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Multi-Decadal Changes In Blue Crab Reproductive Ecology

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Multi-Decadal Changes in Blue Crab Reproductive Ecology

A Dissertation

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In Partial Fulfillment

of the Requirements for the Degree of

Doctor of Philosophy

by

Alexandra K. Schneider

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This dissertation is submitted in partial fulfillment of

the requirements for the degree of

Doctor of Philosophy

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To the Schneiders, for inciting and cultivating my love of the ocean.

Table of Contents

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List of Tables

CHAPTER 1:

CHAPTER 2:

CHAPTER 3:

CHAPTER 4:

List of Figures

CHAPTER 1:

CHAPTER 2:

CHAPTER 3:

CHAPTER 4:

Abstract

Commercial fisheries rely on resource managers to develop and enact fishing regulations that prevent stocks from collapsing. In Chesapeake Bay, the goal for blue crab management is to protect the spawning stock to encourage high levels of egg production and thus juvenile recruitment. Management actions to increase female abundance were implemented in the early 2000s, culminating in 2008, in response to an 84% decline in blue crab spawning stock biomass from 1992 to 2000. Blue crabs are the most valuable fishery in Chesapeake Bay and their decline necessitated severe management actions: the historic spawning sanctuary was expanded, the commercial winter dredge fishery was closed, and the exploitation of female crabs was reduced. The status of this fishery is assessed annually using wintertime spawning stock abundance; however, little research has been done to evaluate the reproductive potential or dynamics of females, especially since 2008. Moreover, blue crab reproductive potential is subject to change with shifts in water temperature, exploitation, and individual characteristics. The primary goal of this dissertation was to holistically evaluate blue crab reproductive ecology in Chesapeake Bay over four decades of environmental and management changes, using a combination of novel biomarkers, fishery-independent data from long-term surveys, field sampling, and lab processing. Each chapter is a separate research question; however, all chapters have interrelated conclusions on the reproductive ecology of blue crabs and inform the female-centric management framework in Chesapeake Bay. Chapter 1 compares the proportion of second-year spawners among years with varying exploitation rates in the spawning grounds during winter, prior to the start of the next spawning season. The chapter also includes models of the probability an individual is a second-year spawner based on individual characteristics. Chapter 2 determines if the observed and potential blue crab spawning season are expanding in association with climate change. Chapter 3 estimates batch fecundity relative to historic estimates, as well as individual size, spawning history, and time of year. Chapter 3 also quantifies and models individual quantities of stored sperm, and is the first study to estimate blue crab brood production using paired fecundity and stored sperm quantity data. Last, Chapter 4 assesses the relative abundance of mature females during spawning and evaluates trends in mean size at maturity over time. Chapter four also explores the impact of changes in abundance and size on total egg production using size-specific fecundity. The results of this research indicate that primiparous blue crabs have a high capacity for reproduction, and females in spring, who are more likely to be primiparous, are becoming more vulnerable to fishing mortality with climate change. Since management actions were implemented, exploitation has been reduced and the proportion of second-year spawners, relative abundance, mean size at maturity, and total egg production of the population have improved; however, improvements are marginal or remain below pre-decline levels (i.e., prior to 1992). Moreover, dramatic variability in these metrics highlights the need for more precautionary fishery management. Specifically, the results suggest that conservation of female blue crabs may be improved if the spawning sanctuary is closed to commercial fishing earlier in the year, in accordance with warming, and female exploitation is reduced in spring.

Author's Note

The chapters within this dissertation were written with the intention to submit each as a peer-reviewed scientific paper. Therefore, each chapter is formatted to the specific guidelines of the target journal, including citation and reporting styles. The stand-alone nature of each chapter has resulted in some redundancy between the introductions of each chapter. Moreover, each chapter has a separate acknowledgement section to highlight the specific contributions of personnel per chapter. Plural pronouns are used to convey the view and contribution of multiple authors. Author details and journal details are included on the title page of each chapter and as follows:

Chapter 1: Schneider, A.K., Fabrizio, M.C., Lipcius, R.N., 2023. Reproductive potential of the blue crab spawning stock across eras and exploitation rates using nemertean worm biomarkers. Marine Ecology Progress Series. 716: 77 – 91.

Chapter 2: Schneider, A.K., Fabrizio, M.C., Lipcius, R.N., 2024. Reproductive phenology of the Chesapeake Bay blue crab population in a changing climate. Frontiers in Ecology and Evolution. 11:1304021.

Chapter 3: Schneider, A.K., Shields, J.D., Fabrizio, M.C., Lipcius, R.N., 2024. Spawning history, fecundity, and potential sperm limitation of female blue crabs in Chesapeake Bay. *In review* at Fisheries Research.

Chapter 4: Schneider, A.K., Fabrizio, M.C., Lipcius, R.N., Long-term trends in female blue crab abundance and size: Consequences for total egg production and fishery stability. *In prep* for ICES Journal of Marine Science.

