Figures 2.9 – 2.10 & A2.14). Atlantic rock crabs in the MAB had differences based on ontogeny with immature crabs found farther south, especially in the spring, compared to mature crabs (Figure 2.7B). This trend was further illustrated in the seasonal KDEs as immature crabs were found more in the southern MAB for all seasons compared to mature crabs that were more in the northern MAB (Figures 2.10 & A2.14). Particularly in the winter, mature male Atlantic rock crabs were found deeper (77.9 m) and farther from shore (63.7 km) compared to immature male Atlantic rock crabs (65 m average depth and 57.4 km average distance from shore; Table 2.15 – 2.16). Significant differences in the distributions of immature and mature male Atlantic rock crabs in the winter were also found in the eCDFs (p-value = 1.80e-10 for depth; p-value = 4.49e-07 for distance to shore; Table 2.18). Mature female Atlantic rock crabs in the winter had a deeper average depth (58.2 m) compared to immature females (45.3 m; Table 2.15). Mature female Atlantic rock crabs were also farther from shore compared to immature females in the winter (p-value = 0.0027; Table 2.18, Figure 2.9). The results of the depth and distance from shore ANOVAs are in Figure A2.31.

Atlantic rock crabs showed greater differences in seasonal patterns based on sex than ontogeny in the MAB. The centroids for each season were similar in GB (Figure 2.7C). Average depths and distances from shore for males and females on GB were similar (Table 2.17; Figures 2.9, 2.11 & A2.15). In the MAB, female Atlantic rock crabs were farther north, especially in the spring, compared to male Atlantic rock crabs (Figure 2.7C). Male Atlantic rock crabs had distributions farther south compared to females in the MAB (Figures 2.11 & A2.15). Female Atlantic rock crabs were also concentrated closer to shore than males for all three seasons (Figures 2.11 & A2.15). Mature male Atlantic rock crabs were about 11 – 14 km farther from shore, on average, than mature females in all seasons in the MAB (Table 2.16). Mature male Atlantic rock crabs also were significantly deeper (p-value = 0.00026 in the winter; p-value = 7.80e-05 in the fall) than mature females in the MAB (Table 2.18; Figure 2.9). Mature male Atlantic rock crabs were distributed farther from shore compared to mature females (p-value = 0.00059 in the winter; p-value = 0.00017 in the fall; Table 2.18; Figure 2.9). Similarly, immature male Atlantic rock crabs in the MAB had average depths nearly 20 m deeper than immature females (Table 2.15). Seasonal centroids that do not have the regions separated are in the appendix (Figures A2.7 – A2.9). A comparison of male and female depth and distance from shore averages from the best ANOVAs in the MAB are in Figure A2.32.

2.5. Discussion

Jonah and Atlantic rock crabs both showed evidence of seasonal movement patterns in which their average location or depth changed for at least one season and region. Generally, Jonah crabs were found in deeper water and more offshore in the winter compared to the other two seasons. Atlantic rock crabs typically were in deeper water and farther from shore in the fall and closer to shore and shallower water in the spring. However, the results for both species do not appear to show coordinated, large-scale movements seasonally that would be considered seasonal migrations. One possibility is the two species are only making small-scale seasonal movements or participating in partial migrations where only a portion of the population migrates. Another possibility is that behavioral differences affect the catchability of crabs by maturity and sex, which may cause catch ratios to change seasonally. It is also possible that both species are participating in ontogenetic migrations where different life stages or sexes move to different habitats seasonally as both species have different seasonal patterns when grouped by sex and maturity. For Jonah crabs, it appears that mature female crabs move inshore in the spring, and mature male crabs follow the inshore movement in the fall. Atlantic rock crabs follow similar seasonal patterns, but female and male crabs tend to have different averages and distributions in depth and distance from shore, except in the spring. Overall, maturity-specific seasonal patterns were more apparent for Jonah crabs, and sex-specific patterns were more evident for Atlantic rock crabs. In both species, male crabs were deeper and farther from shore compared to female crabs, and mature crabs were deeper and farther from shore, on average, compared to immature crabs. Unlike the MAB, Jonah and Atlantic rock crabs on GB also appeared to have similar seasonal patterns.

2.5.1. Jonah crab

Jonah crabs are likely not performing large-scale migrations seasonally, but instead are likely conducting small-scale, seasonal migrations in which a portion of the stock is migrating farther offshore and to deeper water in the winter then migrating to shallower water and closer to shore in the spring and fall. Previous studies have reported that Jonah crabs are most abundant inshore in the summer and early fall seasons, and they have also concluded that seasonal migration is likely occurring (Krouse, 1980; Leland, 2002; Ordzie & Satchwill, 1983). Several studies using commercial lobster traps found an increase in CPUE of Jonah crabs in the summer and fall closer to shore in Rhode Island and Maine (Krouse, 1980; Leland, 2002; Ordzie & Satchwill, 1983). Haefner (1977) using trawl surveys in June, October, and March – April also found that Jonah crabs in the MAB were closer to shore in the fall compared to the other seasons.

However, my results indicated that some Jonah crab groups such as females were generally closest to shore in the spring in the MAB (Table 2.9). These conflicting results could be due to differences in the regions sampled and gear selectivity among studies. Haefner (1977) collected data in Norfolk Canyon and the adjacent continental shelf up to the mouth of the Chesapeake Bay, and my study area encompasses areas farther north up to GB and only offshore areas. Many of the other studies also used passive gear such as lobster traps, which would likely have a lower catchability of smaller crabs, in a smaller study area mostly focused on inshore areas with shorter time series (Krouse, 1980; Leland, 2002; Ordzie & Satchwill, 1983). My study on the other hand focused on a wider and only offshore area of the distribution range for Jonah crabs and also spanned a longer time period. Inconsistencies between studies could also be due to regional differences as Haefner (1977) found Jonah crabs to be the most abundant in 61 – 160 m in the New York Bight and depths greater than 160 m in the Chesapeake Bight in the fall. My results partly agree with a tagging study for Jonah crabs in the Gulf of Maine, GB, and the northern MAB that did not find evidence of the entire population participating in seasonal migrations as the majority of crabs did not travel more than 5 km (ASMFC, 2021; Perry et al., 2019). However, if partial migration is occurring, in which only a portion of the Jonah crab population migrates, or if migratory behavior varies regionally within the MAB, additional tagging studies would be needed to understand these behaviors.

Movement could differ between the sexes because females have been caught more frequently in warmer and shallower waters compared to male Jonah crabs (Ordzie & Satchwill, 1983). I also found that female Jonah crabs were typically closer to shore and in shallower depths compared to males, especially in the spring (Tables 2.8 – 2.9; Figures 2.4). However, mature male and female Jonah crabs had similar depth and distance from shore averages and distributions in the fall (Table 2.8 – 2.9 & 11; Figure 2.4). Mature male and female Jonah crabs also had similar average distance to shore in the winter, which could be when they spawn (Table 2.9). Overall, male Jonah crabs also had a higher catch in the winter compared to female Jonah crabs, and the sex ratio was closer to being equal in the fall (Table 2.2). Other studies that reported the sex ratio of Jonah crabs found that males were more frequent in most seasons, especially in spring (Haefner, 1977) and fall (Ordzie & Satchwill, 1983). However, comparisons are difficult due to studies using different gear and study areas.

Immature Jonah crabs also were more south, closer to shore, and in shallower depths in the study area compared to mature crabs, especially in the MAB (Tables 2.8 – 2.9; Figures 2.2B & 2.5). These differences could be due to an ontogenetic migration where Jonah crabs move to different habitats as they mature. One study that categorized male and female Jonah crabs by size in June found that crabs less than 40 mm CW were found generally shallower at depths approximately 75 – 400 m, and crabs 41 – 80 mm CW were found deeper in depths greater than 150 m (Haefner, 1977). However, the largest size category of Jonah crabs of about 81 – 110 mm CW had a wider depth range of 40 – 400 m (Haefner, 1977). Another study conducted by Haefner (1977) in October found that Jonah crabs less than 40 mm CW and greater than 40 mm CW had overlapping depth distributions, but larger crabs were typically found at deeper depths.

2.5.2. Atlantic rock crab

While my results do not indicate that Atlantic rock crabs are participating in large-scale seasonal migrations, a portion of mature crabs may be participating in seasonal movements where they move more inshore in the spring and offshore in the fall. Atlantic rock crabs were previously described as spending warmer months in deep water and then migrating in the late fall to shallower waters in the MAB (Rebach, 1985), which is slightly different from my results. My results indicated that Atlantic rock crabs in the MAB were closest to shore and at their shallowest depths in the spring and were offshore and at their deepest average depths in the fall (Tables 2.15 – 2.16 & A2.6; Figure 2.8). However, Atlantic rock crabs on GB had similar average depths and distances from shore seasonally, which was different than the MAB (Tables 2.15 – 2.16 & A2.6; Figure 2.8).

Similar to Jonah crabs, several studies have suggested that Atlantic rock crabs have seasonal movement or catchability differences that are sex specific. In the Chesapeake Bay, male Atlantic rock crabs regularly caught by blue crab dredges were found to migrate into the Chesapeake Bay in the late fall and left in May (Haefner & van Engel, 1975). This seasonal pattern was similar to my results in the MAB as mature male Atlantic rock crabs had the closest distance to shore in the early spring and were closer to shore in the winter survey compared to the fall survey (Table 2.16). For Atlantic rock crabs, males represented the majority of landings, especially in the winter through spring (Haefner, 1976; Shotton, 1973). Krouse (1980) found that the sex ratio of Atlantic rock crabs was more equal in the fall, which is similar to my results (Table 2.4).

I also found seasonal differences in location by maturity with immature Atlantic rock crabs in the MAB farther south in the study area than mature Atlantic rock crabs in all seasons (Figures 2.7B & 2.10). However, no other studies have reported on potential movements by maturity for Atlantic rock crab.

2.5.3. Comparison of Jonah and Atlantic rock crabs

Jonah and Atlantic rock crabs are often grouped together in studies because they look similar, especially at smaller sizes, and are both distributed along the western north Atlantic coast. However, I found that Jonah and Atlantic rock crabs respond differently to seasonal changes in the MAB. Jonah crabs were found distributed farthest from shore with deep depths in the winter and closest to shore and in their shallowest depths in the fall and spring (Tables 2.8 – 2.9). In contrast, Atlantic rock crabs were found closest to shore and at their shallowest depths in the spring and farthest from shore and deep depths in the fall (Tables 2.15 – 2.16). However, these seasonal patterns were not regionally consistent as both Jonah and Atlantic rock crabs did not follow the same seasonal patterns in GB. Jonah crabs also had more apparent differences in seasonal patterns when grouped by maturity, and Atlantic rock crabs had more apparent seasonal differences when grouped by sex. However, mature males for both species were observed at deeper depths and farther from shore compared to immature and female crabs.

The inconsistencies between the two regions and seasonal patterns indicate that these crabs are more likely changing their behaviors throughout the year or only a portion of the population for both species are migrating seasonally. For example, mature male Jonah crabs were found at their deepest average depth in the spring at 128.4 m, even though it is not significantly different from their average depth in the winter, and mature female Jonah crabs were the closest to the shore and at their shallowest depths in the spring (Tables 2.8 – 2.9). If there is a portion migrating each year, Atlantic rock crabs might move longer distances compared to Jonah crabs. One laboratory study found that Atlantic rock crabs were at least five times more active than Jonah crabs and therefore, might be able to move greater distances (Jeffries, 1966). I found that at least in the spring, both Jonah and Atlantic rock crabs prefer intermediate temperatures, which might mean that crabs will adjust their location in order to remain in preferred temperatures (Chapter 1). Seasonal temperature changes may provide a cue for Atlantic rock crabs to stay in their preferred temperature range (Rebach, 1987).

2.5.4. Behaviors of Jonah and Atlantic rock crabs

Several studies have proposed that Jonah crabs may migrate inshore in the spring and fall months and move offshore in the winter months (Krouse, 1980; Leland, 2002; Stehlik et al., 1991). Similarly, it has also been suggested that Atlantic rock crabs migrate to deeper waters for the warmer months and move inshore in the late fall (Rebach, 1985). These general seasonal trends for both Jonah and Atlantic rock crabs were found in my results, but they were not consistent. However, there are no direct observations (e.g., tagging) of individuals migrating seasonally for either Jonah or Atlantic rock crabs.

I was not able to track individual crabs, and, therefore, this study does not prove that Jonah and Atlantic rock crabs are migrating. The seasonal differences found in this study could be an indication of seasonal behavioral differences that influence the catchability of Jonah and Atlantic rock crabs. For example, berried females might be less likely to be caught or to enter a trap, which would cause catch to be skewed toward males (Krouse, 1980; Ordzie & Satchwill, 1983). The catch ratio for both Jonah and Atlantic rock crabs found approximately twice as many males caught in the winter compared to females where the other two months were closer to a 1:1 catch ratio (Table 2.2 & 2.4). For Atlantic rock crabs, a decline in the catch for females compared to males in the winter could be due to females preparing to lay eggs during this period and reducing their activity and feeding (Krouse, 1980). Female Atlantic rock crabs might also be burying themselves more during this period as one study that used dredge and trawl surveys speculated that trawls were unable to catch buried crabs well (Stehlik et al., 1991). Female Jonah crabs might also exhibit this behavior. After both species are finished molting and mating, they also might increase their activity. For example, Krouse (1980) hypothesized that male Atlantic rock crabs were more active in the winter and spring after molting and increasing their feeding. It is also possible that changes in catch ratios and seasonal shifts are influenced by crabs moving outside of the study area, especially since my data only included offshore waters. Figure 2.6 shows that female Jonah crabs in the spring have a high intensity along the study area boundary closest to shore in GB, which means female Jonah crabs could be moving outside of the study area closer to shore significantly more than the other two seasons, similar to the seasonal pattern found for mature female Jonah crabs in the MAB (Table 2.9; Figure 2.6). This pattern of female crabs possibly moving outside of the study area is also apparent for Atlantic rock crabs. Female Atlantic rock crab intensities for all three seasons, especially in the winter and spring, were highest along the boundary closest to shore of my study area, which means it is likely that there are some crabs that are moving farther inshore during these times (Figure 2.11). This pattern is also apparent for males, which means they are also possibly moving more seasonally then determined by my results (Figure 2.11).

Tagging studies have found that these crabs move over time, even if those movements are relatively small (Ordzie & Satchwill, 1983; Perry et al., 2019). One tagging study in Rhode Island Sound found that Jonah crabs moved a mean distance of 5.5 km from where they were released and from where they were recaptured after forty days (Ordzie & Satchwill, 1983). Jonah crabs that were tagged and recaptured over eighty days later had a mean distance they traveled of 13.9 km (Ordzie & Satchwill, 1983). Another study that tagged 32,000 Jonah crabs in the Gulf of Maine, GB, and the northern MAB found that over 96% of recaptured individuals moved less than 35 km (Perry et al., 2019). Perry et al. (2019) might indicate that Jonah crabs do not move far distances, but six of the Jonah crabs traveled more than 100 km (ASMFC, 2021). Some of these Jonah crabs were also found to travel between GB and the northern MAB, which indicates that there might be some connectivity of Jonah crab populations between regions (Perry et al.

2019). When grouped by sex, males travelled a distance from 0 to 417 km, and females only traveled 0 to 18 km, but female sample sizes were much lower than males (44 to 695; Perry et al., 2019). Jonah crabs tagged offshore moved the most, especially on GB and in southern New England, and males in these areas moved to shallower depths in the summer and deeper depths in the fall (Perry et al., 2019). This result differs from my results as mature male crabs in the fall were significantly shallower compared to the spring in GB, and mature male Jonah crabs were also shallower in the fall in the MAB but not significantly (Table 2.8). However, more information could be gained from tagging studies with an increase in the number of females recaptured and finding a method to tag and recapture more crabs less than 80 mm CW (Perry et al., 2019).

2.5.5. Regional differences

I analyzed the observations for the GB and MAB regions separately. Regions were separated due to their different characteristics and physical features that could influence the overall seasonal results. GB is about 62 miles offshore and has an area of approximately 30,000 km^2 (Townsend et al., 2006; Wallace et al., 2018). The MAB on the other hand is 850 km long and approximately 110,000 km^2 (Lentz, 2008; Wallace et al., 2018). Therefore, GB is a farther distance offshore but still has shallow average depths around 20 – 100 m, and the MAB is a larger area that generally progressively gets deeper the farther from shore (Wallace et al., 2018). For example, centroids in the appendix that did not analyze the regions separately found greater seasonal movements and some of the centroids were even outside of the study area due to the shape of the Atlantic coast (Figures A2.7 – A2.9). The best ANOVAs for both species also included region effects (Tables 2.5 & 2.12). Jonah and Atlantic rock crabs may have different seasonal distributions by region. In my results, both Jonah and Atlantic rock crabs showed fewer seasonal differences in GB compared to the MAB.

2.5.6. Catchability differences

Inferred movement can be confounded if the catchability of crabs differs among the seasons or if selectivity was different for the two trawls used in this study. The NEFSC winter trawl survey had substantially higher catches of Atlantic rock crabs and Jonah crabs compared to the NEFSC spring and fall trawl surveys. However, the NEFSC winter bottom trawl surveys were conducted using a modified trawl that was different than the NEFSC spring and fall bottom trawl surveys due to the main objective of the winter survey to catch flatfish (Stauffer, 2004). Another potential cause of a difference in catchability not accounted for in the data is that two different vessels were used to conduct the NEFSC bottom trawls during 1992 – 2007. While the R/V *Albatross IV* and the R/V *Delaware II* used the same trawl and protocols, a comparison study between the two vessels found that the R/V *Delaware II* had a higher mean catch per tow for both Jonah and Atlantic rock crabs compared to R/V *Albatross IV* (Byrne & Fogarty, 1985). These catchability differences could have influenced the catch ratios and the number of Jonah and Atlantic rock crabs caught in each season and year.

Similarly, previous studies of Jonah and Atlantic rock crabs were conducted using a range of gears that may have different selectivity and catchabilities. For example, studies used a mixture of Jonah crab traps (Truesdale, 2018), lobster traps (Krouse, 1980; Ordzie & Satchwill, 1983), trawl surveys (Haefner, 1977; Shotton, 1973), and dredge surveys (Haefner & van Engel, 1975; Rebach, 1985). The majority of studies also did not overlap completely with my study area.

Other studies have found that male Jonah crabs were more prevalent in catches in June and July, while female Jonah crabs were more abundant in catches from August to October (Haefner, 1977; Krouse, 1980; Truesdale, 2018). However, Krouse (1980) found more male than female Jonah crabs through early fall in Maine. The timing of data collection for my study did not overlap with the majority of these other studies, but I found that the catch ratio between males and females was approximately 1:1 with slightly more females caught during September – November (Table 2.2). For the winter and spring, more male Jonah crabs were observed with the sex ratio of the catch being 2.24:1 males to females in the winter and 1.59:1 in the spring (Table 2.2). Haefner (1977) also found more male Jonah crabs in the spring with catch sex ratios of 2.9:1 in March and 1.9:1 in April. In Rhode Island, Ordzie & Satchwill (1983) found that males not only were more frequently caught in the spring and summer with a catch ratio of 1.6:1 but were also more often caught in the fall with a catch ratio of 2.8:1, which is different from my 1:1 catch ratio in the fall (Table 2.2). Ordzie & Satchwill (1983) observed that male Jonah crabs were also more inshore during the fall and more females were caught inshore during the spring and summer, which are similar to my results (Tables 2.8 – 2.9). However, it is important to note that differences in the sex ratios of catch could be caused by differences in gear and fishing location, which means direct comparisons are not entirely possible.

For Atlantic rock crabs, males were about twice as abundant as females in the winter possibly due to females molting or burying themselves more than males (Table 2.4). Shotton (1973) found a ratio of about 6:1 more male Atlantic rock crab caught in trawl surveys conducted from February – April in coastal Virginia. However, Shotton (1973) observed that the trawl samples might be biased towards males due to them being larger than female Atlantic rock crabs. Haefner (1976) also found that males were the most abundant in the majority of trawls in the

MAB conducted in June, October, and April. Krouse (1980) on the other hand found that the catches in lobster traps of males and females were nearly equal in the fall in Maine, which is also similar to my catch ratios (Table 2.4). It is important to note that changes in catch ratios could be due to Atlantic rock crabs moving outside the study area or avoiding the traps and trawls. Changes in catchability of Atlantic rock crabs with the highest CPUE in the winter and spring in the MAB with a mixture of passive gear such as traps and active gear such as trawls could suggest seasonal changes in catchability or movements, but it does not prove season migration for the entire population (Ordzie & Satchwill, 1983; Shotton, 1973).

2.5.7. Conclusion

My study demonstrated that Jonah and Atlantic rock crabs have seasonal differences in average depth occupied and distance from shore, particularly in the MAB. However, these patterns were not consistent and were often different based on ontogeny and sex. Therefore, whether these two species undergo seasonal migrations is unclear. My study also did not test causes of potential movement. A portion of Jonah crabs may perform small migrations to deeper waters and farther from shore in the winter months and closer to shore and shallower depths in the fall months, but my results do not fully support that the entire population is moving. Similarly, a portion of Atlantic rock crabs may migrate to deeper water and farther from shore in the fall and shallower depths and closer to shore in the spring in the MAB.

While the Jonah crab fishery was not established until the 1990s, they have increasingly become more popular and commercially important. Atlantic rock crabs have also supported a small fishery in the past and are likely to increase in popularity as other commercially important crustaceans experience declines or move poleward. However, the limited knowledge of Jonah and Atlantic rock crabs presents challenges for management when it comes to understanding how these species will respond to different environmental and anthropogenic stressors. Understanding the migration patterns and seasonal dynamics of Jonah and Atlantic rock crabs is just one step in establishing a sustainable and resilient fishery for Jonah and Atlantic rock crab populations and distributions (ASMFC, 2015).

2.6. Tables

Table 2.1: Jonah crab sample sizes grouped by sex, maturity, and total numbers caught in the Northeast Fishery Science Center winter, spring, and fall trawl surveys in the Mid-Atlantic Bight and Georges Bank during 1992 – 2007.

Season	Male	Female	Mature	Immature	Total
Winter	1,142	511	1,328	332	1,660
Spring	113	71	81	107	188
Fall	236	238	212	265	477

Table 2.2: Ratios of males to females and mature to immature Jonah crabs caught in the Northeast Fishery Science Center bottom trawl surveys in winter, spring, and fall during 1992 – 2007 in the Mid-Atlantic Bight and Georges Bank.

Season	Male:Female	Mature:Immature
Winter	2.24:1	4:1
Spring	1.59:1	1:1.32
Fall	1:1.01	1:1.27

Table 2.3: Atlantic rock crab sample sizes grouped by sex, maturity, and total numbers caught in the Northeast Fishery Science Center for winter, spring, and fall trawl surveys in the Mid-Atlantic Bight and Georges Bank during 1992 – 2007.

Season	Male	Female	Mature	Immature	Total
Winter	906	447	666	727	1,393
Spring	264	223	132	358	490
Fall	401	363	190	596	786

Table 2.4: Ratios of males to females and mature to immature Atlantic rock crabs caught in the Northeast Fishery Science Center bottom trawl surveys in winter, spring, and fall during 1992 – 2007 in the Mid-Atlantic Bight and Georges Bank.

Season	Male:Female	Mature:Immature
Winter	2.02:1	1:1.09
Spring	1.18:1	1:2.72
Fall	1.10:1	1:3.13

Table 2.5: Variables included in the best Jonah crab ANOVA models for the dependent variables depth (m) and distance to shore (dist) (km). Jonah crabs were grouped by sex, maturity, season, and region. The best models were determined using the corrected Akaike's Information Criterion (AICc). The table also includes the degrees of freedom (df) and log likelihood (LL).