Multi-Decadal Changes in Blue Crab Reproductive Ecology

CHAPTER 1: Reproductive potential of the blue crab spawning stock in Chesapeake Bay across eras and exploitation rates using nemertean worms as biomarkers

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Abstract

Assessments of reproductive potential and spawning history of marine and estuarine crabs are limited due to issues with determination of age and spawning history. The spawning stock of the blue crab, *Callinectes sapidus*, in Chesapeake Bay was heavily fished and declined in the 1990s. Management actions were implemented between 2001 and 2008 to reduce spawning stock exploitation and trigger recovery. Whether these actions impacted the demography of female spawners is unknown. We assessed demographics of overwintering mature female crabs in 1992-1996 and 2020-2022 by classifying them as first-year (imminent primiparous) or second-year (primiparous and multiparous) spawners based on presence of mature nemertean worms, *Carcinonemertes carcinophila*, in their gill chambers. We also investigated organismal and environmental predictors of second-year spawners. We provide the first annual estimates of the proportion of multi-year spawners at the population level. Management actions reduced exploitation rates by 41% after 2008, and the proportion of second-year spawners was greater than in the 1990s. Nonetheless, exploitation rate in a given year did not predict proportion of second-year spawners in the following year. Second-year spawners tended to be smaller females, or females with a high gonadosomatic index or longevity indicators (i.e., fouling by barnacles). High proportions of large, highly fecund, overwintering first-year spawners in the 2020s support the need for enhanced protection of females in spring to allow these females to spawn. Finally, nemertean worms are a useful, easily implemented tool to determine spawning history and age-specific reproductive potential of crabs that undergo a terminal molt prior to spawning.

Keywords: Reproduction, Decapoda, symbionts, multiparous, primiparous, Carcinonemertes,

1. Introduction

Estimates of reproductive potential over a lifespan are crucial for the development of effective conservation and management of exploited marine species. Finfish have a well-documented increase in reproductive potential with age and size (Hixon et al. 2014), which allows for protection of larger, older, highly fecund individuals via targeted management actions (Gwinn et al. 2015). Moreover, the accuracy of stock-recruit relationships, which are integral to many stock assessments, can be improved by incorporating the relationship between age and fecundity, a feature that can be assessed with many finfish (Shelton et al. 2012).

Decapod crustaceans comprise a major component of the world's commercial fisheries landings, but assessments of reproductive potential over an individual's lifespan are limited due to problems with determination of age and spawning history. Direct estimates of age using hard parts is not possible because decapods shed their exoskeletons during molting. Efforts to age crustaceans using lipofuscin concentrations (Ju et al. 1999) and gastric mill ossicles (Gnanalingam et al. 2019) are resource intensive and require further validation (Crowley et al. 2014, Becker et al. 2018, Gnanalingam et al. 2019). Moreover, variability in growth per molt, inter-molt period, and the length of the growing season further limit accurate assessments of size and age relationships for crustaceans (Vogt 2012). Alternative approaches to classify spawning history include carapace condition (Somerton & Meyers 1983), presence and coloration of ejaculate within sperm storage organs (i.e., sermathecae, Duluc et al. 2005), presence of egg remnants on pleopods (Churchill 1919), and lab or field experiments examining brood production (Dickinson et al. 2006, Stevens & Swiney 2007, Darnell et al. 2009).

Unfortunately, these methods are subjective (e.g., carapace condition), species specific (e.g., ejaculate coloration), temporally sensitive (e.g., egg remnants), and resource intensive (e.g., mesocosm experiments). An underused and potentially robust approach to assessing spawning history for crustaceans with a terminal molt is the presence of egg predators.

Nemertean worms in the genus Carcinonemertes are egg predators on several decapods, including Alaskan king crabs (Wickham 1986), Dungeness crabs (Wickham 1979), and American lobsters (Aiken et al. 1985). Nemerteans can consume significant numbers of eggs (Roe 1984) and have been linked to brood failure and commercial fishery depletion or collapse in Dungeness crab and red king crab (Wickham 1979, Kuris & Wickham 1987, Kuris et al. 1991, Shields 2012), but the impact on blue crab reproductive potential is unresolved.

The free-swimming larvae of nemertean worms seek female hosts and live in their host's gill cavities or on their carapace as juveniles; *Carcinonemertes carcinophila* feeds on the eggs of blue crabs and other portunid decapods (Humes 1942, Messick 1998, Dickinson et al. 2006). When a female blue crab oviposits her brood, the white, inconspicuous juvenile worms migrate to the brood, feed on eggs, mature, and reproduce (Humes 1942). Upon maturation the worms become a distinct pink or red color (Humes 1942). After the host's eggs hatch, the mature worms return to the gills, where they likely remain until the next batch of eggs is extruded, similarly to *C. carcinophila* in other species of *Callinectes* (Santos & Bueno 2001). Hence, mature worms may be used as indicators of spawning history (Hopkins 1947, Graham et al. 2012) and thus may be useful in assessing the spawning history of the blue crab.

The blue crab supports economically important fisheries along the Atlantic and Gulf coasts of the U.S. where its populations have fluctuated dramatically during the past 30 years, contributing to significant fishery instability (NOAA Fisheries 2022). Across the U.S., blue crab fishery landings declined 25% from 90,265 mt in 2010 to 67,585 mt in 2019 (NOAA Fisheries 2022). In Chesapeake Bay, blue crab landings have followed a similar pattern, experiencing a 28% decline from 38,555 mt in 2010 to 27,669 mt in 2019 (Chesapeake Bay Stock Assessment Committee, 2022; hereafter CBSAC). Blue crab population abundance in Chesapeake Bay declined 81% after 1992 (Lipcius & Stockhausen 2002), rebounded after 2008, and have been low but variable since 2012 (CBSAC 2022)In 2022, blue crab population abundance in the Bay was the lowest on record, and spawning stock abundance has declined since 2017 (CBSAC 2022). The recurrent low abundances in the spawning stock suggest that the efficacy of current management regulations may be limited by an incomplete understanding of the factors affecting the productivity of the blue crab stock in Chesapeake Bay.

From 1990 to 2007, adult female blue crabs in Chesapeake Bay were disproportionately exploited compared with adult males. For instance, from 1994 to 2004, the average annual female exploitation rate was 36%, whereas the average male exploitation rate was 24% (CBSAC 2022). High exploitation of female crabs, coupled with low abundance, prompted resource managers to institute regulations to protect the spawning stock. In particular, the historical blue crab spawning sanctuary in Chesapeake Bay was expanded from 37,814 ha to 240,092 ha in the early 2000s (Lipcius et al. 2001, 2003a, Seitz et al. 2001, Lambert et al. 2006b), and stricter catch restrictions were imposed in 2008 and 2009 (Miller et al. 2011). The target female exploitation rate was lowered to 22.5% and the commercial winter dredge fishery, which preferentially exploited mature females, was closed in 2008 (Miller et al. 2011). During years with a smaller spawning sanctuary and an active winter dredge fishery, high rates of fishery removals of females likely decreased the life span of female blue crabs and therefore decreased the population productivity in Chesapeake Bay. Productivity may decrease through removals of second-year spawners who have not yet reproduced to their full capacity of several broods and by removing first-year spawners who have not yet reproduced at all. Overwintering second-year spawners are entering their second spawning season and include primiparous females, crabs that have spawned once, and multiparous females, crabs that have spawned at least two times (herein, second-year spawners = primiparous and multiparous females). Overwintering first-year spawners are entering their first year of spawning and are imminent primiparous crabs (herein, first-year spawners = imminent primiparous females)

Female blue crabs have a complex reproductive strategy. They have one opportunity to mate during their terminal molt to maturity (Jivoff et al. 2007), which occurs from May through September (Van Engel 1958) in low- and mid-salinity areas of Chesapeake Bay. Females store the sperm of the male in two spermathecae and use stored sperm to inseminate future egg masses (Jivoff et al. 2007). After mating, females migrate to high-salinity zones in the lower Bay, where conditions are conducive to embryogenesis and larval survival (Sandoz & Rogers 1944). Once on the Chesapeake Bay spawning grounds, females may produce one to three egg masses per spawning season (Hines et al. 2003). Females that mate in the upper Bay must migrate long distances, up to 215 km, to high-salinity spawning grounds. Thus, compared with females that mate in the lower Bay, females that mate in the upper Bay arrive at the spawning grounds later in the year (Aguilar et al. 2005). Additionally, females that mate in the lower Bay migrate soon after mating from May to August (Van Engel 1958), whereas females that mate in the upper Bay begin migrating in October, regardless of when mating occurred (Turner et al. 2003, Aguilar et al. 2005) and, thus, arrive after the spawning season. Therefore, females from the upper Bay and females from the lower bay who mate in late summer or early fall do not spawn until the year after mating and migration, whereas females from the lower Bay who mated in spring and early summer may spawn in the same year.

Consequently, females that overwinter on the spawning grounds comprise a wide range of spawning histories, including those that will spawn for the first time and those that have spawned at least one brood. These two classes of females likely contribute unequally to the future reproductive potential of the population, yet neither their composition nor the predictors of first- and second-year spawners on the spawning grounds has been investigated at the population level for any blue crab population and only rarely for any crab species. We emphasize “at the population level” because other studies have characterized features of multiple spawning in the blue crab, including the use of nemertean worms (Coe 1902, Humes 1942, Hopkins 1947, Van Engel 1958, Davis 1965, Graham et al. 2012, Kemberling & Darnell 2020), but none have been done at the population level, which benefits stock assessment.