Model	df	LL	AICc
depth = sex + maturity + region + season + (sex×region) + (season×sex) + (maturity×region) + (maturity×season) + (region×season) + (maturity×region×season)	17	-13218.66	26471.6
dist = sex + maturity + region + season + (sex×maturity) + (sex×season) + (maturity×season) + (region×season) +(sex×maturity×season)	16	-11893.2	23818.6

Table 2.6: Parameter estimates, standard errors (SE), t-values, and p-values for the best Jonah crab ANOVA for depth (m).

Group	Estimate	SE	t-value	p-value
(Intercept)	115.78	10.51	11.017	< 2e-16
Spring	100.20	20.33	4.93	8.86e-07
Winter	4.029	12.02	0.34	0.74
Female	-10.74	9.29	-1.16	0.25
Immature	0.21	11.22	0.018	0.99
Mid-Atlantic Bight	-0.51	12.47	-0.041	0.97
Female: Mid-Atlantic Bight	-14.11	9.52	-1.48	0.14
Spring: Female	-28.30	14.50	-1.95	0.051
Winter: Female	8.91	8.95	1.00	0.32
Immature: Mid-Atlantic Bight	-19.35	14.41	-1.34	0.18
Spring: Immature	-125.22	25.05	-5.00	6.18e-07
Winter: Immature	-1.12	18.97	-0.059	0.95
Spring: Mid-Atlantic Bight	-87.059	21.27	-4.093	4.41e-05
Winter: Mid-Atlantic Bight	2.25	12.98	0.17	0.86
Spring: Immature: Mid-Atlantic Bight	134.05	28.70	4.67	3.19e-06
Winter: Immature: Mid-Atlantic Bight	6.75	21.40	0.32	0.75

Table 2.7: Parameter estimates, standard errors (SE), t-values, and p-values for the best Jonah crab ANOVA distance from shore (km).

Group	Estimate	SE	t-value	p-value
(Intercept)	182.35	5.99	30.44	< 2e-16
Spring	25.34	11.03	2.30	0.022
Winter	11.93	7.03	1.70	0.090
Female	15.52	6.44	2.41	0.016
Immature	4.84	6.31	0.77	0.44
Mid-Atlantic Bight	-108.46	3.91	-27.71	< 2e-16
Female: Immature	-17.05	8.45	-2.017	0.044
Spring: Female	-42.56	11.55	-3.69	0.00023
Winter: Female	-10.95	6.89	-1.59	0.11
Spring: Immature	-26.083	10.83	-2.41	0.016
Winter: Immature	-16.55	6.98	-2.37	0.018
Spring: Mid-Atlantic Bight	-10.96	8.046	-1.36	0.17
Winter: Mid-Atlantic Bight	12.55	5.37	2.34	0.019
Spring: Female: Immature	47.36	16.27	2.91	0.0036
Winter: Female: Immature	-0.42	10.32	-0.040	0.97

Table 2.8: Mean depth estimates from the best ANOVA model by group for Jonah crab. Each group is characterized by season, sex, maturity, and region. The standard error (SE), lower 95% confidence interval (Lower CI), and upper 95% confidence interval (Upper CI) are also included for each estimate. The two regions are Georges Bank (GB) and the Mid-Atlantic Bight (MAB).

Region	Season	Maturity	Sex	Depth (m)	SE	Lower CI	Upper CI
GB	Winter	Mature	Female	118	8.74	100.8	135.1
GB	Winter	Mature	Male	119.8	8.13	103.9	135.8
GB	Winter	Immature	Female	117.1	15.52	86.6	147.5
GB	Winter	Immature	Male	118.9	13.94	91.6	146.2
GB	Spring	Mature	Female	176.9	16.43	144.7	209.2
GB	Spring	Mature	Male	216	18.57	179.6	252.4
GB	Spring	Immature	Female	51.9	18.93	14.8	89.1
GB	Spring	Immature	Male	91	14.68	62.2	119.8
GB	Fall	Mature	Female	105	8.18	89	121.1
GB	Fall	Mature	Male	115.8	10.51	95.2	136.4
GB	Fall	Immature	Female	105.2	9.24	87.1	123.4
GB	Fall	Immature	Male	116	8.09	100.1	131.9
MAB	Winter	Mature	Female	105.6	3.5	98.7	112.5
MAB	Winter	Mature	Male	121.5	2.48	116.7	126.4
MAB	Winter	Immature	Female	92.1	5.28	81.7	102.4
MAB	Winter	Immature	Male	108	4.4	99.4	116.7
MAB	Spring	Mature	Female	75.3	11.01	53.7	96.9
MAB	Spring	Mature	Male	128.4	12.18	104.5	152.3
MAB	Spring	Immature	Female	65	12.76	39.9	90
MAB	Spring	Immature	Male	118.1	8.87	100.7	135.5
MAB	Fall	Mature	Female	90.4	7.18	76.3	104.5
MAB	Fall	Mature	Male	115.3	8.96	97.7	132.8
MAB	Fall	Immature	Female	71.3	8.38	54.9	87.7
MAB	Fall	Immature	Male	96.1	6.33	83.7	108.5

Table 2.9: Mean distance from shore estimates from the best ANOVA model by group for Jonah crab. Each group is characterized by their season, sex, maturity, and region. The standard error (SE), lower 95% confidence interval (Lower CI), and upper 95% confidence interval (Upper CI) are also included for each estimate. The two regions are Georges Bank (GB) and the Mid-Atlantic Bight (MAB).

Region	Season	Maturity	Sex	Distance (km)	SE	Lower CI	Upper CI
GB	Winter	Mature	Female	198.8	3.81	191.4	206.3
GB	Winter	Mature	Male	194.3	3.68	187.1	201.5
GB	Winter	Immature	Female	169.7	5.76	158.4	181
GB	Winter	Immature	Male	182.6	4.27	174.2	190.9
GB	Spring	Mature	Female	180.6	7.7	165.5	195.7
GB	Spring	Mature	Male	207.7	9.26	189.5	225.8
GB	Spring	Immature	Female	189.7	10.59	169	210.5
GB	Spring	Immature	Male	186.4	6.9	172.9	200
GB	Fall	Mature	Female	197.9	4.03	190	205.8
GB	Fall	Mature	Male	182.3	5.99	170.6	194.1
GB	Fall	Immature	Female	185.7	4.96	175.9	195.4
GB	Fall	Immature	Male	187.2	4.01	179.3	195.1
MAB	Winter	Mature	Female	102.9	2.05	98.9	107
MAB	Winter	Mature	Male	98.4	1.42	95.6	101.1
MAB	Winter	Immature	Female	73.8	4.7	64.5	83
MAB	Winter	Immature	Male	86.7	2.67	81.4	91.9
MAB	Spring	Mature	Female	61.2	6.33	48.8	73.7
MAB	Spring	Mature	Male	88.3	7.66	73.3	103.3
MAB	Spring	Immature	Female	70.3	8.98	52.7	87.9
MAB	Spring	Immature	Male	67	4.98	57.3	76.8
MAB	Fall	Mature	Female	89.4	3.8	82	96.9
MAB	Fall	Mature	Male	73.9	5.67	62.8	85
MAB	Fall	Immature	Female	77.2	4.85	67.7	86.7
MAB	Fall	Immature	Male	78.7	3.43	72	85.5

Table 2.10: P-values for Kolmogorov-Smirnov tests for Jonah crab depth (m) and distance to shore (distance) (km) on Georges Bank. Comparisons are presented by maturity and sex categories. Significant differences at the 0.05 level after correcting for multiple comparisons are indicated with bold font.

Group comparison	Winter	Spring	Fall
Depths of female mature crabs vs. female immature crabs	0.68	0.042	0.1
Depths of male mature crabs vs. male immature crabs	0.95	**1.03e-05**	0.25
Depths of female immature crabs vs. male immature crabs	0.61	0.28	0.083
Depths of female mature crabs vs. male mature crabs	0.57	0.071	0.61
Distances of female mature crabs vs. female immature crabs	0.47	0.18	0.51
Distances of male mature crabs vs. male immature crabs	0.91	0.17	0.52
Distances of female immature crabs vs. male immature crabs	0.76	0.83	0.93
Distances of female mature crabs vs. male mature crabs	0.21	0.16	0.078

Table 2.11: P-values for Kolmogorov-Smirnov tests for Jonah crab depth (m) and distance to shore (distance) (km) in the Mid-Atlantic Bight. Comparisons are presented by maturity and sex categories. Significant differences at the 0.05 level after correcting for multiple comparisons are indicated with bold font.

Group comparison	Winter	Spring	Fall
Depths of female mature crabs vs. female immature crabs	**3.98e-08**	0.19	0.069
Depths of male mature crabs vs. male immature crabs	**8.72e-06**	0.029	0.33
Depths of female immature crabs vs. male immature crabs	0.086	0.76	0.48
Depths of female mature crabs vs. male mature crabs	**0.0015**	0.079	0.23
Distances of female mature crabs vs. female immature crabs	**7.29e-09**	0.89	0.054
Distances of male mature crabs vs. male immature crabs	**0.00059**	0.073	0.25
Distances of female immature crabs vs. male immature crabs	0.057	0.98	0.47
Distances of female mature crabs vs. male mature crabs	0.0084	0.018	0.57

Table 2.12: Variables included in the best Atlantic rock crab ANOVA models for the dependent variables depth (m) and distance to shore (dist) (km). Atlantic rock crabs are grouped by sex, maturity, season, and region. The best models were determined using the corrected Akaike's Information Criterion (AICc). The table also includes the degrees of freedom (df) and log likelihood (LL).

Model	df	LL	AICc
depth = sex + maturity + region + season + (sex×region) + (maturity×season) + (region×season)	12	-14581.65	29187.4
dist = sex + maturity + region + season + (sex×maturity) + (maturity×region) + (region×season)	11	-13002.84	26025.8

Table 2.13: Parameter estimates, standard errors (SE), t-values, and p-values for the best Atlantic rock crab ANOVA depth (m).

Group	Estimate	SE	t-value	p-value
(Intercept)	52.24	7.22	7.23	6.24e-13
Female	-2.026	6.42	-0.32	0.75
Immature	4.91	5.65	0.87	0.39
MAB	31.75	6.19	5.13	3.19e-07
Spring	-1.86	10.69	-0.18	0.86
Winter	32.64	14.85	2.20	0.028
Female: Mid-Atlantic Bight	-17.65	7.032	-2.51	0.012
Immature: Spring	-0.74	8.81	-0.084	0.93
Immature: Winter	-17.80	6.70	-2.66	0.0080
Mid-Atlantic Bight: Spring	-28.85	8.95	-3.22	0.0013
Mid-Atlantic Bight: Winter	-38.75	14.26	-2.72	0.0066

Table 2.14: Parameter estimates, standard errors (SE), t-values, and p-values for the best Atlantic rock crab ANOVA distance from shore (km).

Group	Estimate	SE	t-value	p-value
(Intercept)	176.86	4.59	38.50	< 2e-16
Female	-12.16	2.43	-5.0030	6.03e-07
Immature	3.86	4.97	0.78	0.44
Mid-Atlantic Bight	-105.16	4.72	-22.28	< 2e-16
Spring	-5.58	4.15	-1.34	0.18
Winter	-4.42	7.44	-0.60	0.55
Female:Immature	7.72	3.035	2.54	0.011
Immature: Mid-Atlantic Bight	-10.15	4.88	-2.081	0.038
Mid-Atlantic Bight: Spring	-23.61	4.83	-4.89	1.09e-06
Mid-Atlantic Bight: Winter	-3.61	7.69	-0.47	0.64

Table 2.15: Mean depth estimates from the best ANOVA model by group for Atlantic rock crab. Each group is characterized by season, sex, maturity, and region. The standard error (SE), lower 95% confidence interval (Lower CI), and upper 95% confidence interval (Upper CI) are also included for each estimate. The two regions are Georges Bank (GB) and the Mid-Atlantic Bight (MAB).

Region	Season	Sex	Maturity	Depth (m)	SE	Lower CI	Upper CI
GB	Winter	Female	Mature	82.9	14.2	55	110.7
GB	Winter	Female	Immature	70	13.92	42.7	97.3
GB	Winter	Male	Mature	84.9	13.54	58.3	111.4
GB	Winter	Male	Immature	72	13.25	46	98
GB	Spring	Female	Mature	48.3	9.42	29.9	66.8
GB	Spring	Female	Immature	52.5	7.45	37.9	67.1
GB	Spring	Male	Mature	50.4	9.55	31.6	69.1
GB	Spring	Male	Immature	54.5	7.36	40.1	69
GB	Fall	Female	Mature	50.2	6.24	38	62.5
GB	Fall	Female	Immature	55.1	4.85	45.6	64.6
GB	Fall	Male	Mature	52.2	7.22	38.1	66.4
GB	Fall	Male	Immature	57.1	5.2	47	67.3
MAB	Winter	Female	Mature	58.2	3.3	51.7	64.7
MAB	Winter	Female	Immature	45.3	3.14	39.2	51.5
MAB	Winter	Male	Mature	77.9	2.71	72.6	83.2
MAB	Winter	Male	Immature	65	2.73	59.6	70.3
MAB	Spring	Female	Mature	33.6	5.86	22.1	45.1
MAB	Spring	Female	Immature	37.8	4.34	29.2	46.3
MAB	Spring	Male	Mature	53.3	6.03	41.4	65.1
MAB	Spring	Male	Immature	57.4	4.08	49.4	65.4
MAB	Fall	Female	Mature	64.3	5.35	53.8	74.8
MAB	Fall	Female	Immature	69.2	3.9	61.6	76.9
MAB	Fall	Male	Mature	84	5.35	73.5	94.5
MAB	Fall	Male	Immature	88.9	3.62	81.8	96

Table 2.16: Mean distance from shore estimates from the best ANOVA model by group for Atlantic rock crab. Each group is characterized by season, sex, maturity, and region. The standard error (SE), lower 95% confidence interval (Lower CI), and upper 95% confidence interval (Upper CI) are also included for each estimate. The two regions are Georges Bank (GB) and the Mid-Atlantic Bight (MAB).

Region	Season	Sex	Maturity	Distance (km)	SE	Lower CI	Upper CI
GB	Winter	Female	Mature	160.3	8.05	144.5	176.1
GB	Winter	Female	Immature	171.9	7.31	157.5	186.2
GB	Winter	Male	Mature	172.4	8.17	156.4	188.5
GB	Winter	Male	Immature	176.3	7.23	162.1	190.5
GB	Spring	Female	Mature	159.1	5.37	148.6	169.7
GB	Spring	Female	Immature	170.7	3.79	163.3	178.1
GB	Spring	Male	Mature	171.3	5.69	160.1	182.4
GB	Spring	Male	Immature	175.1	3.74	167.8	182.5
GB	Fall	Female	Mature	164.7	4.19	156.5	172.9
GB	Fall	Female	Immature	176.3	2.38	171.6	180.9
GB	Fall	Male	Mature	176.9	4.59	167.8	185.9
GB	Fall	Male	Immature	180.7	2.38	176.1	185.4
MAB	Winter	Female	Mature	51.5	2.03	47.5	55.5
MAB	Winter	Female	Immature	52.9	1.71	49.6	56.3
MAB	Winter	Male	Mature	63.7	1.53	60.7	66.7
MAB	Winter	Male	Immature	57.4	1.42	54.6	60.2
MAB	Spring	Female	Mature	30.4	2.48	25.5	35.2
MAB	Spring	Female	Immature	31.8	2.21	27.5	36.1
MAB	Spring	Male	Mature	42.5	2.41	37.8	47.2
MAB	Spring	Male	Immature	36.2	2	32.3	40.2
MAB	Fall	Female	Mature	59.5	2.46	54.7	64.4
MAB	Fall	Female	Immature	61	2.09	56.9	65.1
MAB	Fall	Male	Mature	71.7	2.3	67.2	76.2
MAB	Fall	Male	Immature	65.4	1.86	61.8	69.1

Table 2.17: P-values for Kolmogorov-Smirnov tests for Atlantic rock crab depth (m) and distance to shore (distance) (km) in Georges Bank. Comparisons are presented by maturity and sex categories. Significant differences at the 0.05 level after correcting for multiple comparisons are indicated with bold font.

Group comparison	Winter	Spring	Fall
Depths of female mature crabs vs. female immature crabs	0.43	0.15	0.97
Depths of male mature crabs vs. male immature crabs	0.39	0.97	0.2
Depths of female immature crabs vs. male immature crabs	0.68	0.089	0.22
Depths of female mature crabs vs. male mature crabs	1	0.94	0.72
Distances of female mature crabs vs. female immature crabs	0.57	0.63	0.5
Distances of male mature crabs vs. male immature crabs	0.33	0.22	0.85
Distances of female immature crabs vs. male immature crabs	0.06	0.98	0.92
Distances of female mature crabs vs. male mature crabs	0.8	0.3	0.99

Table 2.18: P-values for Kolmogorov-Smirnov tests for Atlantic rock crab depth (m) and distance to shore (distance) (km) in the Mid-Atlantic Bight. Comparisons are presented by maturity and sex categories. Significant differences at the 0.05 level after correcting for multiple comparisons are indicated with bold font.

Group comparison	Winter	Spring	Fall
Depths of female mature crabs vs. female immature crabs	0.0049	0.61	0.013
Depths of male mature crabs vs. male immature crabs	**1.80e-10**	0.87	0.048
Depths of female immature crabs vs. male immature crabs	0.031	0.16	0.11
Depths of female mature crabs vs. male mature crabs	**0.00026**	0.24	**7.80e-05**
Distances of female mature crabs vs. female immature crabs	**0.0027**	0.19	0.17
Distances of male mature crabs vs. male immature crabs	**4.49e-07**	0.49	0.038
Distances of female immature crabs vs. male immature crabs	0.15	0.5	0.77
Distances of female mature crabs vs. male mature crabs	**0.00059**	0.34	**0.00017**

2.7. Figures

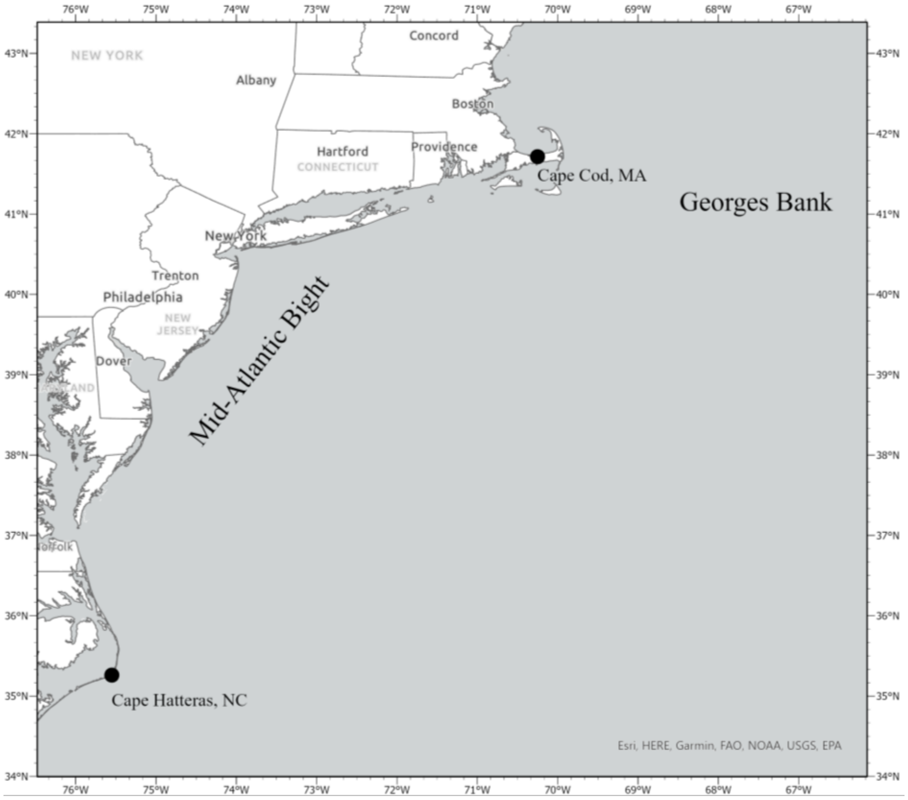

Figure 2.1. The study area includes Georges Bank and the Mid-Atlantic Bight from approximately Cape Cod, MA to Cape Hatteras, NC.

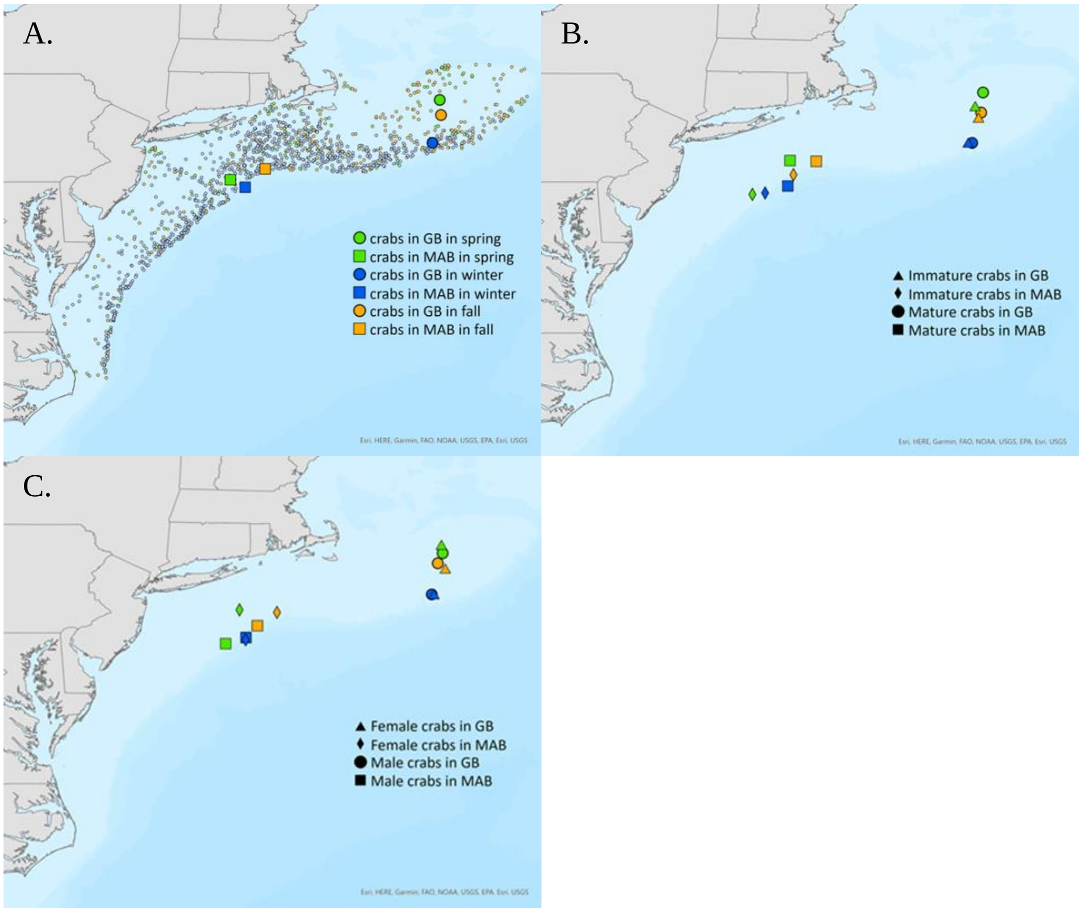

Figure 2.2: Seasonal centroids of A) Jonah crabs, B) Jonah crabs by maturity, and C) Jonah crabs by sex in winter (blue), spring (green), and fall (orange). The legends illustrate the shape that represent each centroid in the Georges Bank and Mid-Atlantic Bight.