Organismal and environmental factors related to the spawning history of a female have not been investigated at the individual level. Organismal factors such as carapace width (CW, measured from lateral spine to lateral spine), gonadosomatic index (GSI), size of fouling barnacles, carapace condition and spermatheca weight, as well as environmental factors such as salinity and location, are directly or indirectly related to female blue crab reproduction and longevity. For example, the size of adult female blue crabs remains constant after their terminal molt to maturity, and although the size of the female does not directly indicate spawning history, mature size may have an indirect effect on the likelihood of being a second-year spawner. Larger females are preferred by crabbers and therefore, larger females may be more likely to be removed from the population than smaller crabs. At high exploitation rates, larger crabs may experience a higher fishing mortality rate than smaller crabs and therefore larger crabs may be less likely to become second-year spawners. For example, size at maturity of female blue crabs decreases in years with high fishing rates in part due to the culling of large crabs (Lipcius & Stockhausen 2002). Furthermore, crab size and reproductive potential are related, with large crabs producing larger egg masses (Hines 1982, Prager et al. 1990). Therefore, a relationship between crab size and spawning year may reflect individual reproductive potential. In addition, the GSI, the ratio of ovary weight to body weight, can be a proxy for the amount of energy allocated to reproduction. With maximum potential clutch size defined by the volume of ovary due to the blue crab's determinate reproduction (Hines 1982, Darnell et al. 2009), GSI may reflect spawning history, and females with smaller relative ovary size may have more recently spawned and not yet rebuilt their full ovarian capacity.

Size of fouling organisms, carapace condition, and spermatheca weight are associated with a female's longevity and thus her spawning potential. Barnacle size correlates with barnacle age (Key et al. 1997, Ewers-Saucedo et al. 2015), such that the age of the largest barnacle on a female's carapace represents the minimum possible age of a mature female's carapace (Ogburn et al. 2019). Carapace condition has been used as a proxy for female age or spawning history under the assumption that as time passes, a female's carapace will become fouled and discolored (Somerton & Meyers 1983, Sainte-Marie 1993, Ogburn et al. 2014, 2019).

Female blue crabs store the sperm of their mate in spermathecae (Hard 1942). As time progresses after mating, the seminal fluid dissipates and the quantity of stored sperm decreases in the spermathecae (Wolcott et al. 2005). Sperm quantity is further depleted after egg fertilization. Sperm quantity is related to spermatheca weight (Ogburn et al. 2019), whereby the weight of a spermatheca may indicate the amount of time that has passed since mating or if a female has reproduced. Consequently, females with smaller and lighter spermathecae would have less sperm stored and would be more likely to be second-year spawners.

In addition to organismal factors, environmental factors such as salinity or location in the Bay may indicate a female's spawning history. Once females migrate towards higher salinities for spawning, they generally do not return to the upper Bay or to its lower-salinity tributaries (Lambert et al. 2006b). Thus, a higher proportion of second-year spawners may be found closer to the Bay mouth, in high-salinity areas.

In this study, we tested hypotheses related to the contributions of first- and second-year spawners to the spawning stock during years with high female fishing pressure (i.e., the 1990s) and years with lower fishing pressure when stricter female management measures were in place (i.e., years after 2008), herein referred to as pre- and post-management eras. We used the presence of the nemertean egg predator *C. carcinophila* in the gills to classify mature female blue crabs as first- or second-year spawners, with the ultimate objective to identify (1) differences in the proportion of overwintering second-year spawners across years and variable female exploitation rates; and (2) the influence of environmental and individual-level factors on the proportion of second-year spawners that overwinter on the spawning grounds.

2. Methods

2.1. Sample collection

Blue crabs were collected by the Winter Dredge Survey (WDS), a long-term monitoring program for Chesapeake Bay blue crabs that samples between December and March each winter; Sharov et al. (2003) and CBSAC (2022) provide full details of survey design and methodology. For this study, we used sampling stations south of 37.4 °N (Fig. 1), hereafter referred to as the lower Bay, which encompasses most of the blue crab spawning grounds and is characterized by high abundance of ovigerous crabs during the spawning season (Lipcius et al. 2003a, b). During winter, this region also harbors mature females that will likely spawn the following summer (Sharov et al. 2003). All live, mature females, classified by abdomen shape (Van Engel 1958), and collected by the WDS during two time periods (1992-1996 and 2020-2022), were measured on board for carapace width (CW) to the nearest 0.1 mm. Females were classified as first- or second-year spawners using the presence of the nemertean worm *C. carcinophila* in the gills, an approach that has been used and validated (Coe 1902, Humes 1942, Hopkins 1947, Van Engel 1958, Davis 1965, Graham et al. 2012, Kemberling & Darnell 2020). Females with mature (vibrant pink or red) worms within the gills were classified as second-year spawners, whereas those with immature (white, inconspicuous) worms within the gills, or without worms, were classified as first-year spawners. These designations based on color and location of worms are up to 97% accurate (Hopkins 1947). Further sample processing varied by year due to changes in WDS protocol and is described below.