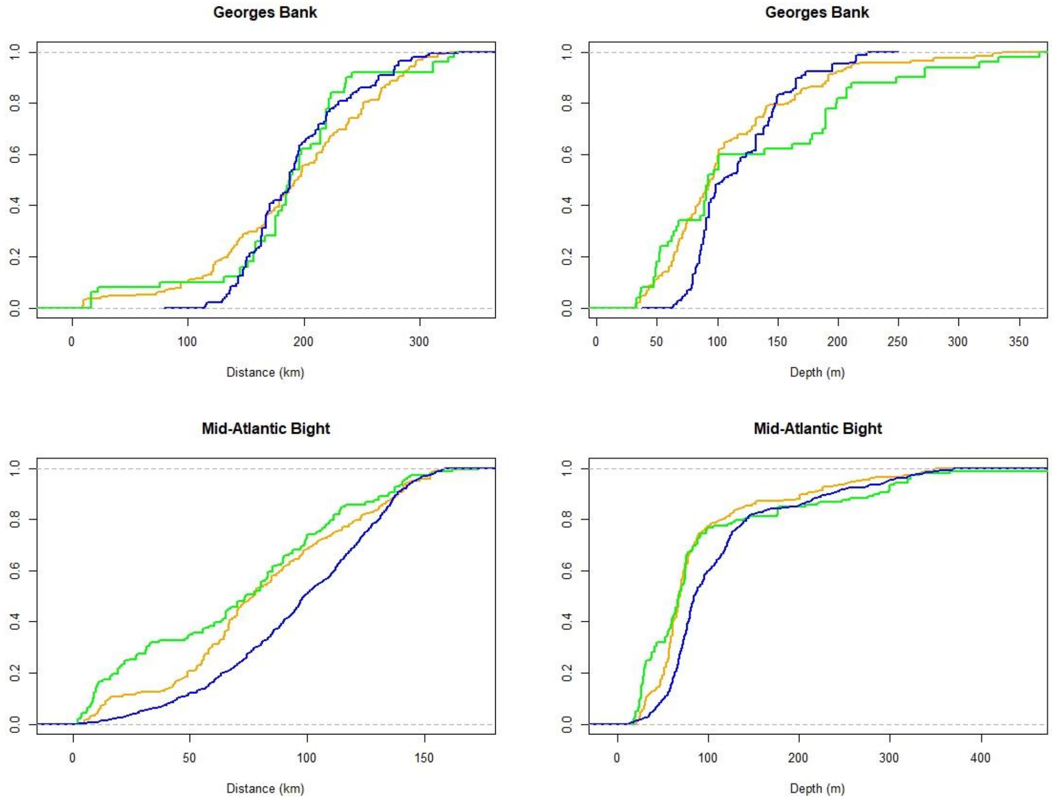

Figure 2.3: Jonah crab empirical cumulative distribution functions for distance to shore (distance) (km) and depth (m) in the winter (blue), spring (green), and fall (orange) for the Mid-Atlantic Bight and Georges Bank. The Kolmogorov-Smirnov (KS) tests for depth and distance to shore in Georges Bank and the Mid- Atlantic Bight can be found in Table A2.3.

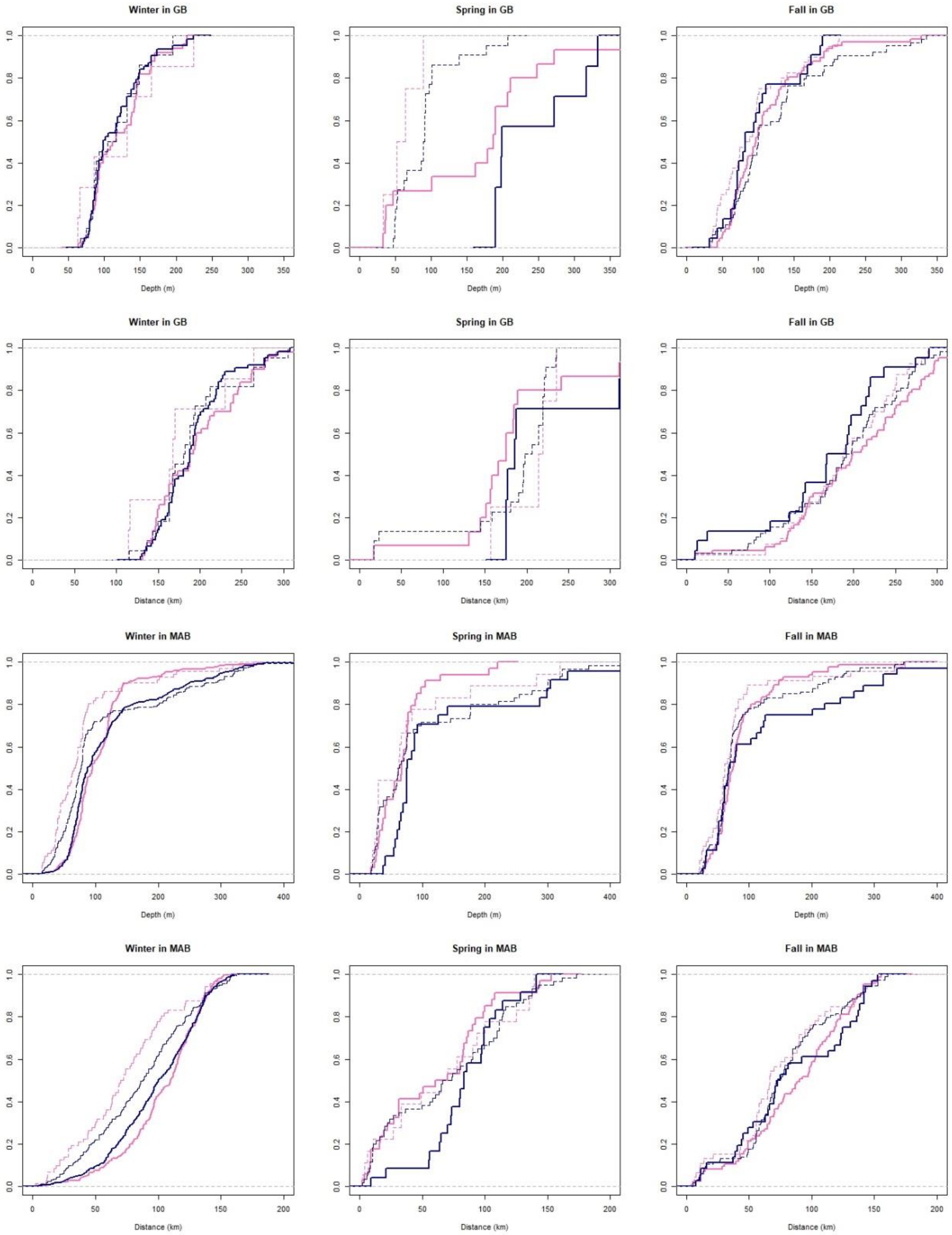

Figure 2.4: Jonah crab empirical cumulative distribution functions for depth (m) and distance to shore (distance) (km) for winter, spring, and fall. Female crabs are represented by pink, male crabs are represented by blue, mature crabs are represented by a solid line, and immature crabs are represented by a dotted line. Kolmogorov-Smirnov (KS) tests can be found in Table 2.10 for Georges Bank and Table 2.11 for the Mid-Atlantic Bight.

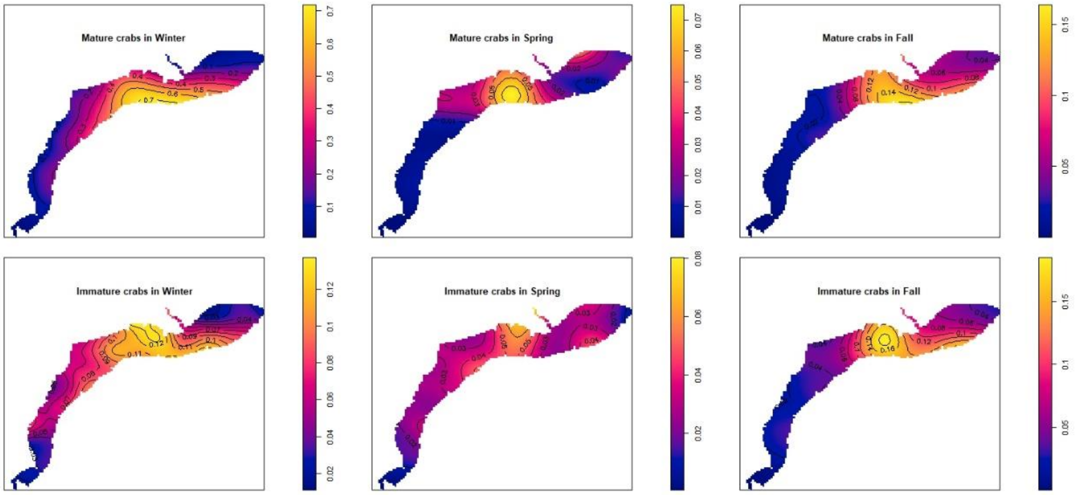

Figure 2.5: Jonah crab kernel density estimates by maturity in winter, spring, and fall with warmer colors (yellow) representing areas with high intensities of Jonah crabs and cool colors (blue) represent areas with low intensities of Jonah crabs. The scales for each season are different as seen on each scale.

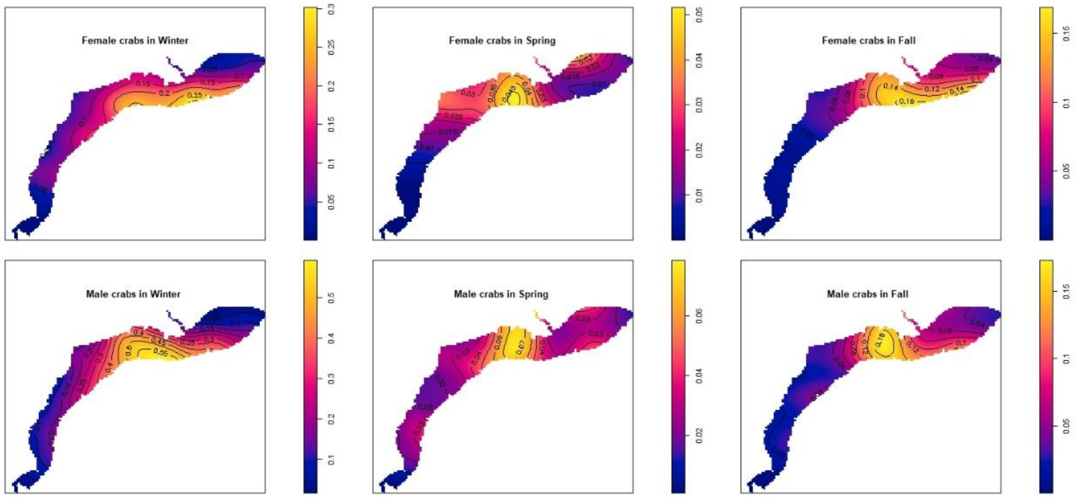

Figure 2.6: Jonah crab kernel density estimates by sex in winter, spring, and fall with warmer colors (yellow) representing areas with high intensities of Jonah crabs and cool colors (blue) represent areas with low intensities of Jonah crabs. The scales for each season are different as seen on each scale.

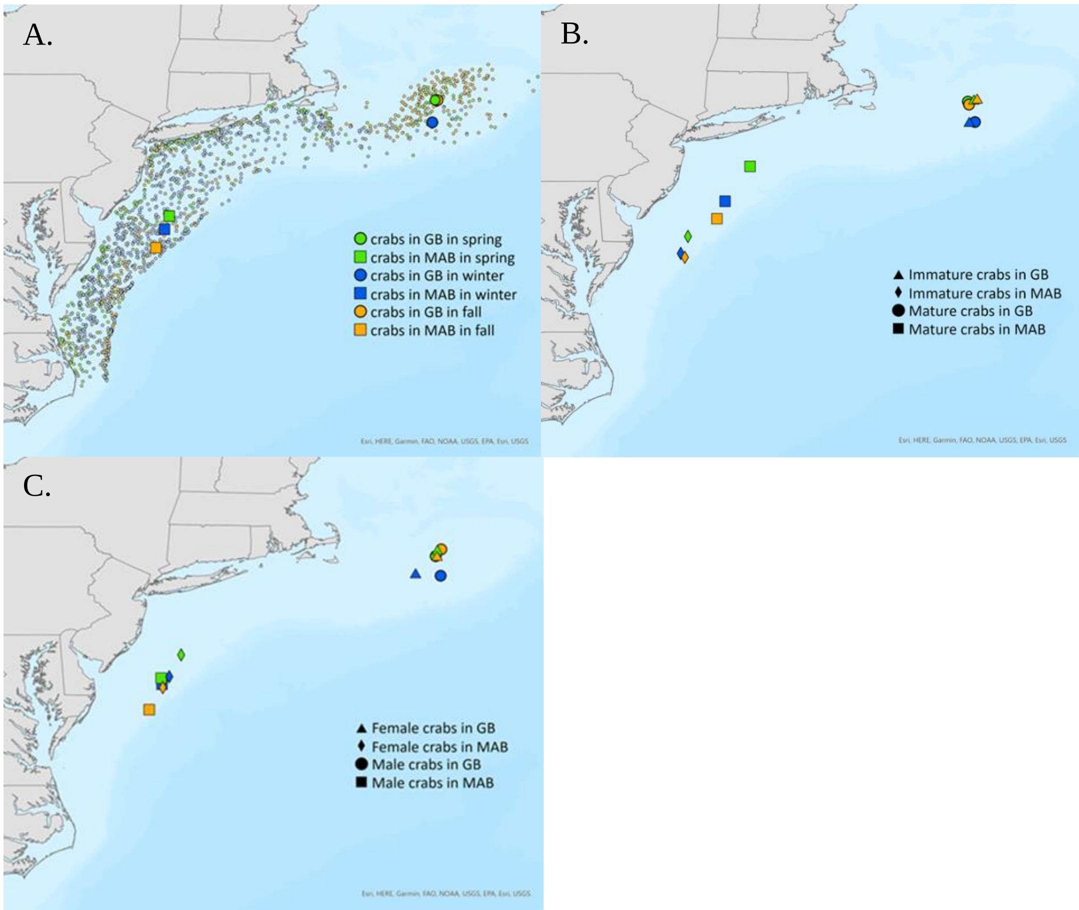

Figure 2.7: Seasonal centroids of A) Atlantic rock crabs, B) Atlantic rock crabs by maturity, and C) Atlantic rock crabs by sex in winter (blue), spring (green), and fall (orange). Centroids were calculated for the Mid-Atlantic Bight (MAB) and Georges Bank (GB).

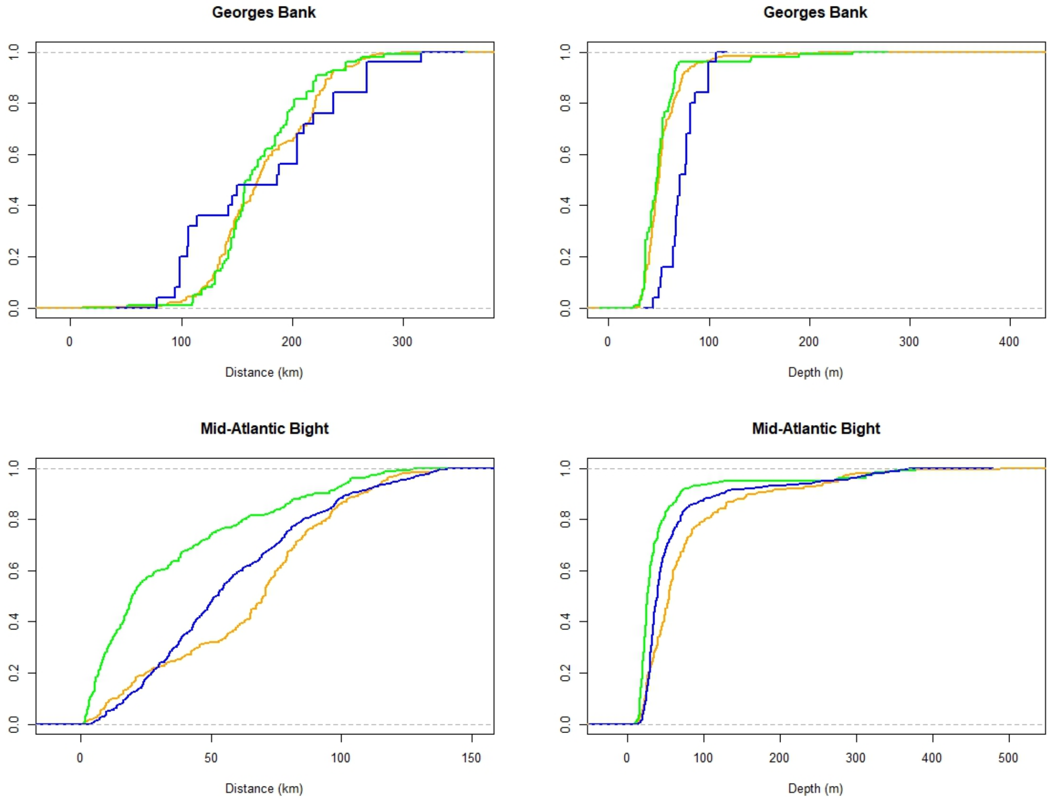

Figure 2.8: Atlantic rock crab empirical cumulative distribution functions for distance to shore (distance) (km) and depth (m) in the winter (blue), spring (green), and fall (orange) for the Mid-Atlantic Bight and Georges Bank. The Kolmogorov-Smirnov (KS) tests for depth and distance to shore in Georges Bank and the Mid- Atlantic Bight can be found in Table A2.6.

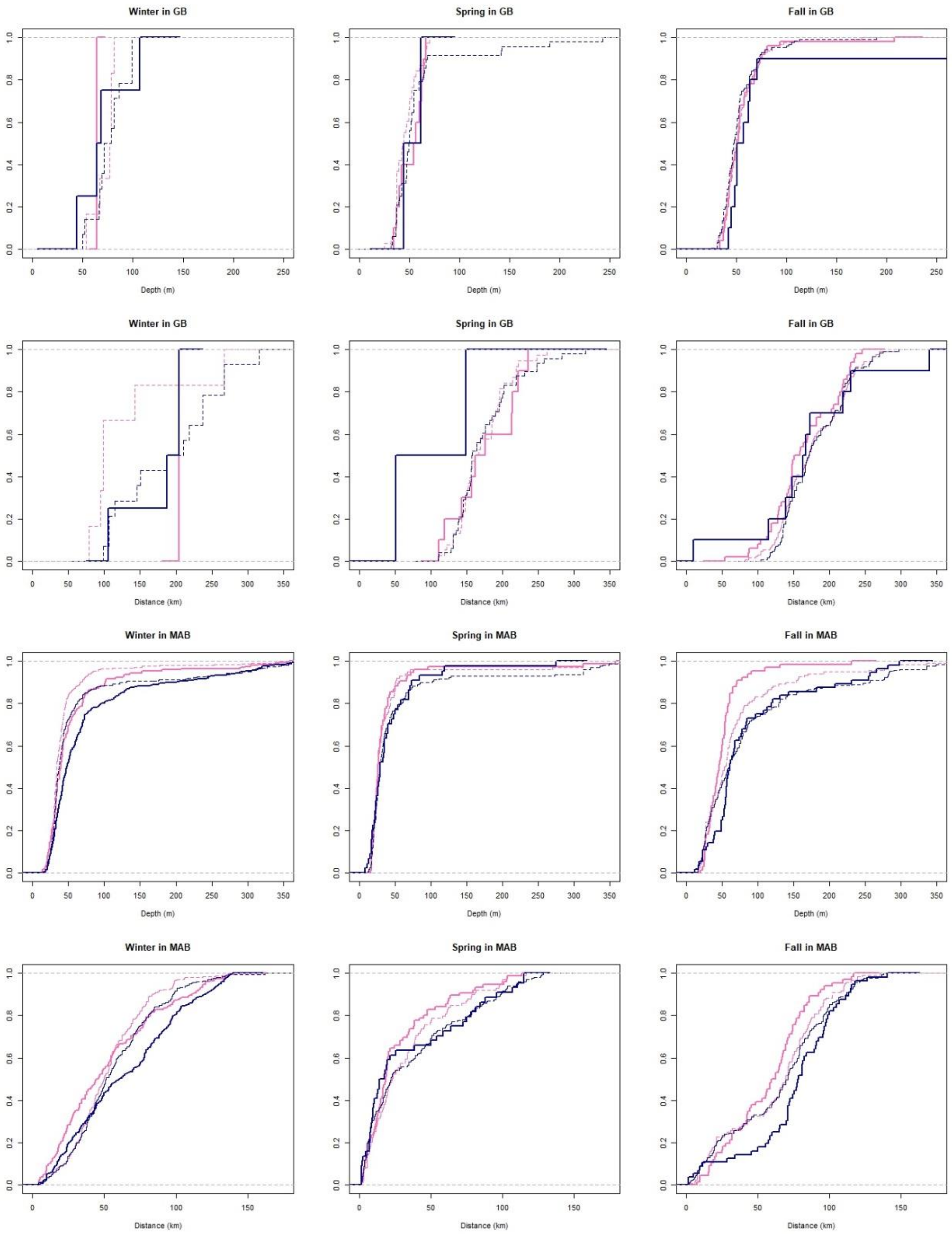

Figure 2.9: Atlantic rock crab empirical cumulative distribution functions for depth (m) and distance to shore (distance) (km) for winter, spring, and fall. Female crabs are represented by pink, male crabs are represented by blue, mature crabs are represented by a solid line, and immature crabs are represented by a dotted line. Kolmogorov-Smirnov (KS) tests can be found in Table 2.17 for Georges Bank and Table 2.18 for the Mid-Atlantic Bight.

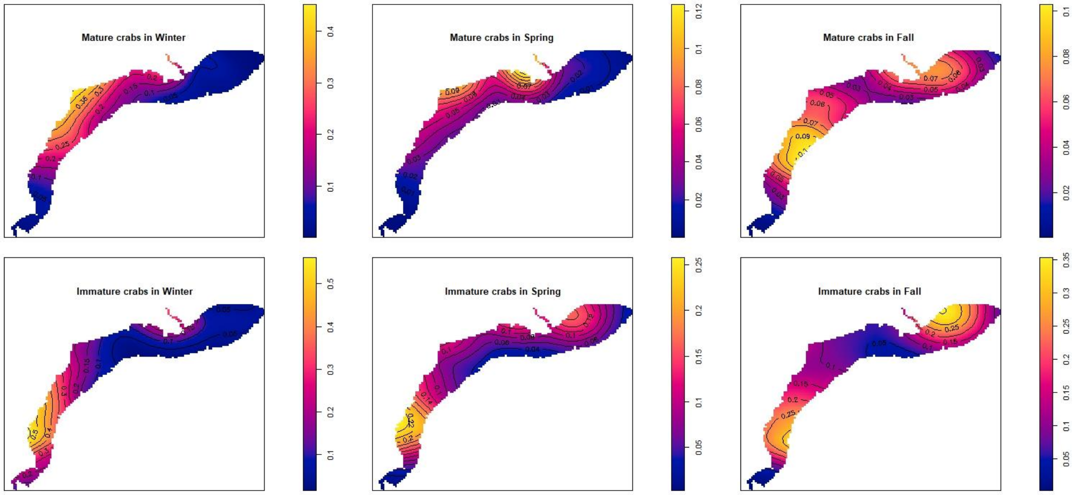

Figure 2.10: Atlantic rock crab kernel density estimates by maturity in winter, spring, and fall with warmer colors (yellow) representing areas with high intensities of Atlantic rock crabs and cool colors (blue) represent areas with low intensities of Atlantic rock crabs. The scales for each season are different as seen on each scale.