2.2. Blue crab characteristics

In a subset of years (due to methodological changes in WDS protocol, years include 1992, 1993, 2020, and 2021), GSI was calculated as ovary weight divided by total weight. Crabs were weighed to the nearest 0.01 g wet weight, after which ovaries were removed, staged as immature, developing, or developed (see section 2.5 for details), and weighed to the nearest 0.001 g wet weight. In 1992 and 1993, about 30% of females had ovary weight measurements but no body weight measurements. We estimated these missing weight data using a nonlinear least-squares regression with crab weight as a function of CW: Weight = $a(CW^b)$. To reflect natural variation of blue crab weight at size, a normal distribution parameterized with the standard deviation of the model residuals was created, sampled at random, and these residuals were added to the modeled weight estimates (see Section S1, Fig. S1, and Table S1 in the Supplement).

In 2020 and 2021, carapace condition and the presence of fouling organisms, i.e., barnacles, were also recorded. Acorn barnacles, *Chelonibia spp.*, were enumerated, and the largest was measured. Spermathecae were removed and weighed to the nearest 0.001 g. Carapace condition was assessed as clean (pearly white), partially dirty (light yellow to light brown discoloration), or dirty (dark brown or black coloration) based on a female's abdomen coloration.

2.3. Proportion of second-year spawners and exploitation rates

The relationship between the proportion of second-year spawners in a given year and the overall exploitation rate during the previous year was described with a linear model, with the hypothesis that years with low exploitation rates would be associated with a high proportion of second-year spawners in the following year. We excluded 1992 and 1993 from the analysis of exploitation and proportion because exploitation rates for those years were unreliable. Survey methods were not fully standardized until 1994 and these were years of high female abundance, prior to spawning stock biomass decline in 1994 and therefore were not reflective of the spawning stock status during the population decline (CBSAC 2022). The proportion of second-year spawners in 1992 and 1993 (Fig. 1 and Section S2 in supplement) and crabs captured in 1992 and 1993 were included in models of individual spawning history (see section 2.6).

The annual proportion of second-year spawners was estimated as the number of females with mature nemerteans in the gills divided by the total number of females examined in a given sampling year. The standard error was estimated by: $(p \times (1-p))/n^{0.5}$, where p is the proportion of the population infected with mature nemerteans and n is the total number of blue crabs examined (Fleiss et al. 2003). Annual female exploitation rates were retrieved from the Chesapeake Bay Stock Assessment Committee's annual report (G. Davis, pers. comm.) for 1993-1995 and 2019-2021. These exploitation rates are relevant for the crabs sampled by the WDS during 1994-1996 and 2020-2022 because a WDS year refers to sampling conducted during the first part of winter in year t-1 through the end of winter in year t, such that the relevant year of exploitation rates is year t-1. For example, crabs sampled in 2022 were sampled December 2021 through March 2022, and thus, the relevant annual exploitation rate is the rate estimated for 2021.

2.4. Probability of second-year spawners in two eras

Generalized linear models (GLMs) were used to model the relationship between eras, i.e., pre- (1994 to 1996) and post-management (2020 to 2022) years, and the probability of a mature female being a second-year spawner using the logit link for modeling the probabilities of binary outcomes. The odds ratio was used to assess the probability of observing a second-year spawner in the post-management era. Other potential predictors of spawning year such as carapace width were excluded from this analysis because the effects of regulations and exploitation may have also affected such predictors. For example, blue crab CW is inversely related to exploitation rate (Lipcius & Stockhausen 2002). Moreover, GSI was not available for 1994 to 1996.

2.5. Probability of second-year spawners as a function of individual condition

GLMs were used to model the relationship between individual characteristics and the probability of a mature female being a second-year spawner using the logit link for modeling the probabilities of binary outcomes. Independent predictors included GSI, CW, salinity, year, distance from the mouth of the Bay, carapace condition, maximum barnacle size, spermathecae wet weight, and the interaction between distance and year (Table 1).

Observations were limited to individuals with a mature ovary, and excluded crabs with immature and undeveloped or exhausted ovaries. Females were considered to have an immature ovary if it was small and inconspicuous and their spermathecae still contained seminal fluid. Females were considered to have an exhausted ovary if it was collapsed, small and dark gray or brown color and their spermathecae only contained sperm packets (i.e., no fluid). In years where ovary stage was not documented (i.e., 1992 and 1993), crabs were considered mature if their ovary wet weight was greater than 2.5 g, regardless of CW (Appendix 3).

Year (1992, 1993, 2020, and 2021) was included as a fixed variable in the GLMs to account for interannual differences, such as yearly abundance and management policies (CBSAC 2022). Distance between each station and the mouth of the Chesapeake Bay was calculated in km as the shortest in-water distance using a least-cost distance algorithm to the location 37°01’04.5” N, 76°02’30.4” W, which we used to designate the mouth of the Bay. An interaction between distance and year was also included because aggregations and distributions of females during winter vary among years (Lipcius et al. 2003b, Jensen & Miller 2005, Saluta 2012). Therefore, we surmised that the locations of first- and second-year spawners varied among years (Fig. 1).

Carapace condition, maximum barnacle size, and spermathecae weight were considered in the GLM of individual spawning year because these factors are associated with the age of the female. If no barnacles were present on a female’s carapace, the barnacle diameter was denoted 0.

2.6. GLM model validation and selection

To allow comparison of effect sizes among predictors, all continuous predictors were standardized by subtracting the mean and dividing by two standard deviations (Gelman 2008, Schielzeth 2010). Two sets of candidate models were evaluated based on covariate data availability (Table 1): two-year models including 2020 and 2021, and four-year models including

1992-1993 and 2020-2021. One female crab from 2020 was removed from the analysis because limb loss reduced its weight well below the expected weight for its CW. Similarly, 21 crabs collected in 2020 were excluded from the two-year model set because their spermathecae weights were not recorded.

All crabs were treated as independent observations (Appendix 4). Models were checked for overdispersion by dividing the Pearson χ^2 by the degrees of freedom, with values greater than 1.0 indicating that the model is overdispersed relative to the assumed distribution (Stroup 2013). Goodness of fit was tested with the Hosmer-Lemeshow test using an α level of 0.05 (Hilbe 2009). The appropriateness of the logit link function was tested visually by assessing the linear relationship between the observed and model-predicted proportions. Due to poor fit with the logit link, the two-year model set was re-tested with a complementary log-log link (Stroup 2013), which improved model fit to a satisfactory level. Collinearity was assessed a priori with Pearson's correlation coefficients and *a posteriori* with variance inflation factors. Potential collinearity between CW and GSI and between salinity and distance to the mouth of the Bay were the primary concern as CW and GSI are both morphological features of an individual, and salinity and distance from the Bay mouth may be correlated, however both correlations were non-significant (Pearson's correlation coefficient, <0.20 between CW and GSI, <0.15 between salinity and distance for all model sets). Variance inflation factors were <4.5 for all models, indicating lack of collinearity amongst predictors (Montgomery & Peck 1992). All analyses were performed using R statistical computing language (R Core Team 2021). Models were cross-validated with 10-fold validation using the cv.glm function in the boot package in R (Davison & Hinkley 1997, Canty & Ripley 2021).

Each model set included a global model in which all predictors were considered. Additional candidate models sequentially excluded carapace condition, salinity, and spermathecae weight. These variables were hypothesized to be of lesser importance because of the subjective nature of assigning carapace condition (Hard 1942), the temporal relevance of a static measure of salinity at the time of sample collection versus dynamic salinity conditions during the spawning season, and the variable relationship between spermathecae weight and sperm count (Ogburn et al. 2014). Within sets, models were evaluated within an information theoretic framework (Burnham & Anderson 2007) to determine which model(s) produced the best description of the data from among the models considered. Akaike's Information Criterion corrected for small sample size (AICc) and weighted model probabilities (w_i) were used to determine the probability that a particular model was the best-fitting model within each set of two-year and four-year models (Anderson 2008).

3. Results

3.1. Annual Exploitation Rates of Female Blue Crabs

Annual exploitation rates (mean ± SE) of female crabs averaged 0.34 ± 0.015 from 1990 to 2007 (Fig. 2) and declined significantly by 41% after 2008 (Tukey test, $p < 0.001$); during 2008 to 2021 annual exploitation rates averaged 0.20 ± 0.017. Among the years during which nemertean worms were assessed, the lowest annual exploitation rates occurred in 2019 (0.14) and 2020 (0.19), and the highest rate occurred in 1994 (0.35; Fig. 2). Exploitation rates averaged 0.31 ± 0.013 from 1993 to 1995, and were 55% greater than those from 2019 to 2021, when annual exploitation rates averaged 0.20 ± 0.06 (Tukey test, $p = 0.051$).

3.2. Proportion of second-year spawners and exploitation rates

We classified 2,855 mature female crabs from 1992 to 1996 and 2020 to 2022 as first- or second-year spawners (Table S2) based on the presence and color of *C. carcinophila* in the gills. For 1994 to 1996 and 2020 to 2022, the proportion (± SE) of second-year spawners was highest in 2020 (0.19 ± 0.040) and lowest in 1996 (0.02 ± 0.007; Fig. 3). The average proportion of second-year spawners during the pre-management years (1994-1996) was 0.056 ± 0.007, whereas the average proportion in the post-management years (2020-2022) was 0.110 ± 0.012, which reflected a 96% increase after management intervention.