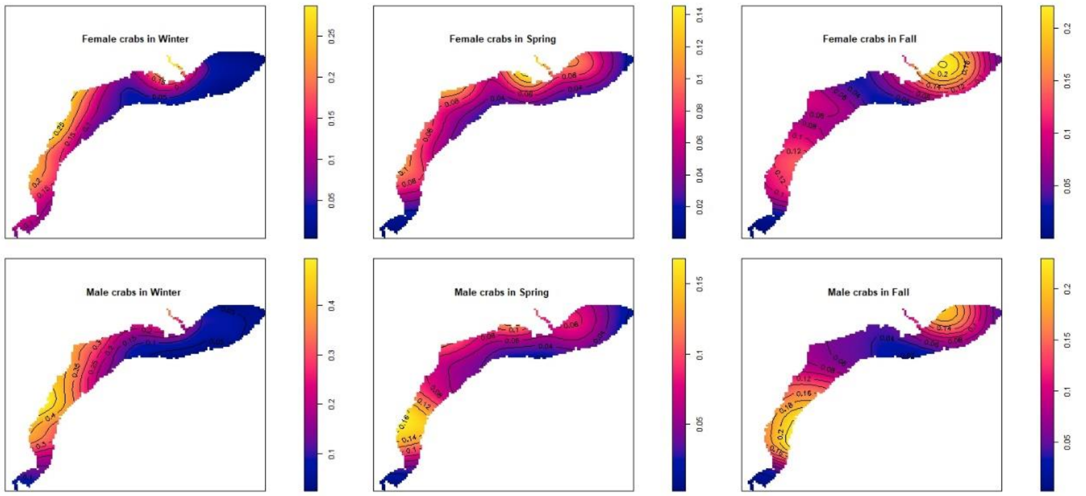

Figure 2.11: Atlantic rock crab kernel density estimates by sex in winter, spring, and fall with warmer colors (yellow) representing areas with high intensities of Atlantic rock crabs and cool colors (blue) represent areas with low intensities of Atlantic rock crabs. The scales for each season are different as seen on each scale.

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Appendices

Chapter One Appendix

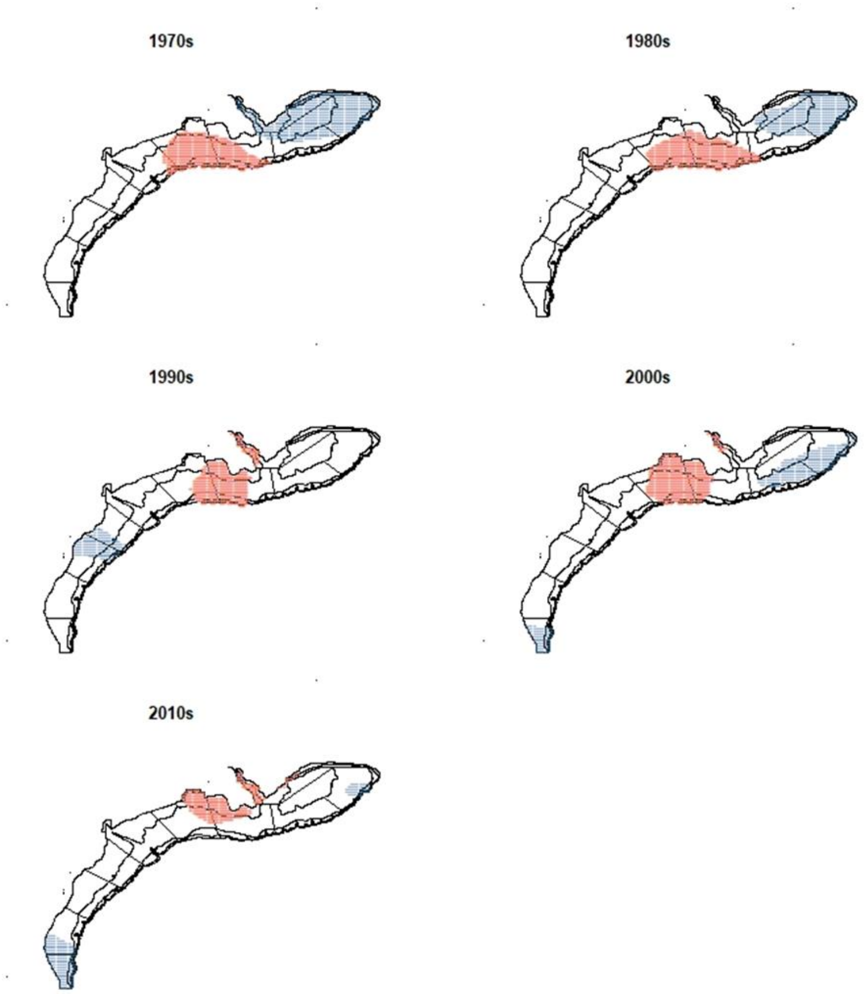

Figure A1.1: Jonah crab kernel density estimates for each decade from 1970s – 2010s that show areas that have a high intensity of Jonah crabs compared to the absences used as a control. Each KDE is created from 1,000 Monte Carlo permutations that divide points as being positively significant with Jonah crab presences, negatively significant with Jonah crab presences, or not significant. Areas in blue represent negative significance in finding Jonah crab presences, and red regions represent areas where the crabs are significantly likely to be present. These were compared with KDE plots in Figure 1.2 to analyze the significance of the changes found.

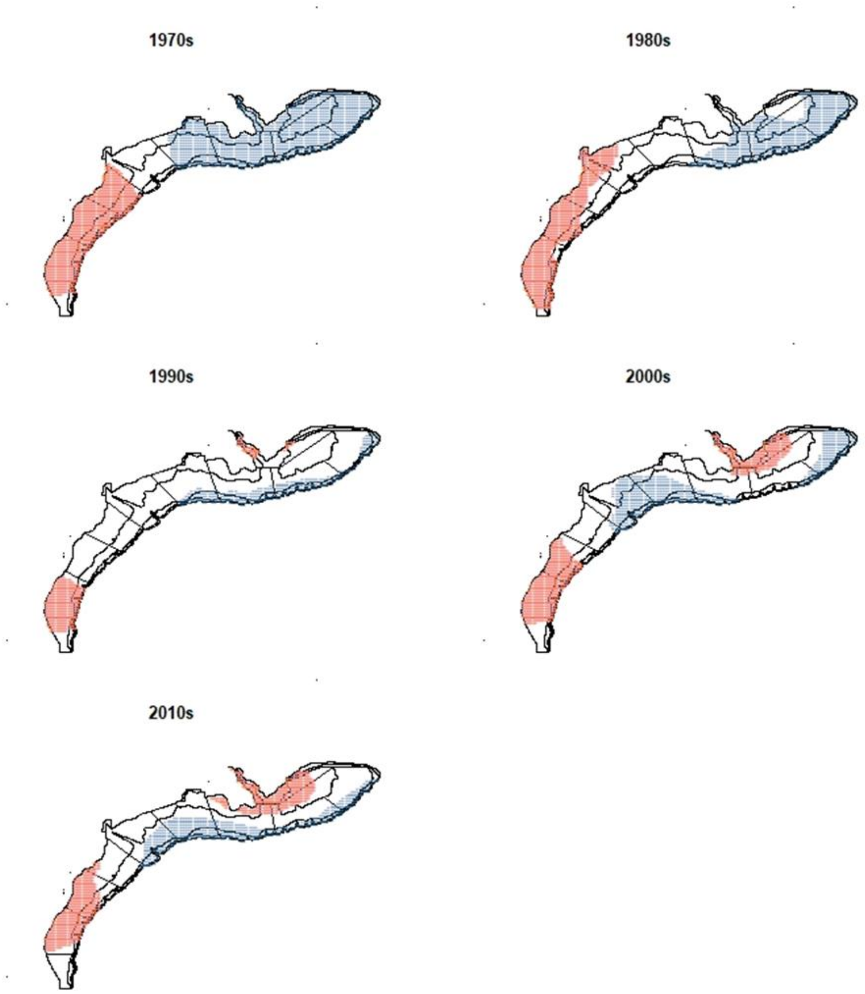

Figure A1.2: Atlantic rock crab kernel density estimates for each decade from 1970s – 2010s that show areas that have a high intensity of Atlantic rock crabs compared to the absences used as a control. Each KDE is created from 1,000 Monte Carlo permutations that divide points as being positively significant with Atlantic rock crab presences, negatively significant with Atlantic rock crab presences, or not significant. Areas in blue represent negative significance in finding Atlantic rock crab presences, and red regions represent areas where the crabs are significantly likely to be present. These were compared with KDE plots in Figure 1.3 to analyze the significance of the changes found.

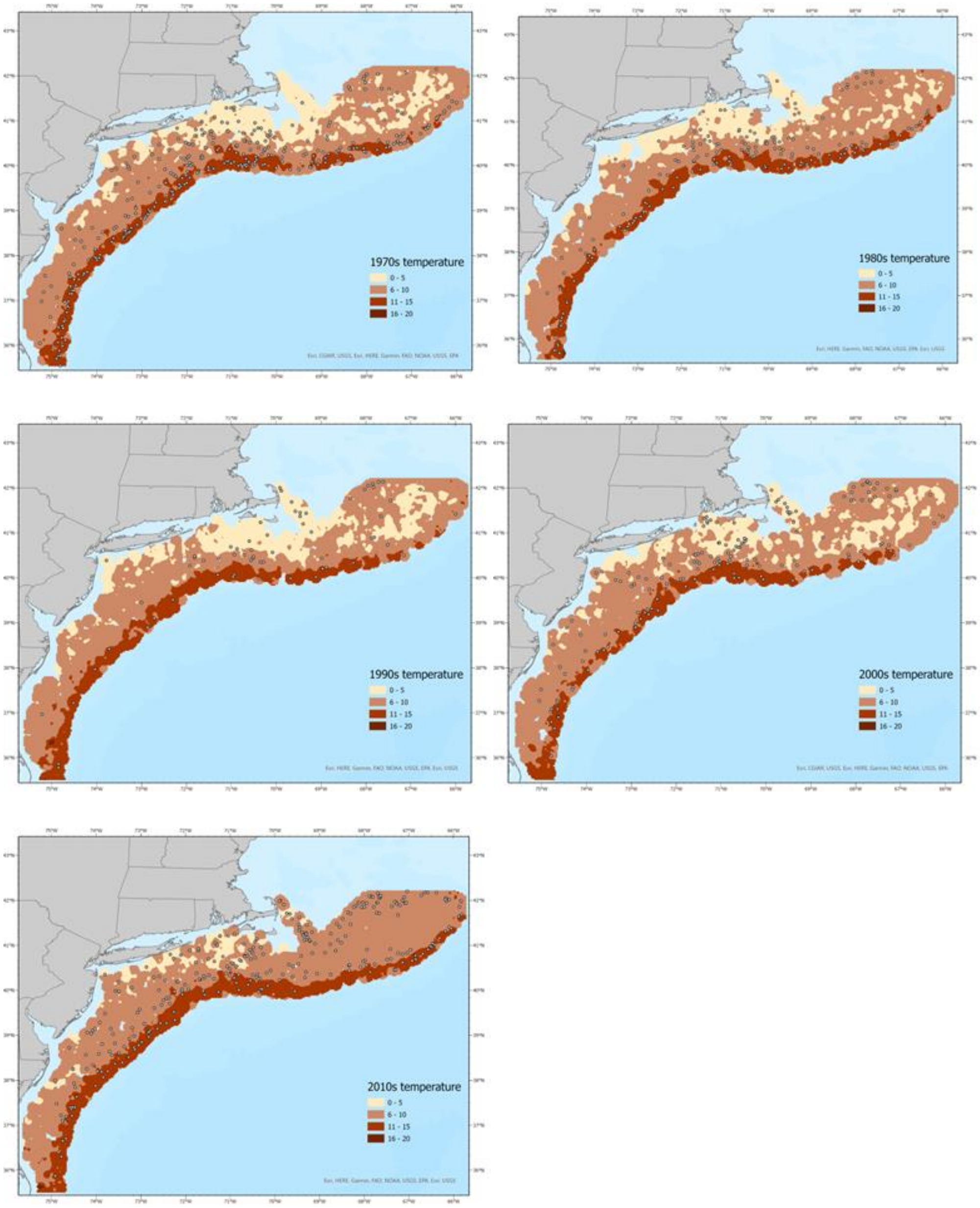

Figure A1.3: The presences of Jonah crabs and the average temperature by decade during the 1970s – 2010s using the inverse distance weighted tool in ArcGIS Pro.

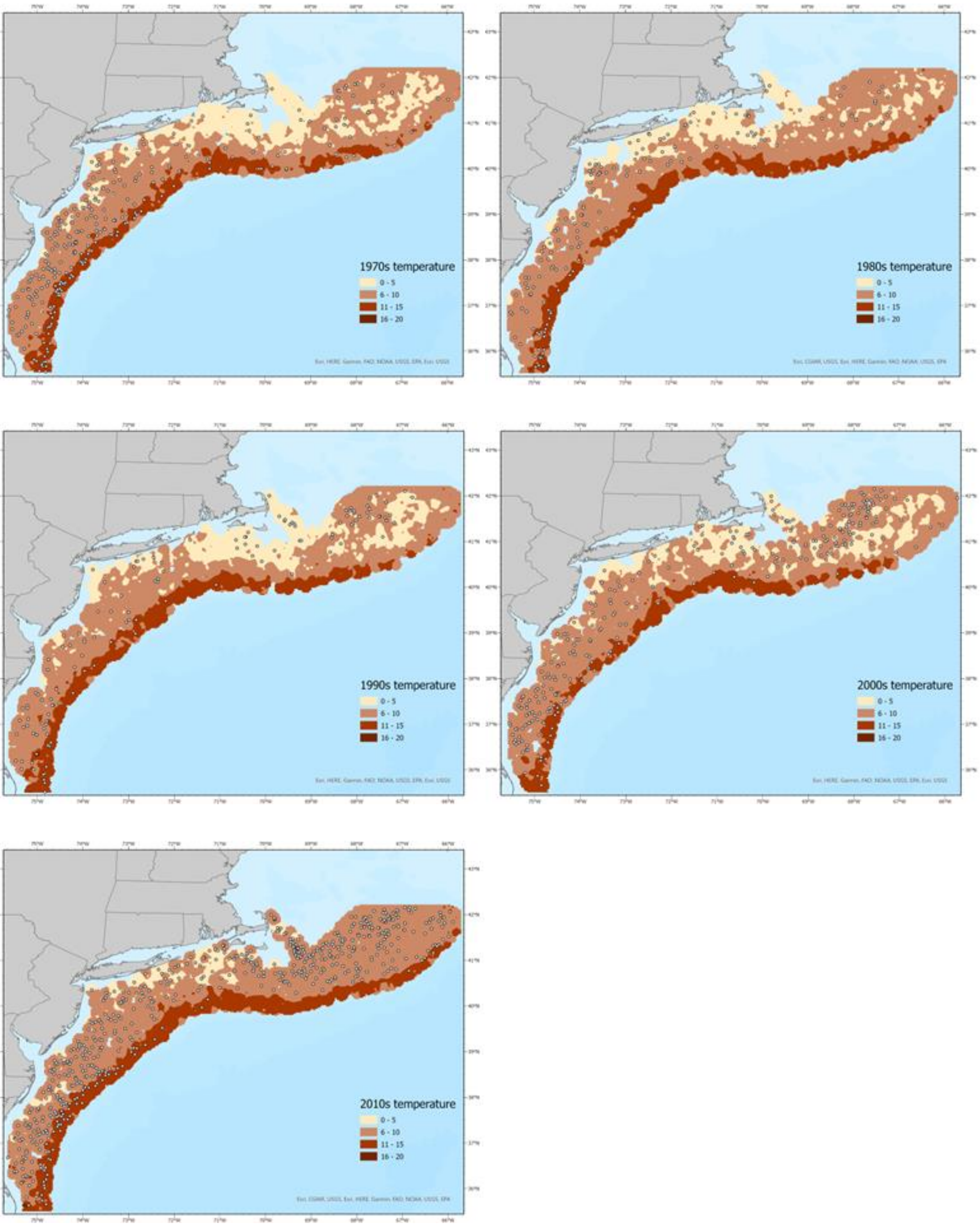

Figure A1.4: The presences of Atlantic rock crabs and the average temperature by decades from 1970s – 2010s using the inverse distance weighted tool in ArcGIS Pro.

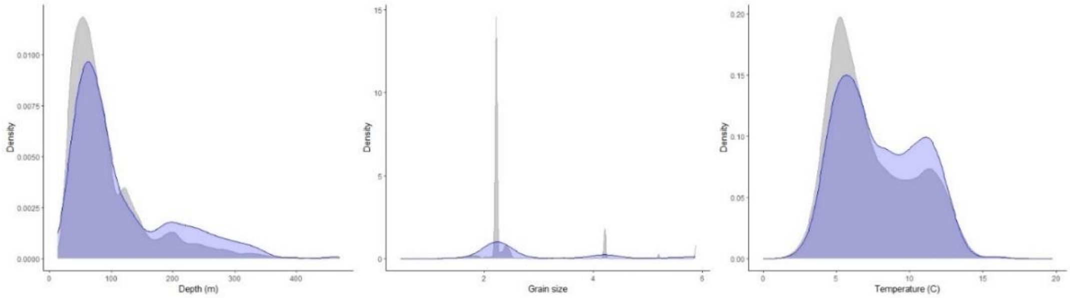

Figure A1.5: Jonah crab habitat utilization plots for A) Depth, B) Grain size, and C) Temperature. The blue area represents the density of crab presences and the gray area represents all the tow observations.

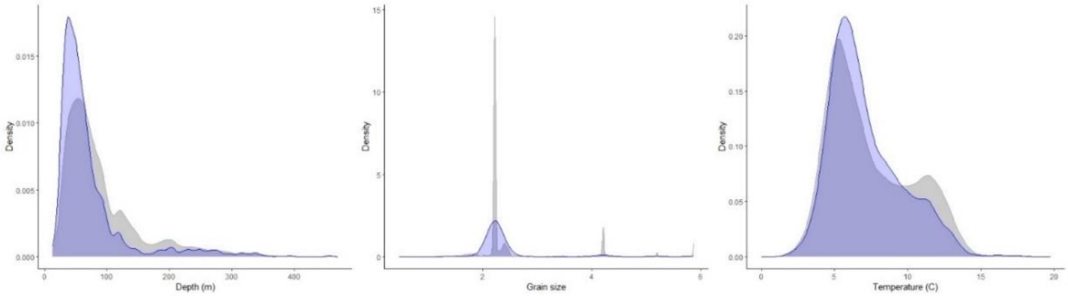

Figure A1.6: Atlantic rock crab habitat utilization plots for A) Depth, B) Grain size, and C) Temperature. The blue area represents the density of crab presences and the gray area represents all the tow observations.

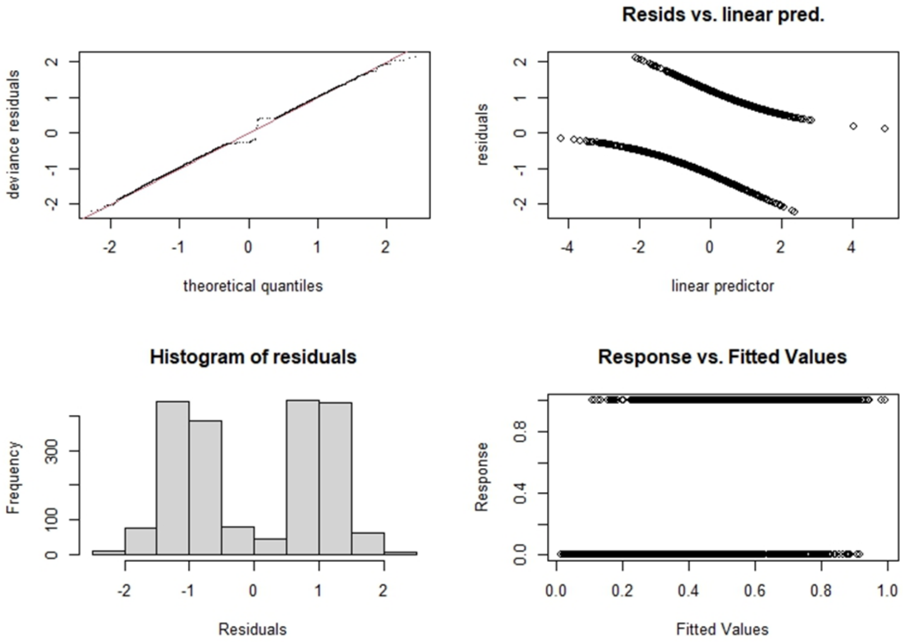

Figure A1.7: Residual plot diagnostics for the Jonah crab presences and absences for the best binomial generalized additive model found in Table 1.3.

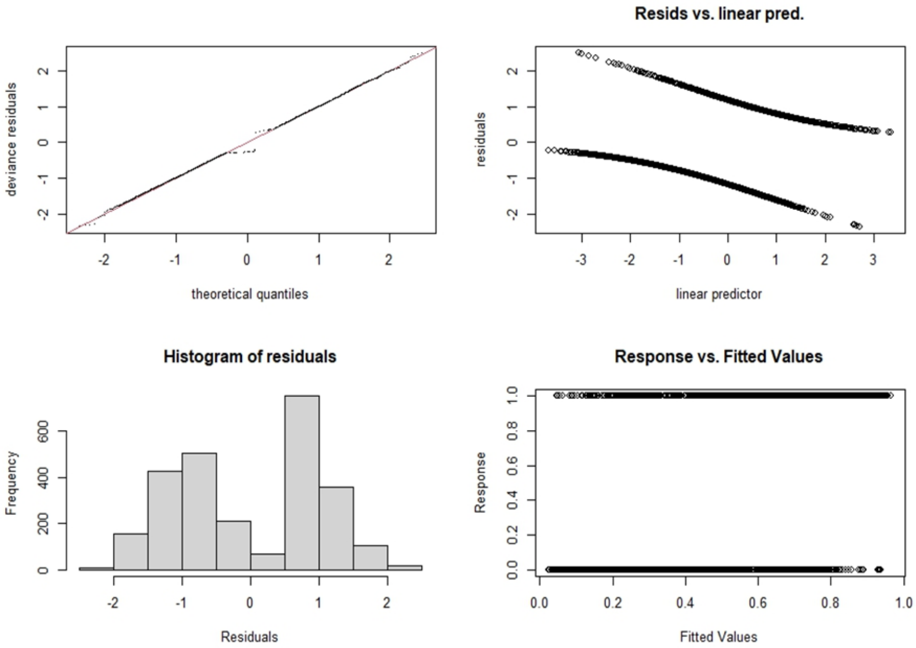

Figure A1.8: Residual plot diagnostics for the Atlantic rock crab presences and absences for the best binomial generalized additive model found in Table 1.4.