The relationship between female exploitation rate and the proportion of second-year spawners (Fig. 3) was negative (slope ± SE: -0.46 ± 0.26). This is consistent with our hypothesis that the proportion is inversely related to exploitation rate, though the regression was highly influenced by observations from 1995 and 2020 (Cook's Distance > 1.0) and we were unable to detect a statistically significant difference between the estimated slope and 0 (linear regression, r2 = 0.44, F = 3.097, p = 0.15), likely due to low sample size.

3.3. Between-era comparison of the probabilities of being a second-year spawner

Average exploitation rates were 55% higher (0.31 vs. 0.20) and the proportions of second-year spawners were 49.9% lower (0.056 vs. 0.11) in the 1990s compared with the 2020s. The model coefficient for the effect of era on the probability of being a second-year spawner was 0.69 ± 0.19 ($p < 0.001$). The odds ratio for era implies that compared with the pre-management era, mature female blue crabs in the post-management era were 2.0 times more likely to be a second-year spawner, although the model explained only 1.5% of the total deviance. Despite this, the 95% confidence interval for the odds ratio indicates that females in the 2020s were 1.38 to 2.89 times more likely to be second-year spawners than females in the 1990s.

3.4. Probability of being a second-year spawner and organismal characteristics

Across both model sets, the top-performing models included similar suites of variables. Within the four-year model set, model C1 had the lowest AICc and a weighted probability of 0.997; this model included CW, salinity, distance from the mouth of the Bay, year, the interaction of year and distance, and GSI as predictors of a female being a second-year spawner (Table 2). Results are not presented for other models due to their low weighted probabilities. The best model in the two-year set was model T4, which had the lowest AICc and a weighted probability of 0.70. Model T4 included CW, year, distance from the mouth of the Bay, GSI, and maximum barnacle size, and the interaction of year and distance (Table 3). Model T3 had a weighted probability of 0.25, and considered the same predictors as model T4, but also included salinity as a predictor. Due to the low ΔAICc between model T3 and T4 (Δ = 2) and the support for including salinity in the four-year model set (model C1, Table 2), model T3 was chosen for interpretation; the interpretations from models T3 and T4 were qualitatively similar.

Across both model sets, predictors had similar effects on the probability of a mature female blue crab being a second-year spawner, which was inversely related to CW, and positively related to increasing GSI, and maximum barnacle size (Table 4). In general, the probability of being a second-year spawner increased with decreasing distance from the bay mouth, but the rate varied significantly by year (significant year x distance interaction; Figs. 4 &

5). Comparison of year effects across the model sets was not possible because each model set considered different years and predictors, and because of the significant interaction between year and distance.

The deviance explained by the best models was lower for the four-year model set, 29%, than for the two-year model set, 63%. In both model sets, cross-validation error rates were <10%. The deviance statistics were generally close to 1, at 0.98 and 1.04 for models C1 and T3, respectively, indicating that the distributions were appropriate for the binomial response variable.

4. Discussion

4.1. Key findings

This study is the first to document spawning history of a blue crab spawning stock at the population level. We did so by collecting females randomly from the Chesapeake Bay population’s spawning stock, and then classifying females as first- or second-year spawners over multiple years using stages of nemertean worms. The combination of blue crab population sampling and nemertean-based reproductive classification represents a novel approach for evaluating individual spawning histories in decapod crustaceans with a terminal molt, and may be extended to species with indeterminate growth whose nemerteans transfer during molting (Wickham et al. 1984). Annual estimates of the proportion of second-year spawners are relative measures of age structure and can inform estimates of reproductive potential in stock assessments. The probability of a female being a second-year spawner was accurately predicted by crab size, salinity, GSI, maximum barnacle size, and the interaction between year and distance from the mouth of the bay, whereas spermatheca weight and carapace condition were uninformative predictors.

4.2. Proportion of second-year spawners and population exploitation rates

We expected that the annual proportion of second-year spawners would be higher following a year with low exploitation rates of females because under low exploitation rates, removal of primiparous or multiparous females would be less likely than in years under high exploitation rates. Although our results were consistent with this hypothesis, low sample sizes precluded us from detecting a strong statistical relationship. An alternative hypothesis for the statistically insignificant relationship between annual proportion of second-year spawners and exploitation may be related to the recent decline in spawning stock and population abundance (CBSAC 2022). The drivers of low population abundance, which are not fully understood but may be caused by a variety of factors (e.g., overharvesting, nursery habitat deterioration, increased predation), may have also decreased mature female survival and the proportion of second-year spawners that overwintered in the 2020s. Moreover, we could not quantify the effect of the winter dredge fishery on overwintering females from 1992-1996 because the spawning-history composition of the commercial harvest remains unknown.