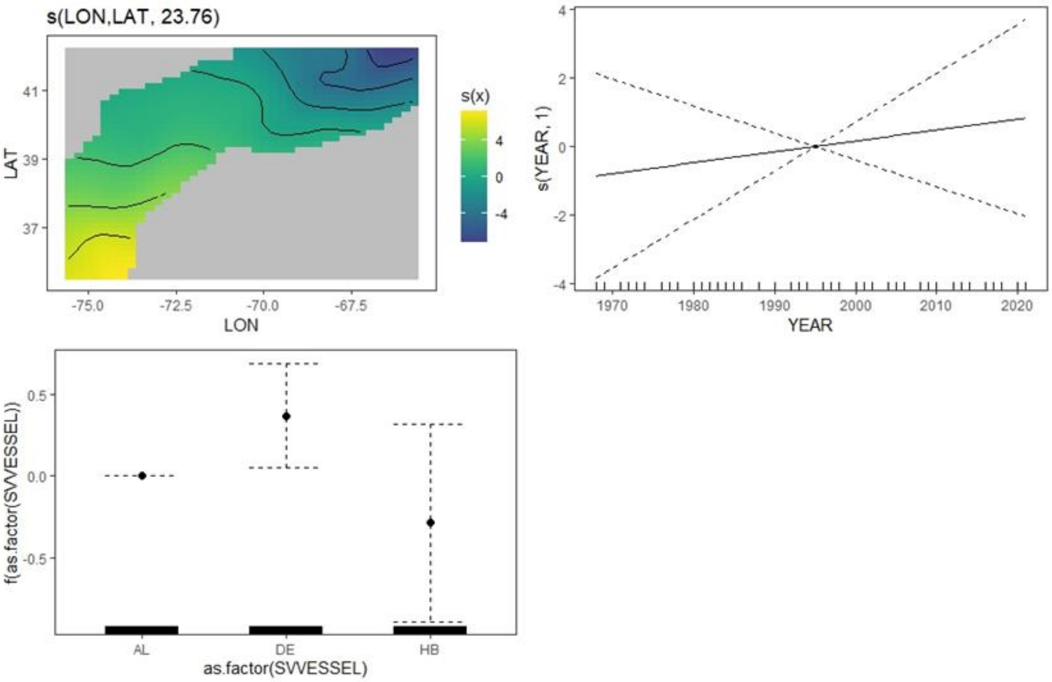

Figure A1.9: Effect plots for the spatial interaction between latitude (LAT) and longitude (LON), year, and the vessel (SVVESSEL) changes throughout the years from the best generalized additive model for Jonah crabs found in Table 1.3. The vessel names include R/V Albatross IV (AL), R/V Delaware II (DE), and R/V Henry B. Bigelow (HB). These figures were created using the mgcViz package in R.

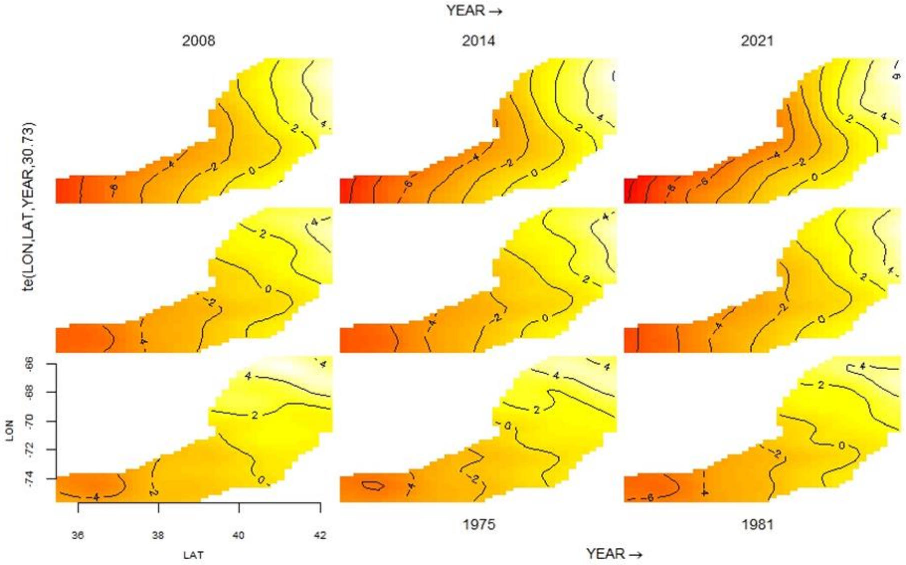

Figure A1.10: The effect plot for the interaction between spatial (LAT,LON) and temporal (YEAR) variables using a tensor product in the best generalized additive model for Jonah crabs found in Table 1.3.

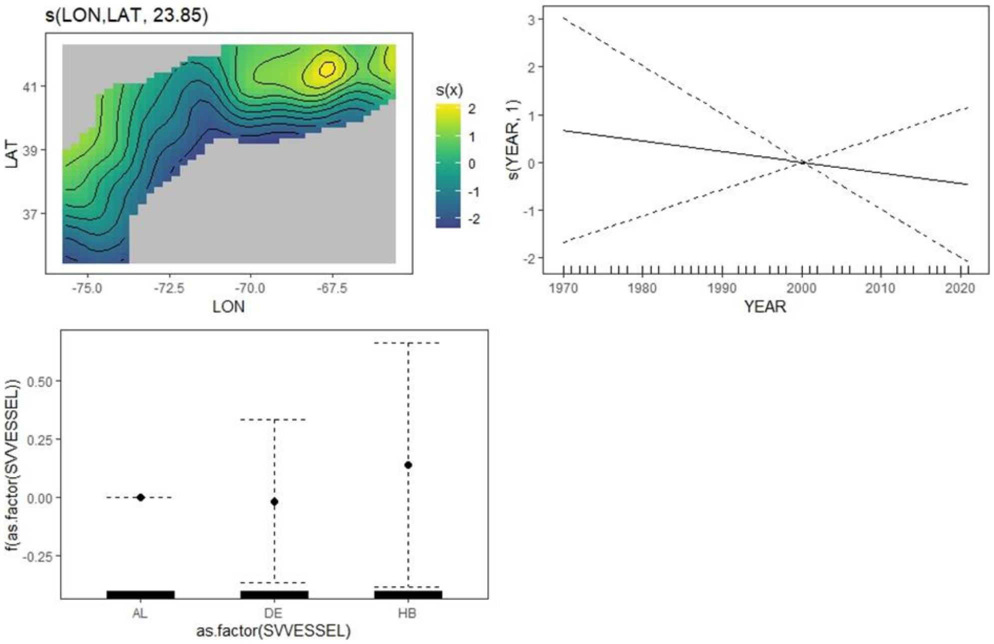

Figure A1.11: Effect plots for the spatial interaction between latitude (LAT) and longitude (LON), year, and the vessel (SVVESSEL) changes throughout the years from the best generalized additive model for Atlantic rock crabs found in Table 1.4. All variables included in the model had a smoothing spline (s). The vessel names include R/V Albatross IV (AL), R/V Delaware II (DE), and R/V Henry B. Bigelow (HB). These figures were created using the mgcViz package in R.

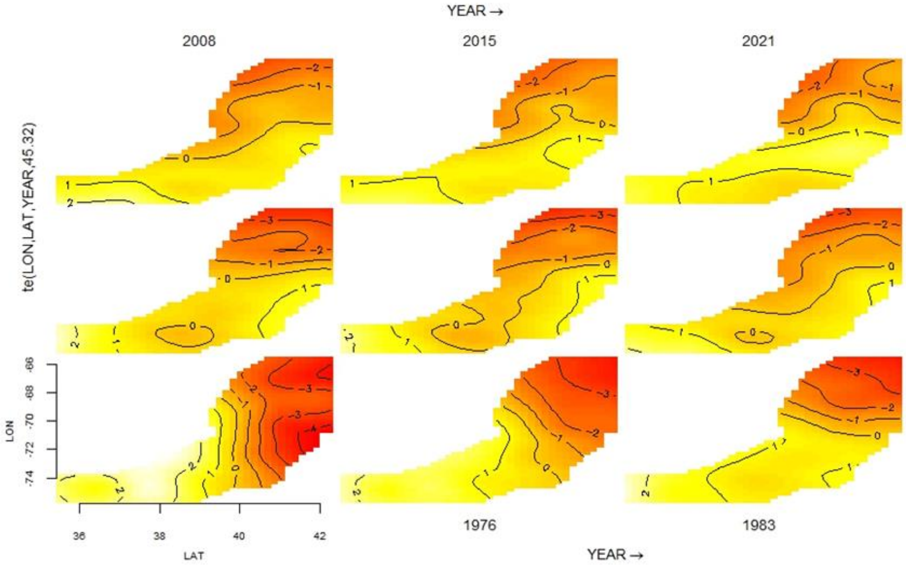

Figure A1.12: The effect plot for the interaction between spatial (LAT,LON) and temporal (YEAR) variables using a tensor product in the best generalized additive model for Atlantic rock crabs found in Table 1.4.

Table A1.1: The generalized additive models for Jonah and Atlantic rock crabs only including environmental variables temperature (temp), depth, and grain size (grain) with their degrees of freedom (df), Akaike information criterion (AIC), specificity (spec), sensitivity (sen), area under the curve (AUC), root mean square error (RMSE), mean area error (MAE), cover between the actual and predicted testing set values, and explained deviance. These results are also found in Table 1.3 for Jonah crabs and Table 1.4 for Atlantic rock crabs.

GAM models	df	AIC	spec	sen	AUC	RMSE	MAE	cover	explained deviance
Jonah crabs: s(temp) + s(depth) + s(grain)	16.93	2620.85	0.55	0.71	0.69	0.61	0.37	0.63	6.32%
Atlantic rock crabs: s(temp) + s(depth) + s(grain)	18.47	3247.76	0.67	0.66	0.71	0.58	0.34	0.66	10.80%

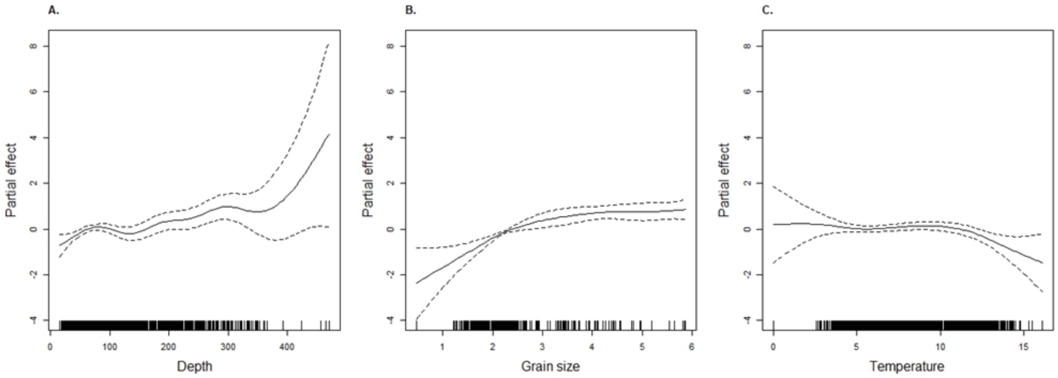

Figure A1.13: Jonah crab generalized additive model effect plots from the model in Table A1.1 with smoothing splines for the three environmental variables A) depth (m), B) grain size (ϕ), and C) temperature (°C).

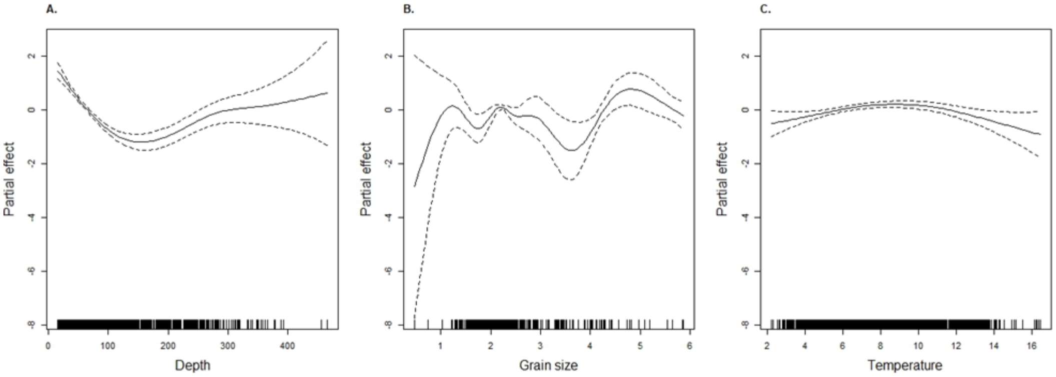

Figure A1.14: Atlantic rock crab generalized additive model effect plots from the model in Table A1.1 with smoothing splines for the three environmental variables A) depth (m), B) grain size (ϕ), and C) temperature (°C).

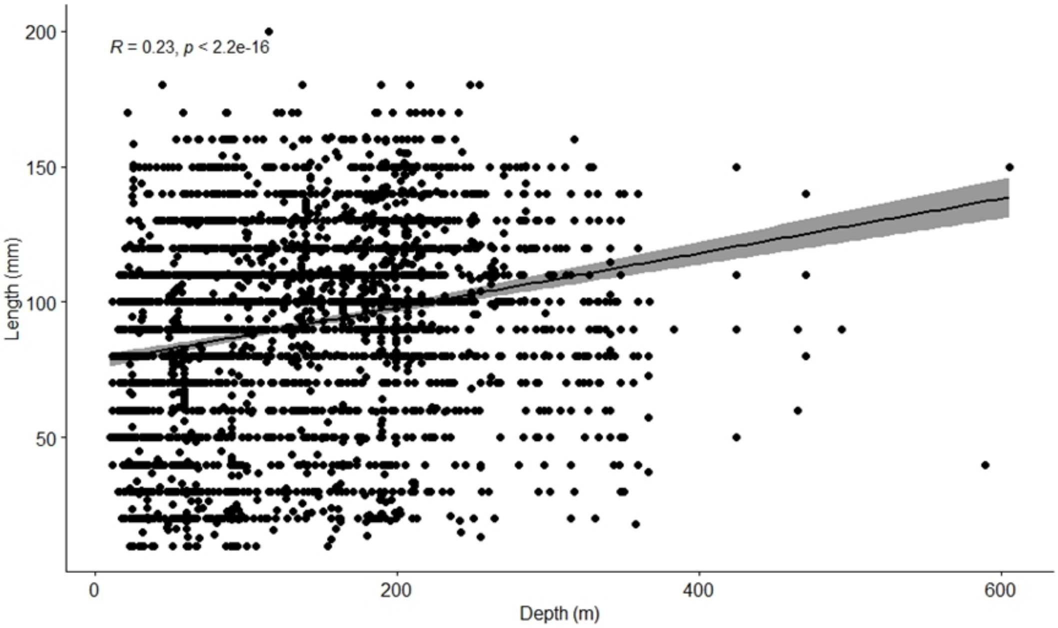

Figure A1.15: The length (mm) of the carapace width of Jonah crabs and depths (m) they were found in the NEFSC trawl surveys from 1968 – 2021.

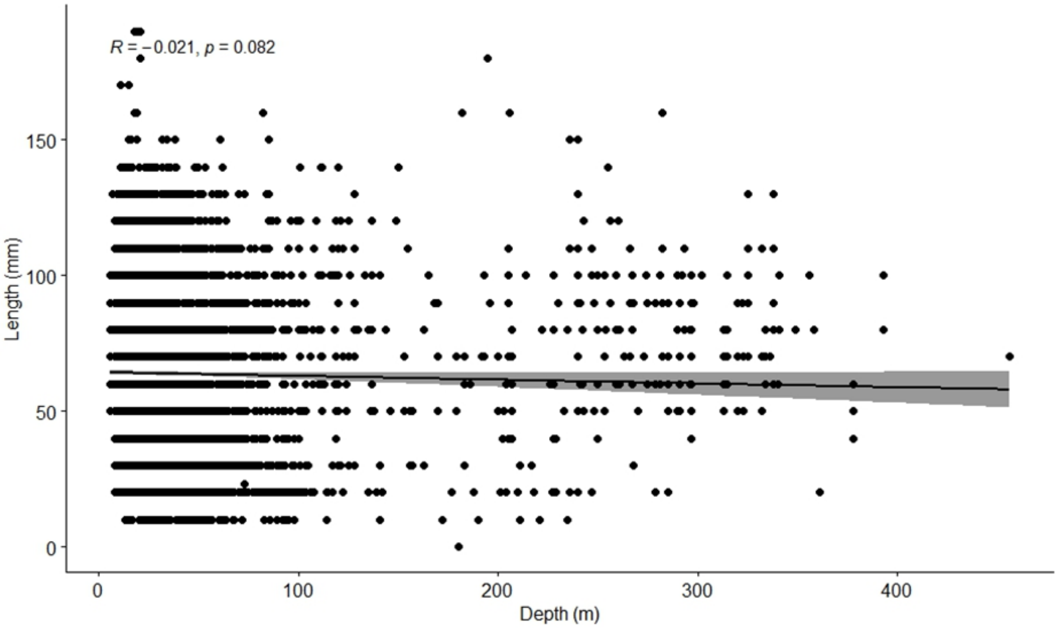

Figure A1.16: The length (mm) of the carapace width of Atlantic rock crabs and depths (m) they were found in the NEFSC trawl surveys from 1968 – 2021.

Chapter Two Appendix

Table A2.1: The top analysis of variances (ANOVAs) for Jonah crabs and depth (m) grouped by sex, maturity, region, and season. The ANOVAs are evaluated by degrees of freedom (df), log likelihood (LL), Akaike information criterion (AICc), and the difference between the AICc of the model and the best model.

Model	df	LL	AICc	AICc difference
depth = sex + maturity + region + season + (sex×region) + (season×sex) + (maturity×region) + (maturity×season) + (region×season) + (maturity×region×season)	17	-13218.66	26471.6	0
depth = sex + maturity + region + season + (sex×season) + (maturity×region) + (maturity×season) + (region×season) +(maturity×region×season)	16	-13219.76	26471.8	0.2
depth = sex + maturity + region + season + (sex×maturity) + (sex×region) + (sex×season) + (maturity×region) + (maturity×season) + (region×season) + (sex×maturity×season) + (maturity×region×season)	20	-13216.16	26472.7	1.1
depth = sex + maturity + region + season + (sex×maturity) + (sex×region) + (sex×season) + (maturity×region) + (maturity×season) + (region×season) + (sex×maturity×region) + (sex×maturity×season) + (maturity×region×season)	21	-13215.26	26472.9	1.3
depth = sex + maturity + region + season + (sex×maturity) + (sex×season) + (maturity×region) + (maturity×season) + (region×season) + (sex×maturity×season) + (maturity×region×season)	19	-13217.31	26473	1.4
depth = sex + maturity + region + season + (sex×maturity) + (sex×region) + (sex×season) + (maturity×region) + (maturity×season) + (region×season) + (maturity×region×season)	18	-13218.42	26473.1	1.5
depth = sex + maturity + region + season + (sex×maturity) +	17	-13219.52	26473.3	1.7

(sex×season) + (maturity×region) + (maturity×season) + (region×season) + (maturity×region×season)

Table A2.2: The top analysis of variances (ANOVAs) for Jonah crabs and distance from shore (km) grouped by sex, maturity, region, and season. The ANOVAs are evaluated by degrees of freedom (df), log likelihood (LL), Akaike information criterion (AICc), and the difference between the AICc of the model and the best model.

Model	df	LL	AICc	AICc difference
dist = sex + maturity + region + season + (sex×maturity) + (sex×season) + (maturity×season)+ (region×season) + (sex×maturity×season)	16	-11893.2	23818.6	0
dist = sex + maturity + region + season + (sex×maturity) + (sex×region) + (sex×season) + (maturity×season) + (region×season) + (sex×maturity×season)	17	-11892.5	23819.2	0.6
dist = sex + maturity + region + season + (sex×maturity) + (sex×region) +(sex×season) + (maturity×region) + (maturity×season) + (region×season) + (sex×maturity×season)	18	-11891.5	23819.3	0.7
dist = sex + maturity + region + season + (sex×maturity) + (sex×season) + (maturity×region) + (maturity×season) + (region×season) + (sex×maturity×season)	17	-11892.7	23819.8	1.2

Table A2.3: Jonah crab Kolmogorov – Smirvnov (KS) test p-values for depth (m) and distance to shore (km) between the three seasons (winter, spring, and fall) for Georges Bank and the Mid-Atlantic Bight.

Season comparison	Distance (km) p-value	Depth (m) p-value
GB: winter and fall	0.016	**5.44e-06**
GB: winter and spring	0.38	**0.00072**
GB: fall and spring	0.056	0.024
MAB: winter and fall	**1.19e-11**	**1.78e-15**
MAB: winter and spring	**6.22e-08**	**8.90e-10**
MAB: fall and spring	**0.0012**	0.0070

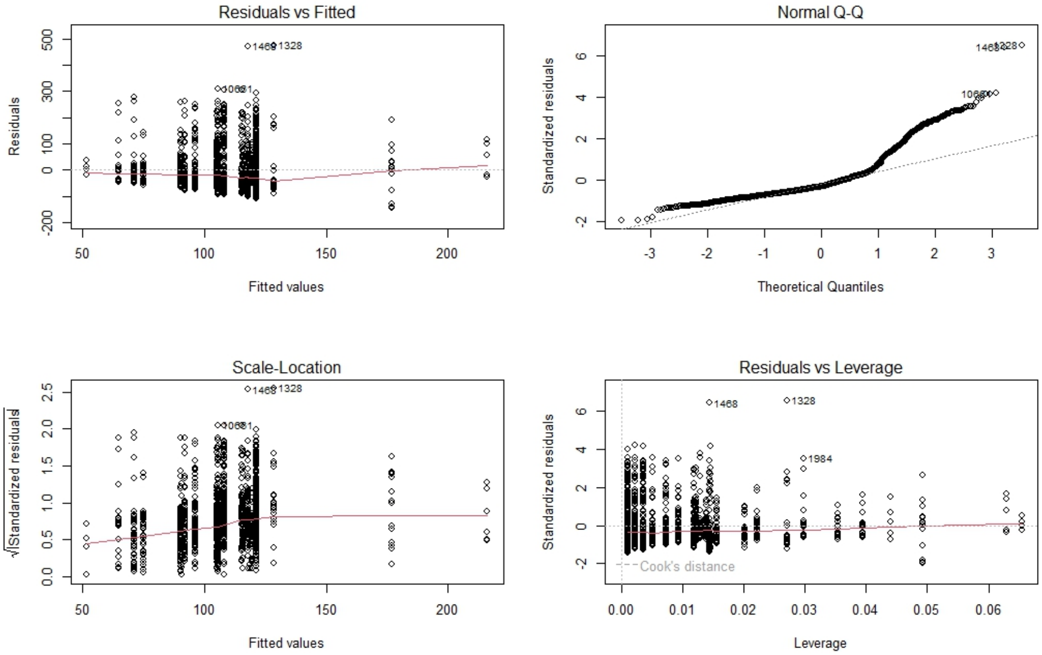

Figure A2.1: Residuals from the best analysis of variance (ANOVA) model for the depths of the observations of Jonah crabs grouped by sex, maturity, season, and maturity. The best model is found in Table A2.1 and Table 2.5.

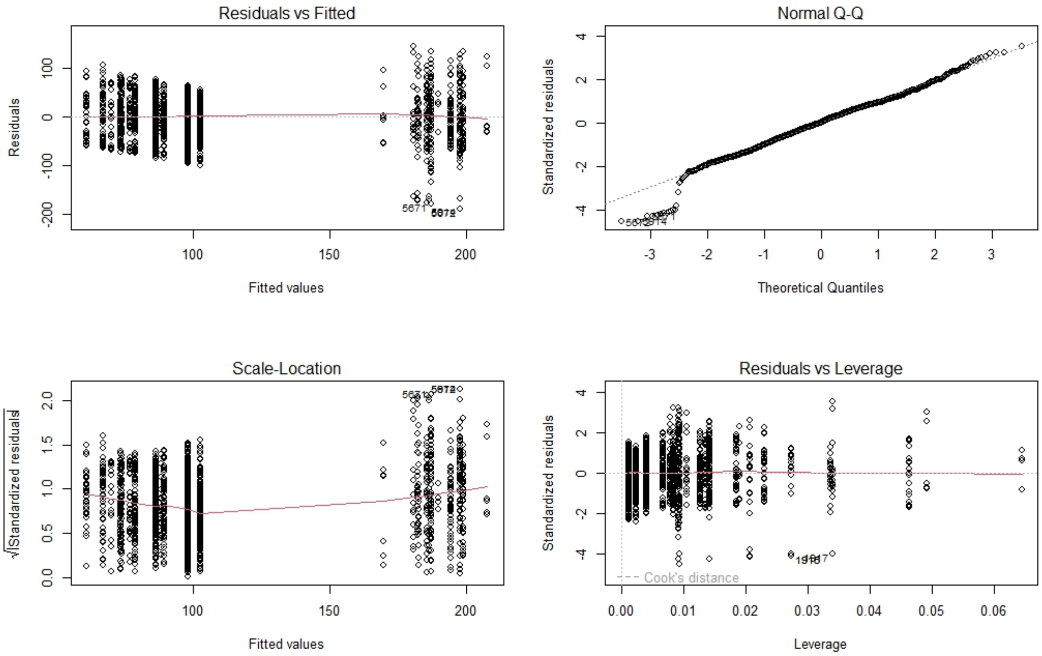

Figure A2.2: Residuals from the best analysis of variance (ANOVA) model for the distance to shore (km) of the observations of Jonah crabs grouped by sex, maturity, season, and maturity. The best model is found in Table A2.2 and Table 2.5.

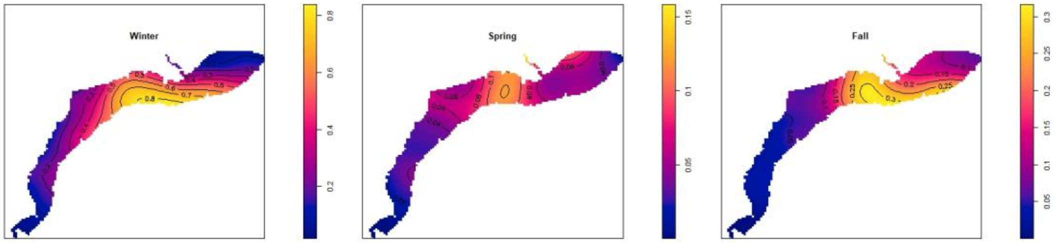

Figure A2.3: Kernel density estimates for Jonah crab by winter, spring, and fall with warmer colors (yellow) representing areas with high intensities of Jonah crabs and cool colors (blue) represent areas with low intensities of Jonah crabs. The scales for each season are different as seen on each scale.

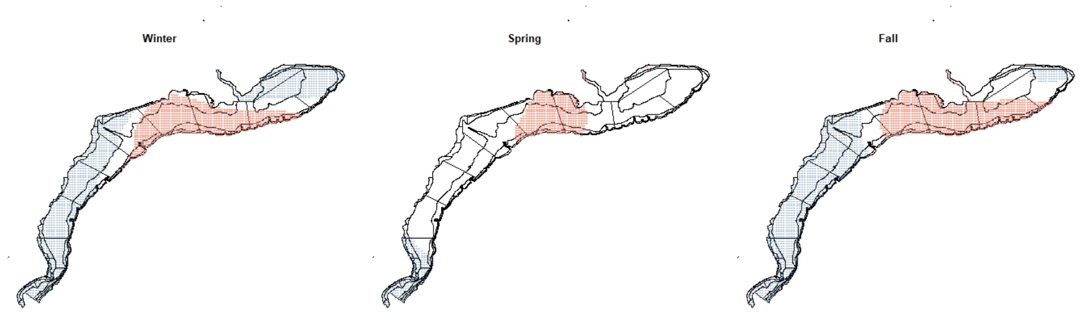

Figure A2.4: Kernel density estimates with 1,000 Monte Carlo permutations for Jonah crab in winter, spring, and fall. The area in red indicates places where there is a significant high probability of Jonah crabs, and areas in blue represent places where there is a significant low probability of finding a Jonah crab.

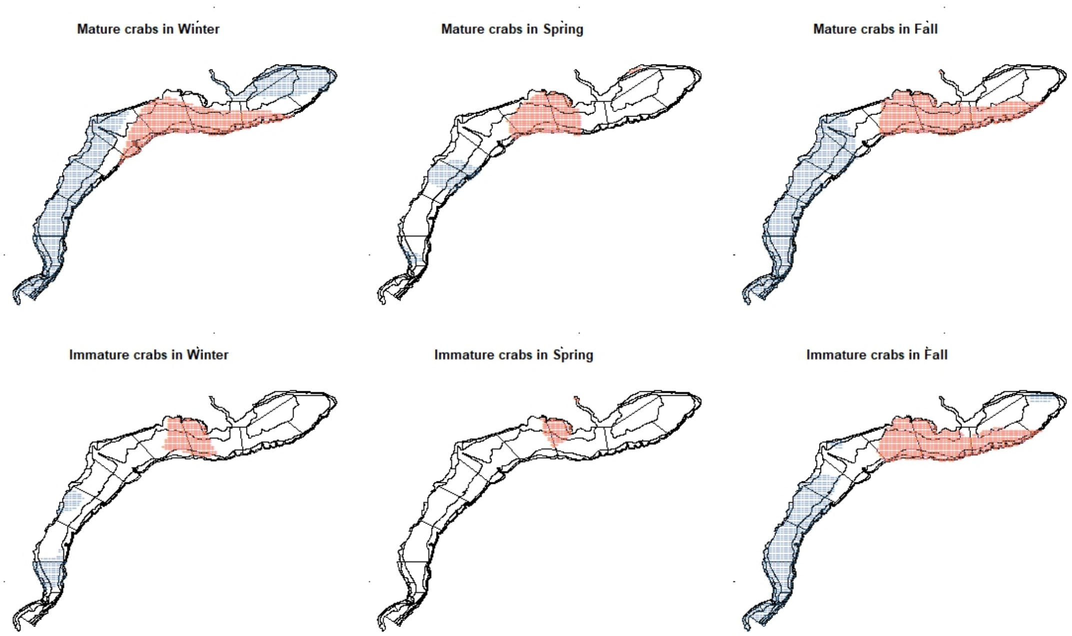

Figure A2.5: Kernel density estimates with 1,000 Monte Carlo permutations for Jonah crabs by maturity in winter, spring, and fall. The area in red indicates places where there is a significant high probability of Jonah crabs, and areas in blue represent places where there is a significant low probability of finding a Jonah crab.

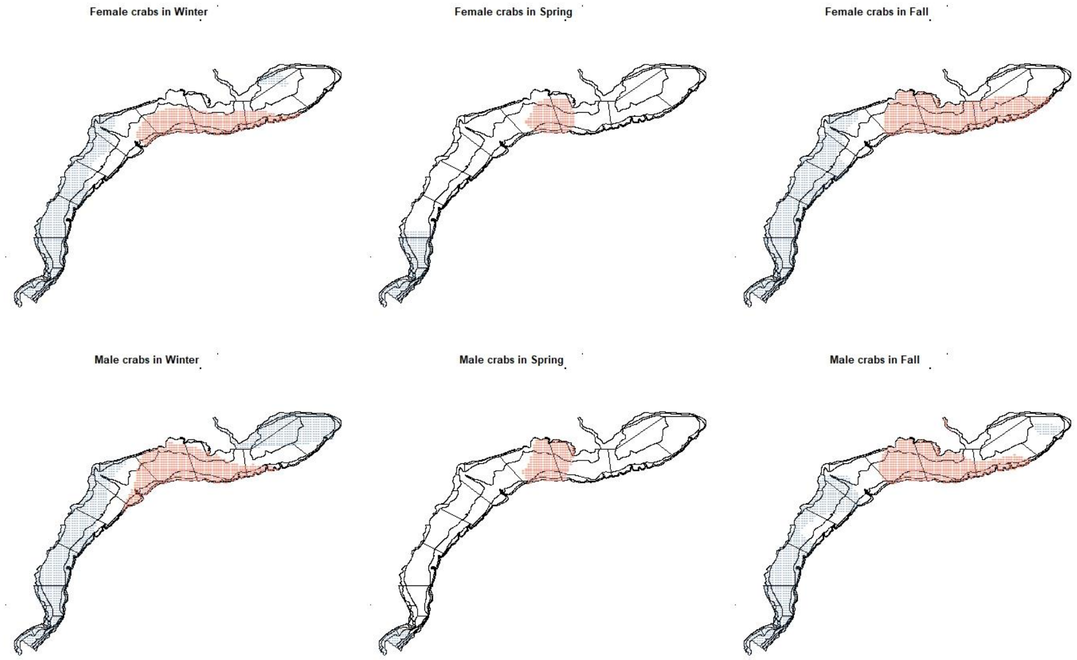

Figure A2.6: Kernel density estimates with 1,000 Monte Carlo permutations for Jonah crabs by maturity in winter, spring, and fall. The area in red indicates places where there is a significant high probability of Jonah crabs, and areas in blue represent places where there is a significant low probability of finding a Jonah crab.

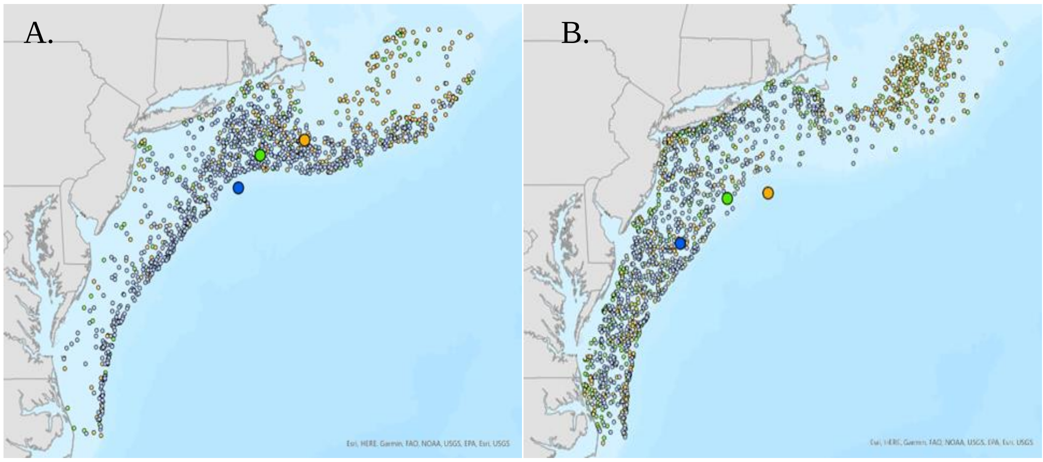

Figure A2.7: Seasonal centroids of A) Jonah crabs and B) Atlantic rock crabs in winter (blue), spring (green), and fall (orange).

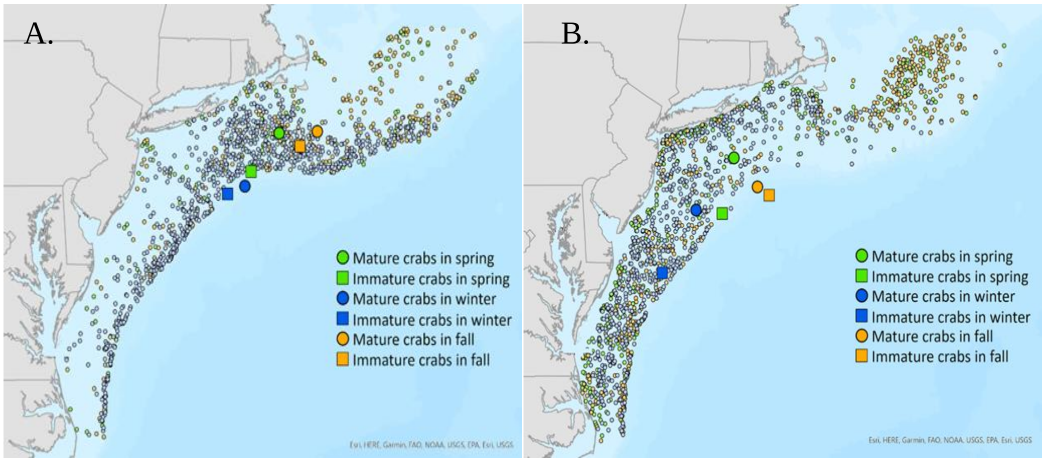

Figure A2.8: Seasonal centroids for A) Jonah crabs and B) Atlantic rock crabs by maturity (mature = circles; immature = squares) in winter (blue), spring (green), and fall (orange).

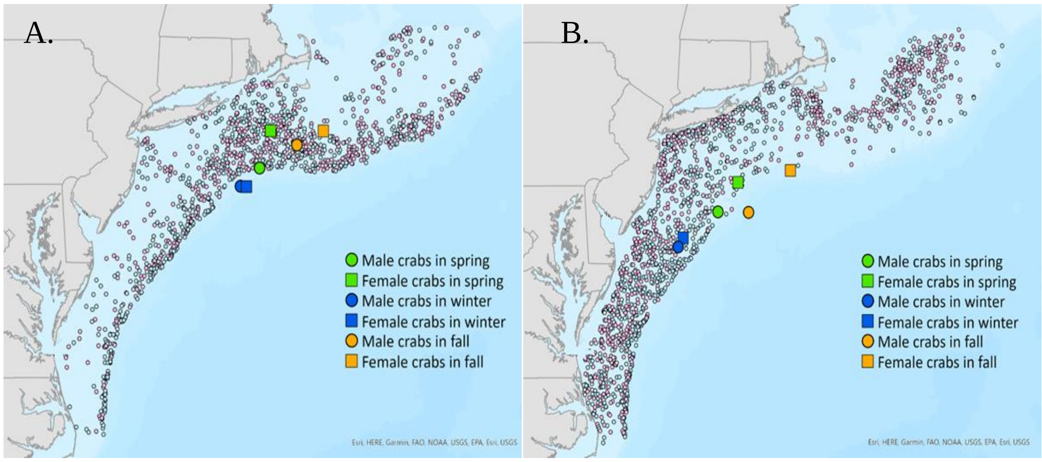

Figure A2.9: Seasonal centroids for A) Jonah crabs and B) Atlantic rock crabs by sex (male = circle; female = square) in winter (blue), spring (green), and fall (orange).

Table A2.4: The top analysis of variances (ANOVAs) for Atlantic rock crabs and depth (m) grouped by sex, maturity, region, and season. The ANOVAs are evaluated by degrees of freedom (df), log likelihood (LL), Akaike information criterion (AICc), and the difference between the AICc of the model and the best model.

Model	df	LL	AICc	AICc difference
depth = sex + maturity + region + season + (sex×region) + (maturity×season) + (region×season)	12	-14581.65	29187.4	0
depth = sex + maturity + region + season + (sex×region) + (maturity×region) + (maturity×season) + (region×season)	13	-14580.65	29187.4	0
depth = sex + maturity + region + season + (sex×maturity) + (sex×region) + (maturity×region) + (maturity×season) + (region×season)	14	-14580.43	29189	1.6
depth = sex + maturity + region + season + (sex×maturity) + (sex×region) + (maturity×season) + (region×season)	13	-14581.56	29189.3	1.9

Table A2.5: The top analysis of variances (ANOVAs) for Atlantic rock crabs and distance from shore (dist) (km) grouped by sex, maturity, region, and season. The ANOVAs are evaluated by degrees of freedom (df), log likelihood (LL), Akaike information criterion (AICc), and the difference between the AICc of the model and the best model.

Model	df	LL	AICc	AICc difference
dist = sex + maturity + region + season + (sex×maturity) + (maturity×region) + (region×season)	11	-13002.84	26025.8	0
dist = sex + maturity + region + season + (sex×maturity) + (sex×region) + (sex×season) + (maturity×region) + (region×season) + (sex×maturity×region) + (sex×region×season)	17	-12996.2	26026.6	0.8
dist = sex + maturity + region + season + (sex×maturity) + (sex×region) + (maturity×region) + (region×season) + (sex×maturity×region) + (sex×region×season)	13	-13000.55	26027.2	1.4
dist = sex + maturity + region + season + (sex×maturity) + (maturity×region) + (maturity×season) + (region×season)	13	-13000.57	26027.3	1.5
dist = sex + maturity + region + season + (sex×maturity) + (sex×region) +(sex×season) + (maturity×region) + (maturity×season) + (region×season) + (sex×maturity×region) + (sex×region×season) + (maturity×region×season) + (sex×maturity×region×season)	25	-12988.47	26027.4	1.6
dist = sex + maturity + region + season + (sex×maturity) + (sex×region) + (sex×season) + (maturity×region) + (maturity×season) + (region×season) + (sex×maturity×region) + (sex×region×season)	21	-12992.63	26027.6	1.8
dist = sex + maturity + region + season + (sex×maturity) + (sex×region) + (maturity×region) + (region×season)	12	-13001.79	26027.7	1.9

Table A2.6: Atlantic rock crab Kolmogorov – Smirnov (KS) test p-values for depth (m) and distance to shore (km) between the three seasons (winter, spring, and fall) for Georges Bank and the Mid-Atlantic Bight.

Season comparison	Distance (km) p-value	Depth (m) p-value
GB: winter and fall	**0.017**	**1.99e-09**
GB: winter and spring	0.031	**1.40e-09**
GB: fall and spring	0.061	0.17
MAB: winter and fall	**1.78e-15**	**< 2.2e-16**
MAB: winter and spring	**< 2.2e-16**	**< 2.2e-16**
MAB: fall and spring	**< 2.2e-16**	**< 2.2e-16**

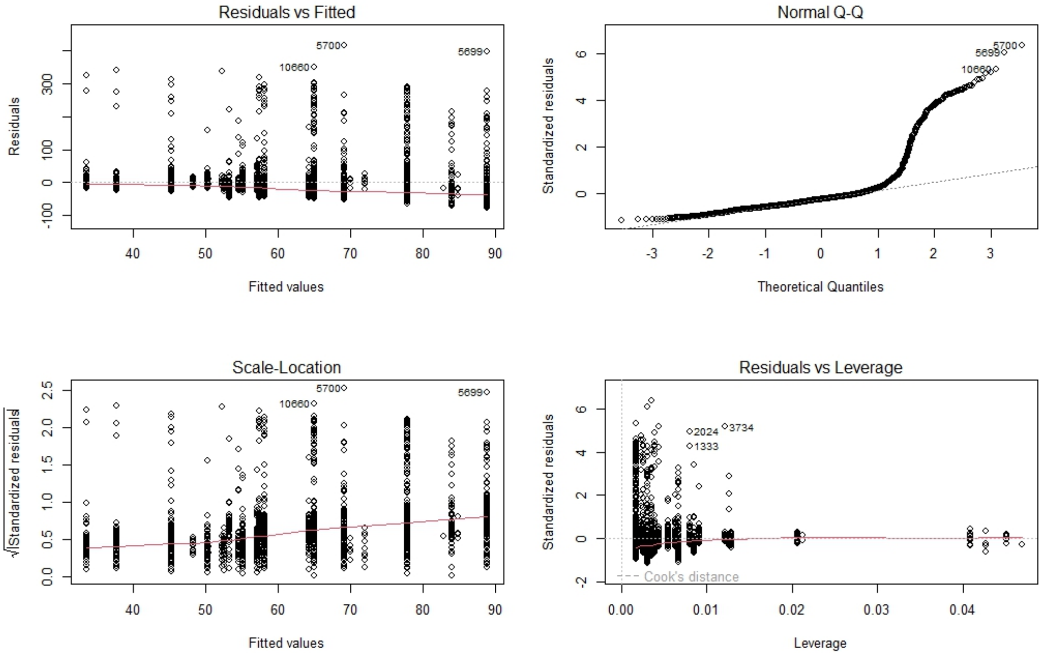

Figure A2.10: Residuals from the best analysis of variance (ANOVA) model for the depths of the observations of Atlantic rock crabs grouped by sex, maturity, season, and maturity. The best model is found in Table A2.4 and Table 2.12.

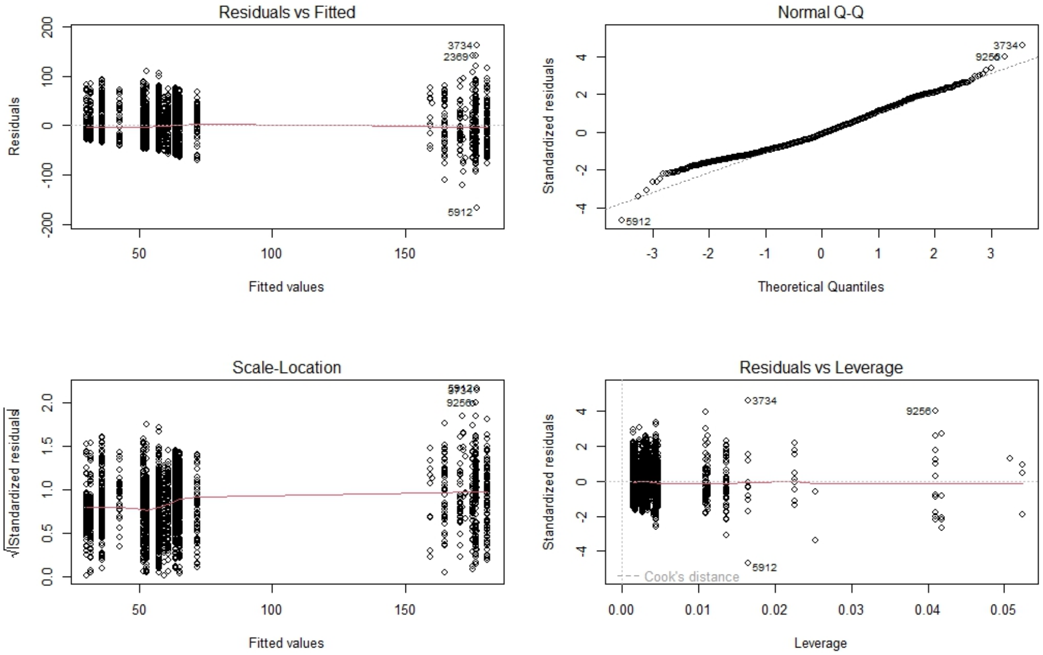

Figure A2.11: Residuals from the best analysis of variance (ANOVA) model for the distance to shore (km) of the observations of Atlantic rock crabs grouped by sex, maturity, season, and maturity. The best model is found in Table A2.5 and Table 2.12.

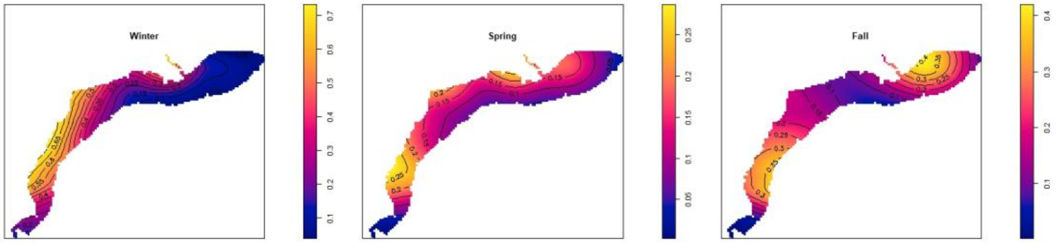

Figure A2.12: Kernel density estimates of Atlantic rock crabs by winter, spring, and fall with warmer colors (yellow) representing areas with high intensities of Atlantic rock crabs and cool colors (blue) represent areas with low intensities of Atlantic rock crabs. The scales for each season are different as seen on each scale.

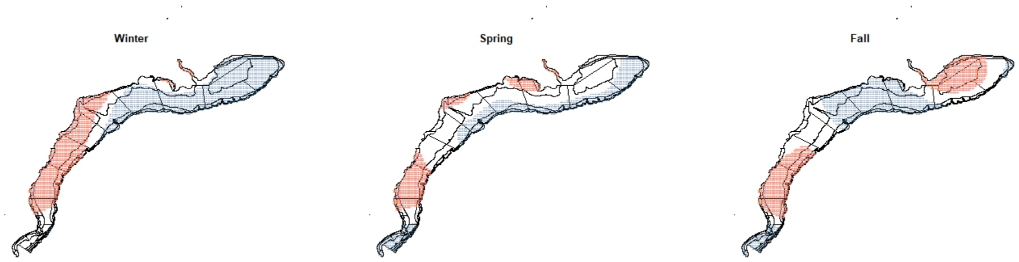

Figure A2.13: Kernel density estimates with 1,000 Monte Carlo permutations for Atlantic rock crabs in winter, spring, and fall. The area in red are places where there is a significant high probability of Atlantic rock crabs, and areas in blue represent places where there is a significant low probability of finding an Atlantic rock crab.

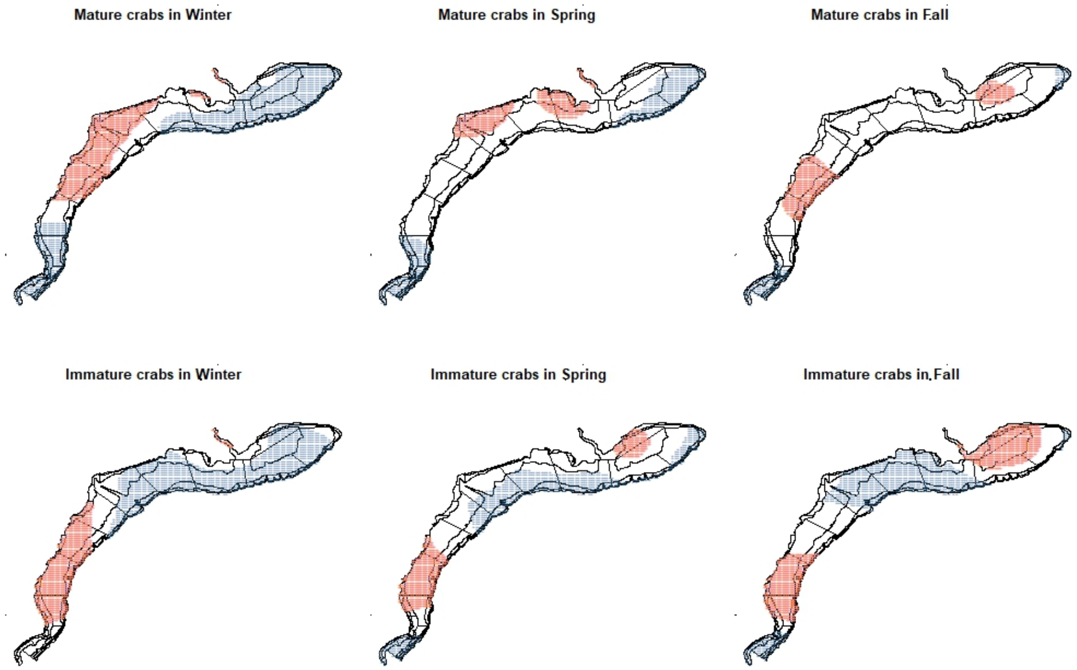

Figure A2.14: Kernel density estimates with 1,000 Monte Carlo permutations for Atlantic rock crabs by maturity in winter, spring, and fall. The area in red are places where there is a significant high probability of Atlantic rock crabs, and areas in blue represent places where there is a significant low probability of finding an Atlantic rock crab.

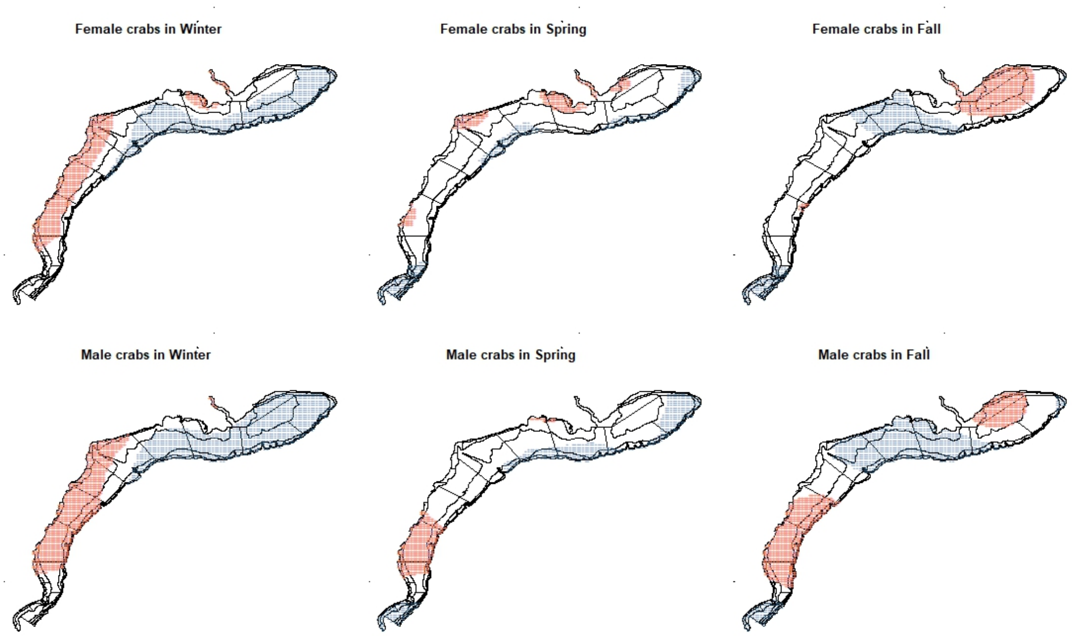

Figure A2.15: Kernel density estimates with 1,000 Monte Carlo permutations for Atlantic rock crabs by sex in winter, spring, and fall. The area in red are places where there is a significant high probability of Atlantic rock crabs, and areas in blue represent places where there is a significant low probability of finding an Atlantic rock crab.

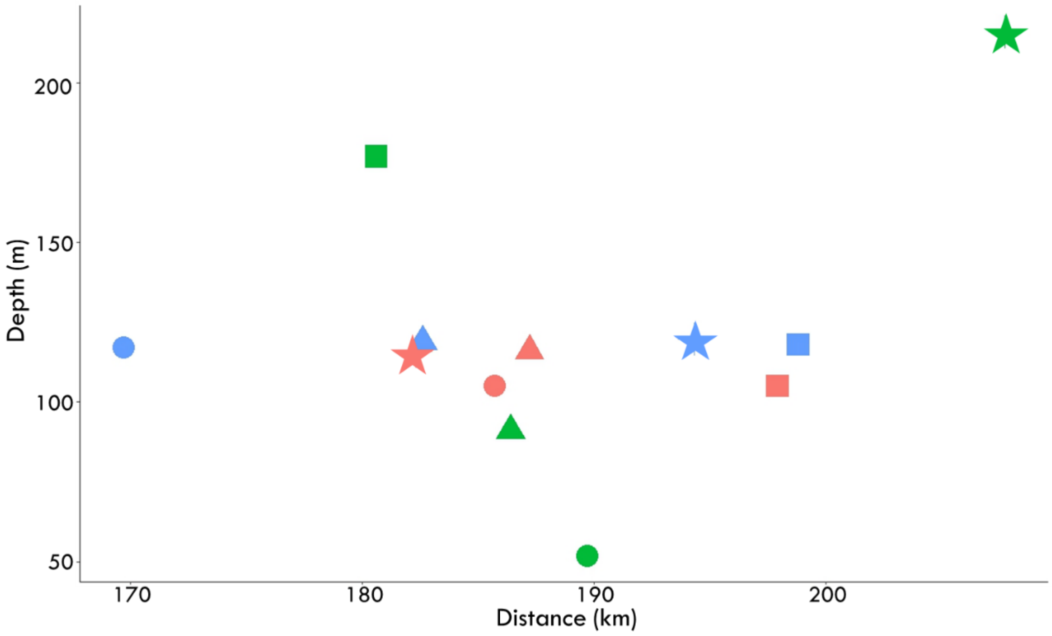

Figure A2.16: Seasonal differences in average distance from shore (km) and depth (m) for Jonah crabs Georges Bank from the best ANOVAs. Each group is represented by a different symbol with mature males as stars, mature females as squares, immature males as triangles, and immature females as circles. Seasons are represented by colors with winter as blue, spring as green, and pink as fall.

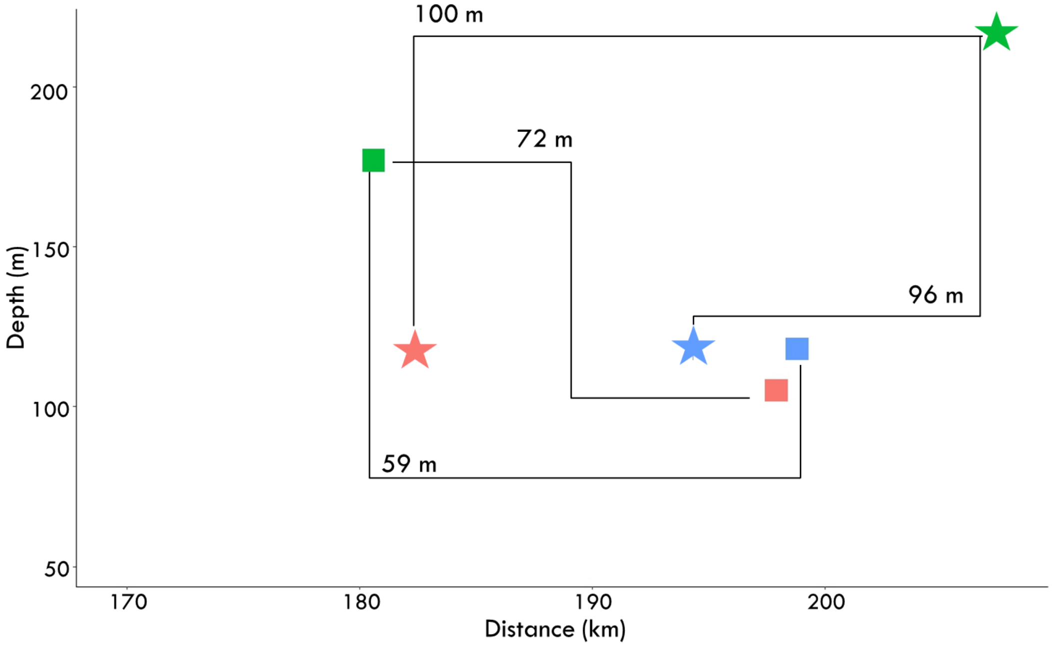

Figure A2.17: Seasonal differences in average distance from shore (km) and depth (m) for Jonah crabs in Georges Bank from the best ANOVAs. Each group is represented by a different symbol with mature males as stars and mature females as squares. Seasons are represented by colors with winter as blue, spring as green, and pink as fall. Black lines represent differences between two seasonal averages that do not have overlapping confidence intervals.

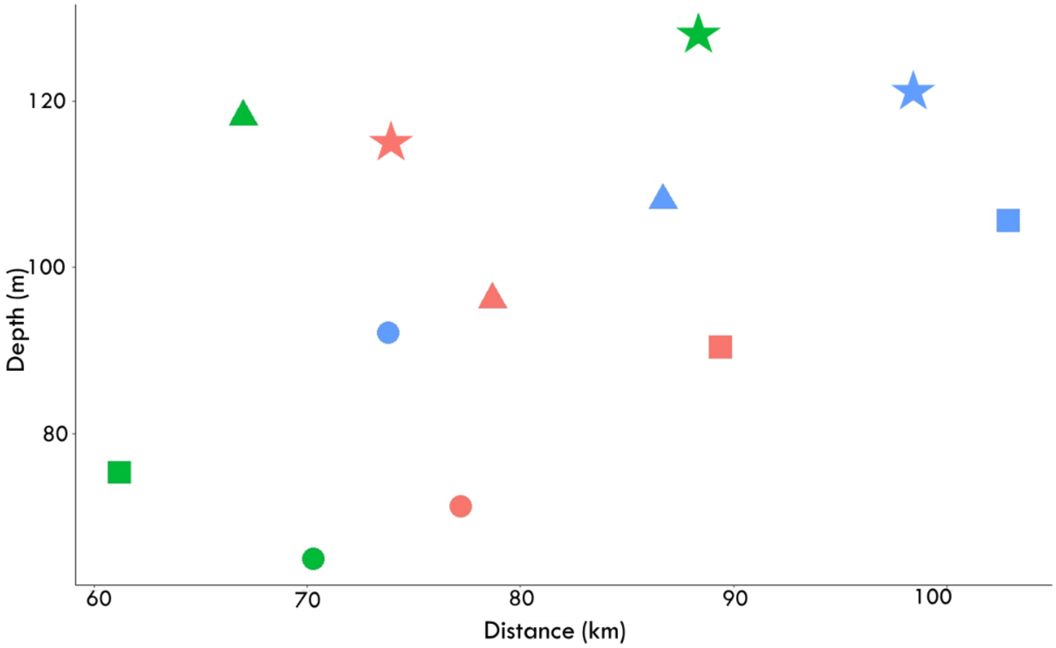

Figure A2.18: Seasonal differences in average distance from shore (km) and depth (m) for Jonah crabs in the Mid-Atlantic Bight from the best ANOVAs. Each group is represented by a different symbol with mature males as stars, mature females as squares, immature males as triangles, and immature females as circles. Seasons are represented by colors with winter as blue, spring as green, and pink as fall.

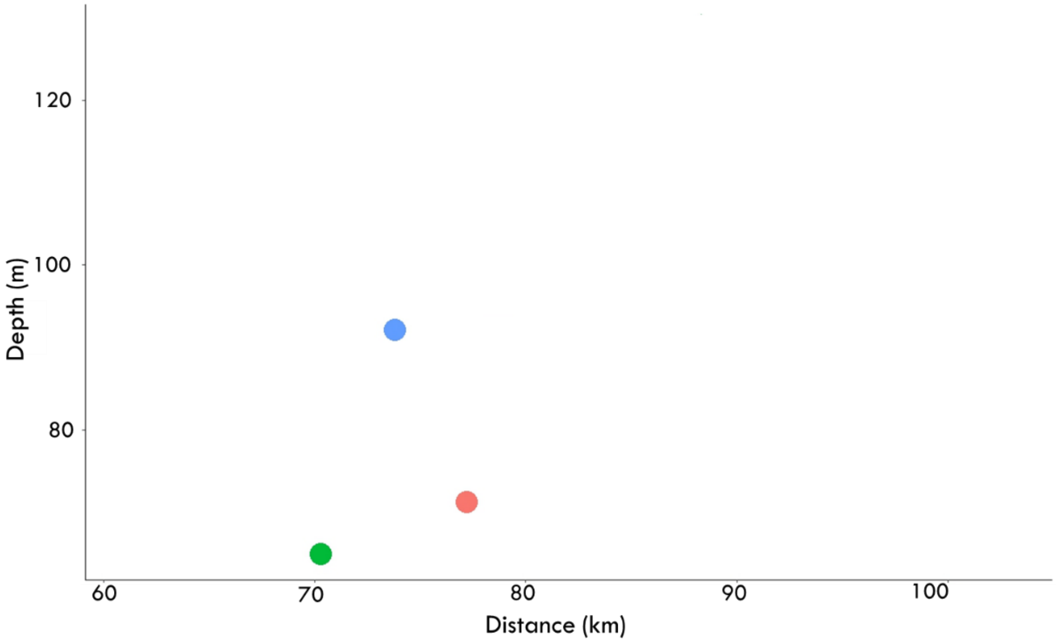

Figure A2.19: Seasonal differences in average distance from shore (km) and depth (m) for immature female Jonah crabs in the Mid-Atlantic Bight from the best ANOVAs. Seasons are represented by colors with winter as blue, spring as green, and pink as fall.

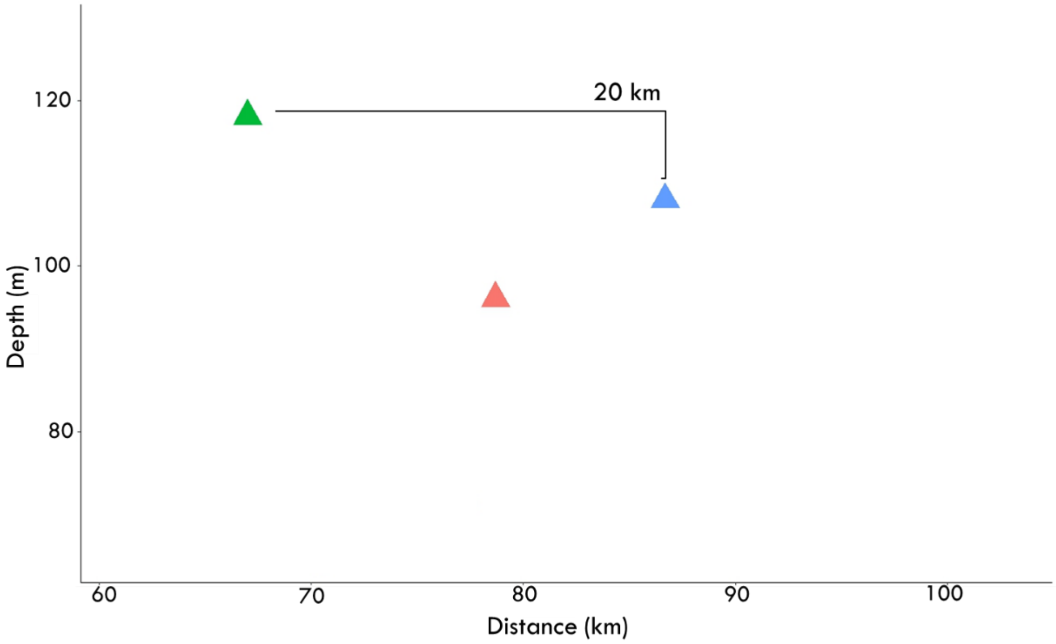

Figure A2.20: Seasonal differences in average distance from shore (km) and depth (m) for immature male Jonah crabs in the Mid-Atlantic Bight from the best ANOVAs. Seasons are represented by colors with winter as blue, spring as green, and pink as fall. Black lines represent differences between two seasonal averages that do not have overlapping confidence intervals.

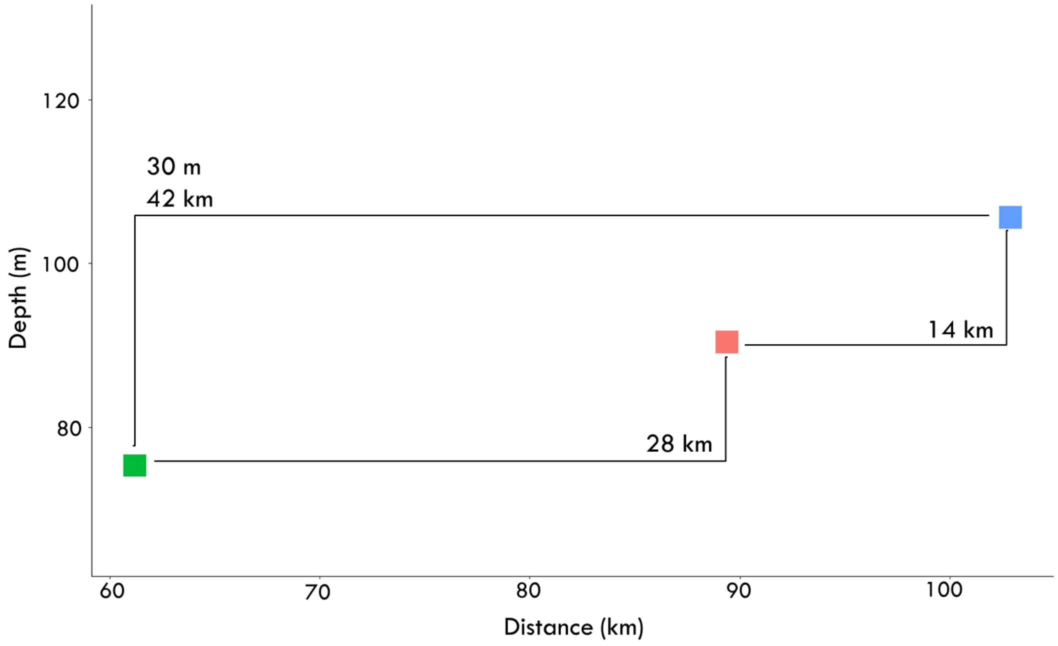

Figure A2.21: Seasonal differences in average distance from shore (km) and depth (m) for mature female Jonah crabs in the Mid-Atlantic Bight from the best ANOVAs. Seasons are represented by colors with winter as blue, spring as green, and pink as fall. Black lines represent differences between two seasonal averages that do not have overlapping confidence intervals.

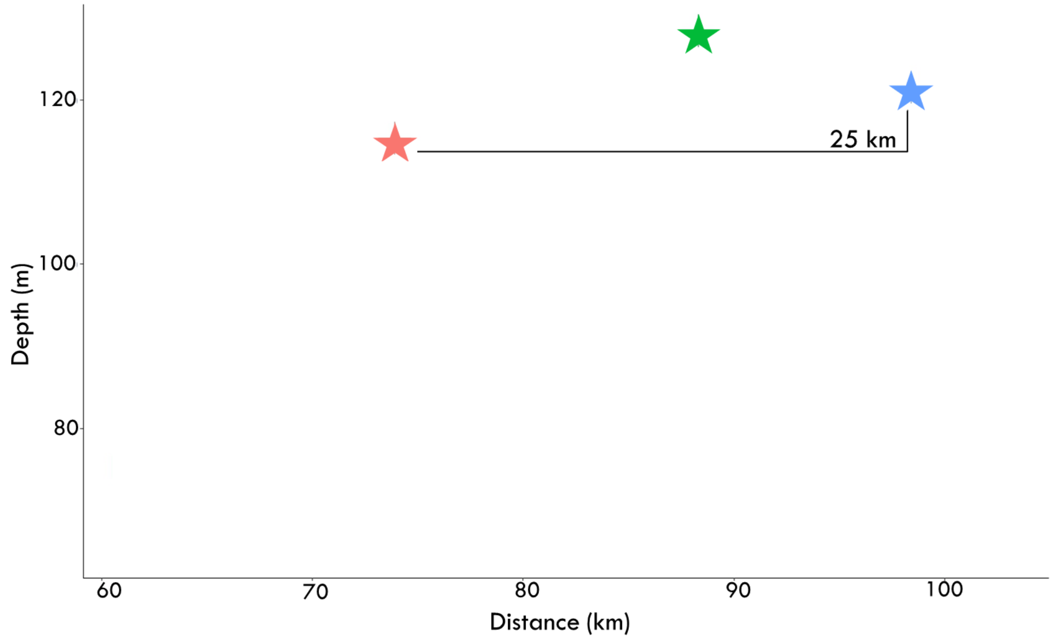

Figure A2.22: Seasonal differences in average distance from shore (km) and depth (m) for mature male Jonah crabs in the Mid-Atlantic Bight from the best ANOVAs. Seasons are represented by colors with winter as blue, spring as green, and pink as fall. Black lines represent differences between two seasonal averages that do not have overlapping confidence intervals.

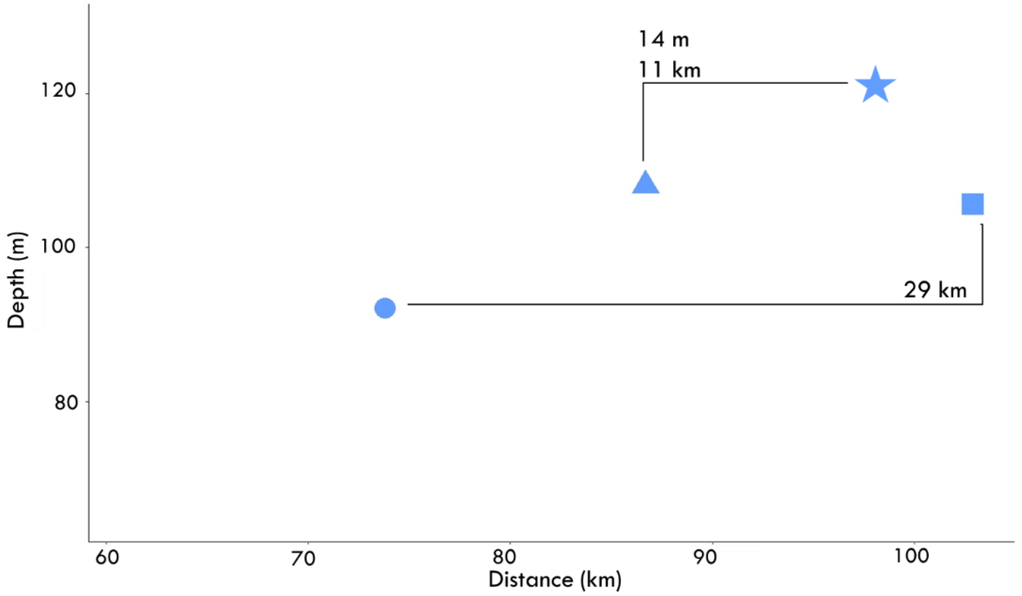

Figure A2.23: Seasonal differences in average distance from shore (km) and depth (m) for Jonah crabs in the Mid-Atlantic Bight from the best ANOVAs. Each group is represented by a different symbol with mature males as stars, mature females as squares, immature males as triangles, and immature females as circles. Seasons are represented by colors with winter as blue. Black lines represent differences between mature and immature winter averages that do not have overlapping confidence intervals.

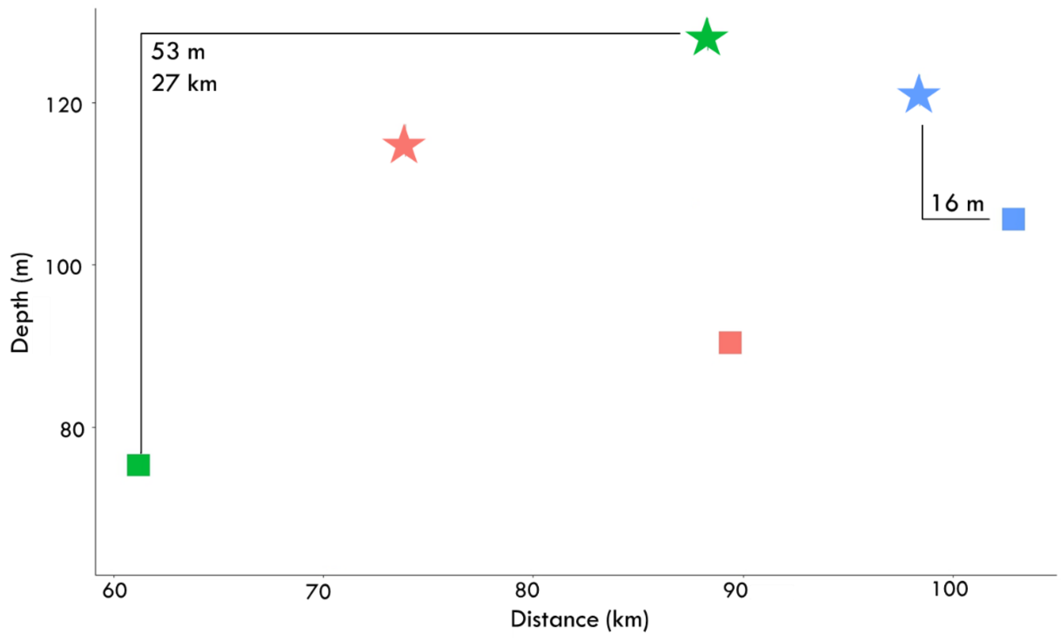

Figure A2.24: Seasonal differences in average distance from shore (km) and depth (m) for Jonah crabs in the Mid-Atlantic Bight from the best ANOVAs. Each group is represented by a different symbol with mature males as stars and mature females as squares. Seasons are represented by colors with winter as blue, spring as green, and fall as pink. Black lines represent differences between male and female averages that do not have overlapping confidence intervals.

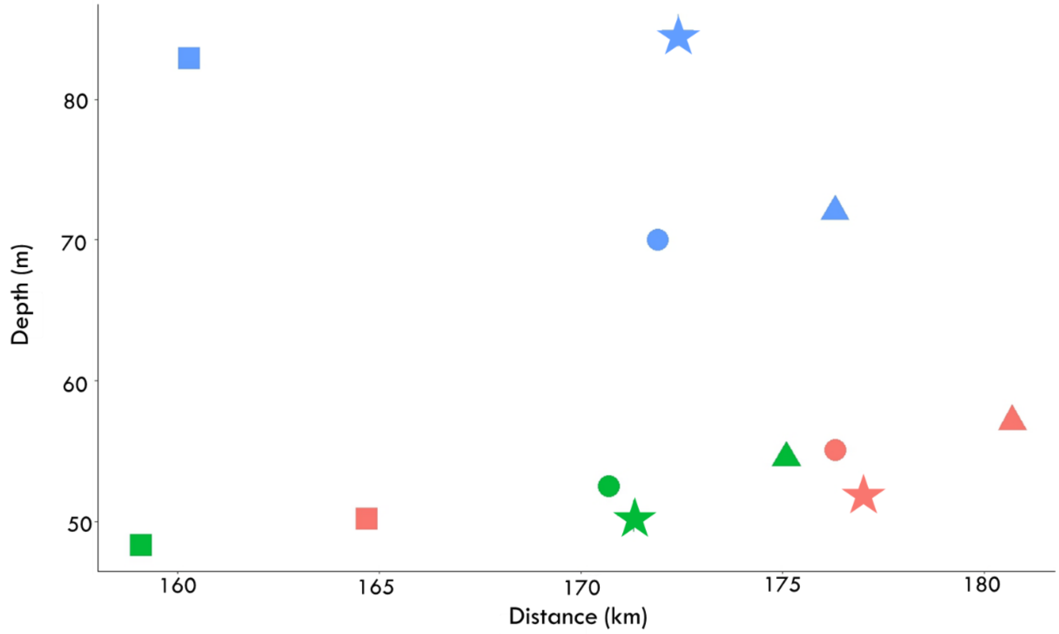

Figure A2.25: Seasonal differences in average distance from shore (km) and depth (m) for Atlantic rock crabs in Georges Bank from the best ANOVAs. Each group is represented by a different symbol with mature males as stars, mature females as squares, immature males as triangles, and immature females as circles. Seasons are represented by colors with winter as blue, spring as green, and pink as fall.

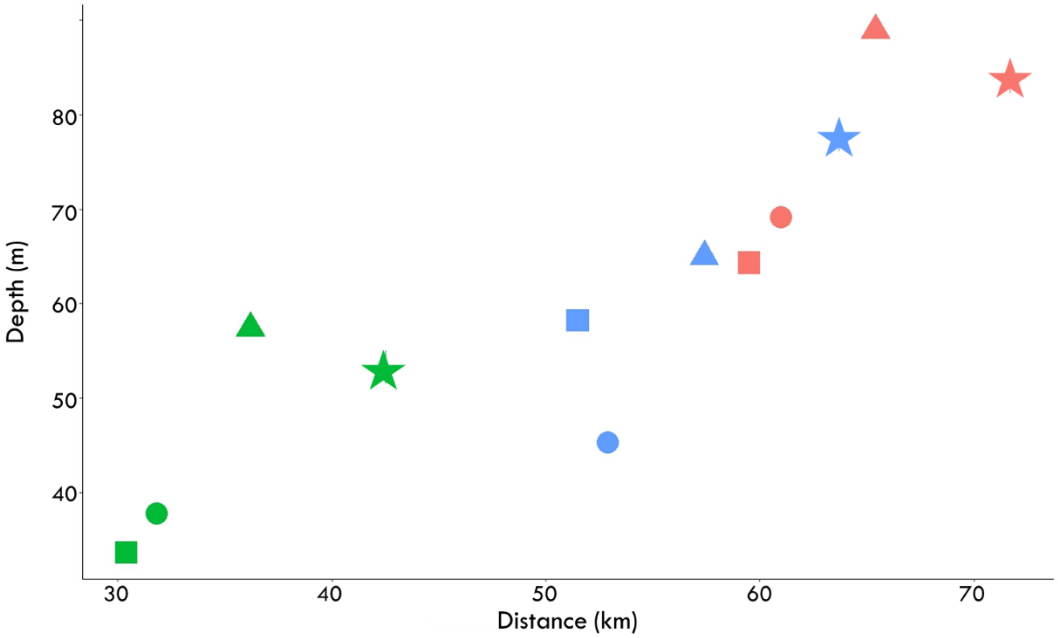

Figure A2.26: Seasonal differences in average distance from shore (km) and depth (m) for Atlantic rock crabs in the Mid-Atlantic Bight from the best ANOVAs. Each group is represented by a different symbol with mature males as stars, mature females as squares, immature males as triangles, and immature females as circles. Seasons are represented by colors with winter as blue, spring as green, and pink as fall.

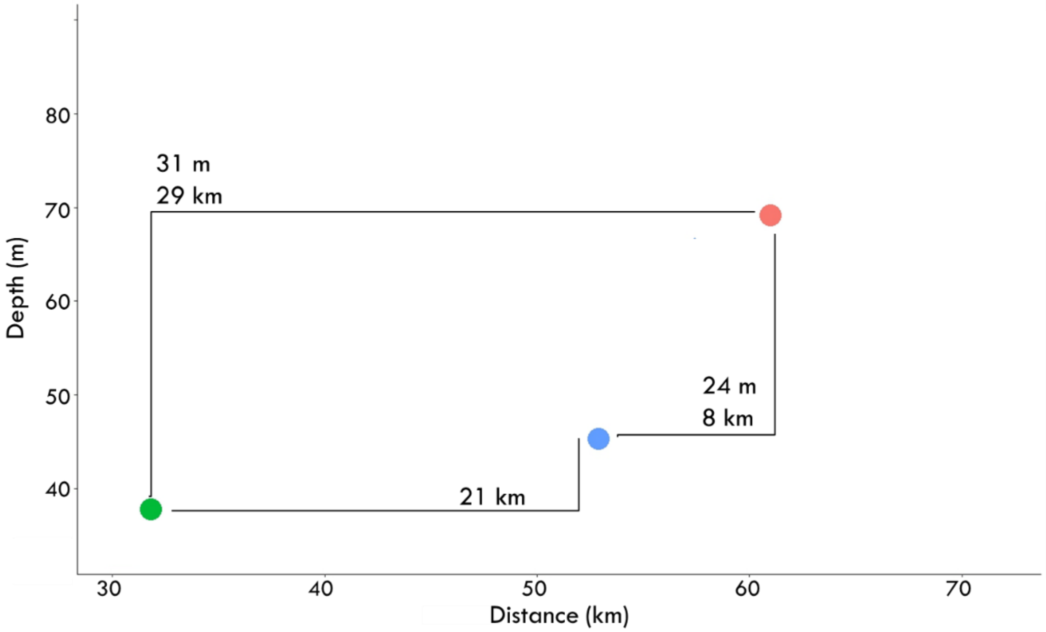

Figure A2.27: Seasonal differences in average distance from shore (km) and depth (m) for immature female Atlantic rock crabs in the Mid-Atlantic Bight from the best ANOVAs. Seasons are represented by colors with winter as blue, spring as green, and pink as fall. Black lines represent differences between two seasonal averages that do not have overlapping confidence intervals.

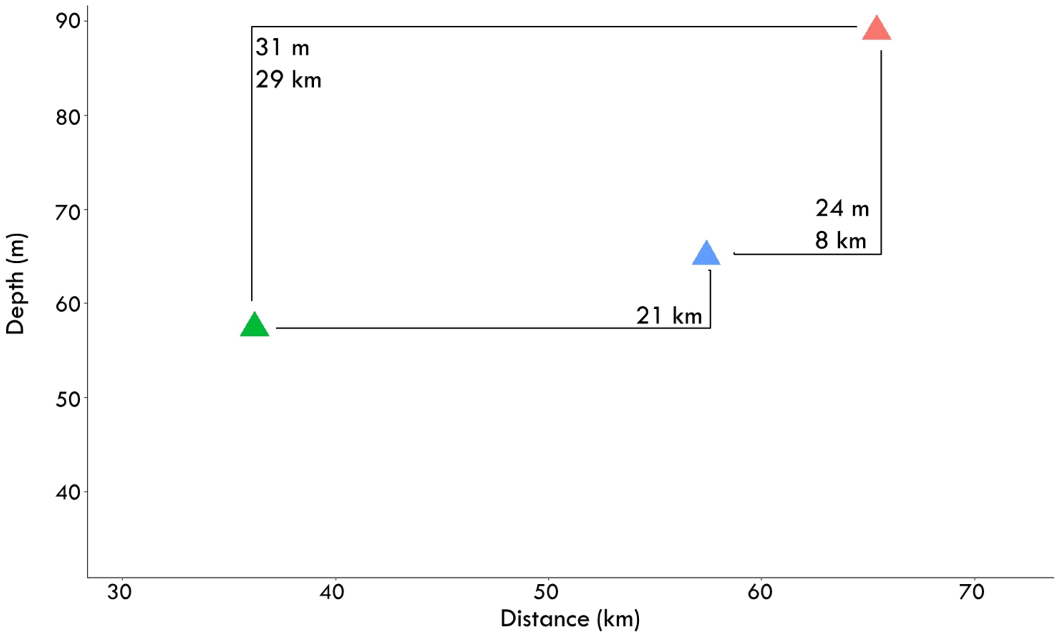

Figure A2.28: Seasonal differences in average distance from shore (km) and depth (m) for immature male Atlantic rock crabs in the Mid-Atlantic Bight from the best ANOVAs. Seasons are represented by colors with winter as blue, spring as green, and pink as fall. Black lines represent differences between two seasonal averages that do not have overlapping confidence intervals.

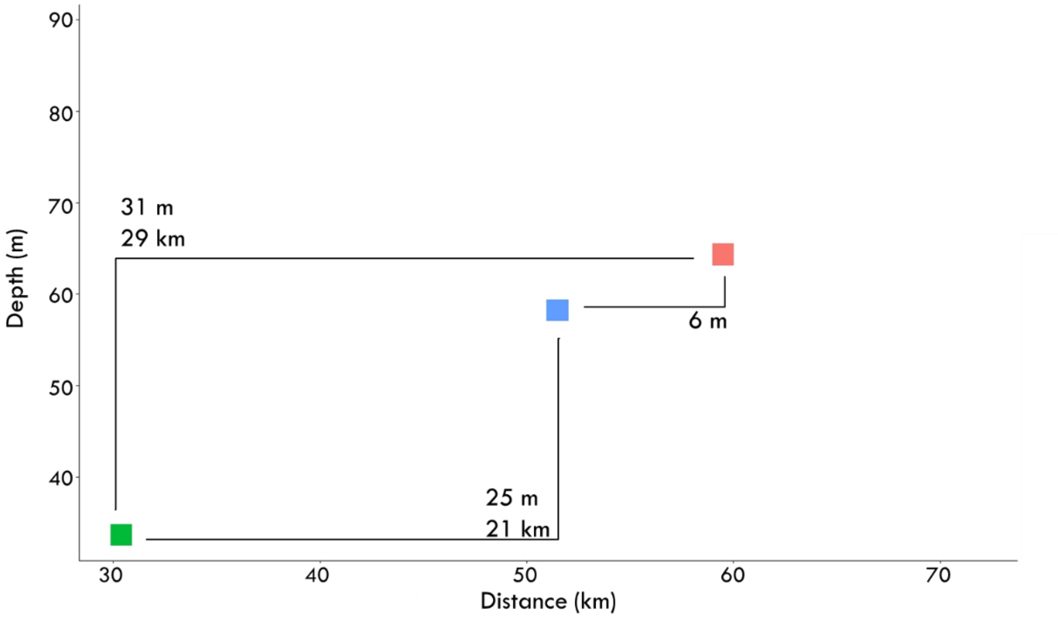

Figure A2.29: Seasonal differences in average distance from shore (km) and depth (m) for mature female Atlantic rock crabs in the Mid-Atlantic Bight from the best ANOVAs. Seasons are represented by colors with winter as blue, spring as green, and pink as fall. Black lines represent differences between two seasonal averages that do not have overlapping confidence intervals.

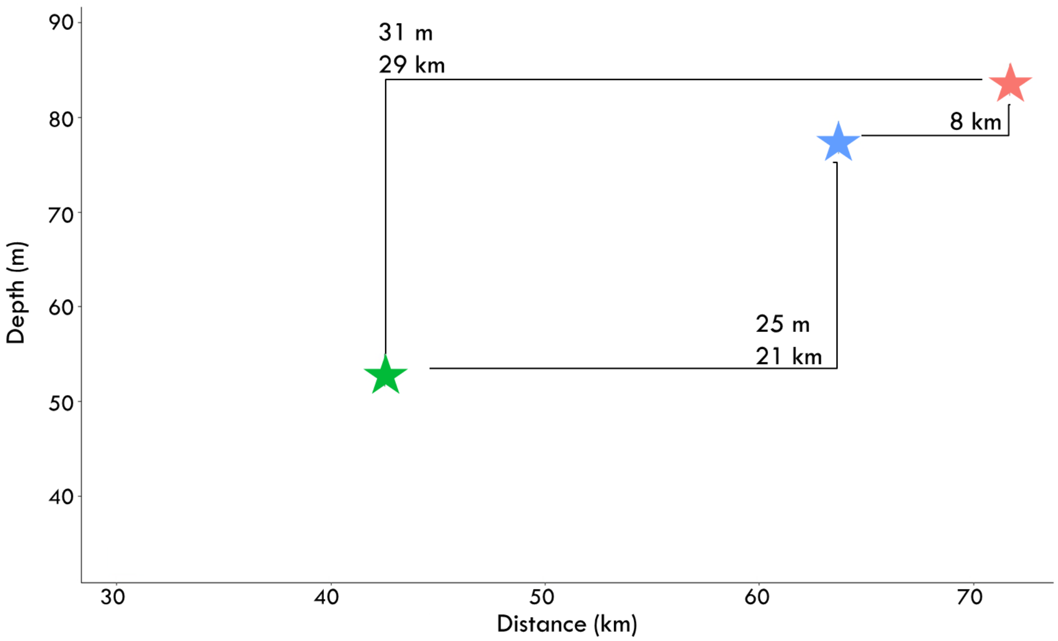

Figure A2.30: Seasonal differences in average distance from shore (km) and depth (m) for mature male Atlantic rock crabs in the Mid-Atlantic Bight from the best ANOVAs. Seasons are represented by colors with winter as blue, spring as green, and pink as fall. Black lines represent differences between two seasonal averages that do not have overlapping confidence intervals.

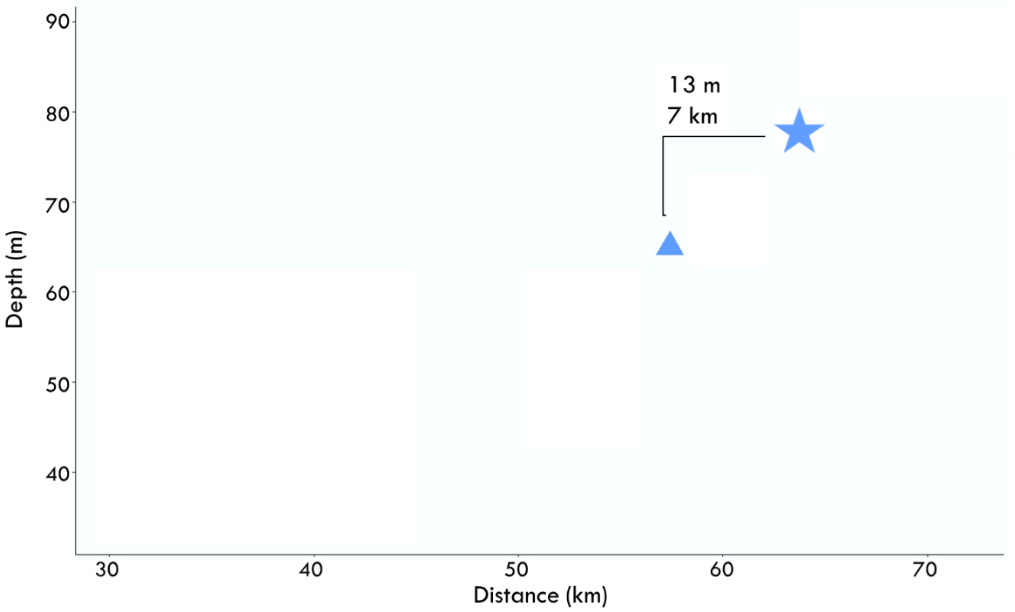

Figure A2.31: Seasonal differences in average distance from shore (km) and depth (m) for Atlantic rock crabs in the Mid-Atlantic Bight from the best ANOVAs. Each group is represented by a different symbol with mature males as stars and immature males as triangles. Seasons are represented by colors with winter as blue. Black lines represent differences between mature and immature winter averages that do not have overlapping confidence intervals.

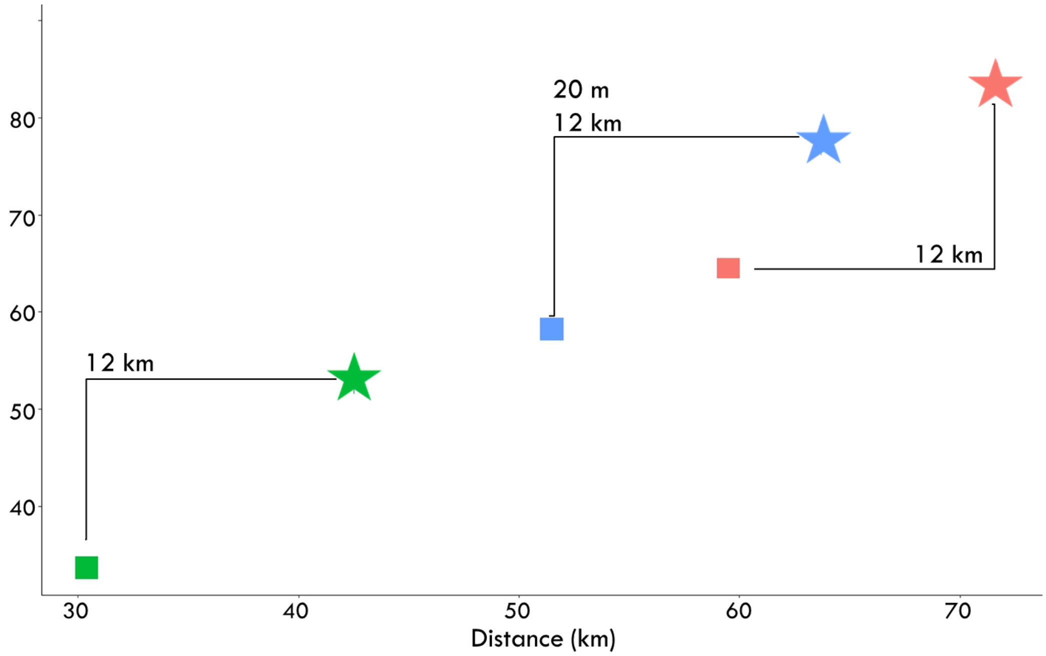

Figure A2.32: Seasonal differences in average distance from shore (km) and depth (m) for Atlantic rock crabs in the Mid-Atlantic Bight from the best ANOVAs. Each group is represented by a different symbol with mature males as stars and mature females as squares. Seasons are represented by colors with winter as blue, spring as green, and fall as pink. Black lines represent differences between mature and immature winter averages that do not have overlapping confidence intervals.

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