Based on low estimates of annual survival rates (0.08) of female blue crabs in Chesapeake Bay (Lambert et al. 2006a), we would not expect a high proportion of females to survive to their second spawning year. The proportions of second-year spawners in 1992 to 1996 (0.08) and in 2020 to 2022 (0.12) were slightly higher than the proportion of female crabs infested with nemerteans in winter of 1945-1946 (0.056, Hopkins 1947) and comparable to that in winter and autumn of 1990-1992 (0.12, Messick 1998). Unfortunately, both studies aggregated infestations of immature and mature nemertean worms and female crab maturity, precluding direct comparisons of estimates of second-year spawners.

Our estimates of second-year spawners are likely conservative. We assumed that all second-year spawners were infected with pink or red worms (Hopkins 1947). Nemerteans must consume eggs from their female host to mature (Cheng 1984), mature worms are not found on male blue crabs or immature female blue crabs (Humes 1942), and mature worms are prevalent in ovigerous crabs at high percentages (Hopkins 1947, Rogers-Talbert 1948, A. Schneider unpublished data). As some second-year spawners may not host pink or red worms (Hopkins 1947), our results would result in risk-averse management if used as a benchmark to protect the spawning stock.

4.3. Alternative spawning indicators

The probability of a female being a second-year spawner increased with the presence of large barnacles, which is associated with spawning activity (Ogburn et al. 2019). Consequently, presence of large barnacles is a useful and non-lethal indicator of spawning history, but it is overly conservative, likely because barnacle (Chelonibia sp.) settlement on mature females is affected by salinity (Reilly 2019). In 2020 through 2022, we classified 19%, 8.9% and 8.4% of females as second-year spawners based on nemertean worm presence, but only 11%, 4%, and 3% of female blue crabs had barnacles. Therefore, barnacle presence may provide a minimum, relative estimate of multiple spawning events.

Carapace condition was not a significant predictor, possibly due to alternative causes of carapace discoloration such as poor water quality or sediment characteristics. We agree with Hard (1942) and discourage the use of carapace condition or coloration as an indicator of spawning history for blue crabs. Similarly, spermatheca weight was not a significant predictor, probably because spermatheca weight only partially explains variation in sperm quantity and the relationship is variable at low spermatheca weights (Ogburn et al. 2019). Sperm quantity may perform better than spermatheca weight, but estimating sperm quantity is resource intensive.

The interaction between year and distance from the bay mouth was a significant predictor in four-year models, but not in two-year models. The probability of being a second-year spawner declined with distance from the mouth of the bay, though the rate of decline varied by year. In the four-year models we anticipated a higher probability of second-year spawners in 2020 and 2021 relative to 1992 and 1993 because of female-centric management strategies implemented in the 2000s. However, the probability of being a second-year spawner was greater in 2020 across all distances and in 2021 at relatively short distances from the mouth of the Bay. As the distance increased, the probability of a second-year spawner in 2021 decreased more rapidly than in 1992 and 1993, likely due to interannual variation in the spatial distribution of mature females or the high abundance of mature females in 1992 and 1993 (CBSAC 2022). The spatial distribution of second-year spawners may be non-stationary and could have been affected by annual differences in density-dependent aggregations or the winter dredge fishery's removal of mature females from overwintering hotspots in the pre-management era. Evidence of the latter is provided by density estimates of mature female blue crabs by the WDS; density of mature female crabs declined from December through March when the commercial winter dredge fishery was operating in the pre-management era (R. Lipcius, unpublished data).

The hypothesized positive relationship between salinity and the occurrence of second-year spawners was inconsistent across years. Mature females migrate to high-salinity areas to reproduce because embryos and larvae require high salinities to develop (Sandoz & Rogers 1944, Van Engel 1958). In four-year models, salinity was positively correlated with the probability of being a second-year spawner, but not in two-year models, possibly due to weak salinity gradients in the lower Bay. In addition, if mature females migrate outside the Bay mouth before the WDS, estimates of the probability of being a second-year spawner would be biased. However, in the only documented winter survey of female blue crabs outside the Bay mouth, no female blue crabs were captured there (Lipcius et al. 2003b).

4.4. Crab size and GSI

The probability of being a second-year spawner was inversely related to crab size. Larger females produce larger clutches than smaller females (Hines 1982), and the first brood, which is the largest brood, contains the highest proportion of viable eggs (Dickinson et al. 2006, Darnell et al. 2009). Therefore, after winter dormancy first-year spawners may produce disproportionately more eggs per clutch than smaller second-year spawners who produce their second or third clutch after winter dormancy. This may be the mechanism underlying higher fecundities in large, first-time spawners in the Gulf of Mexico during spring (Graham et al. 2012).

The positive relationship between GSI and the probability of being a second-year spawner suggests that second-year spawners will spawn earlier in the spawning season than first-year spawners. Second- year spawners will have a larger relative ovary size in spring because they likely had more time to develop their ovaries prior to winter. First-year spawners, however, would need to continue to develop their gonads, possibly spawning later in the spring.

Three size-related phenomena, driven by the terminal molt in female blue crabs, may explain the inverse relationship between crab size and the probability of being a second-year spawner. First, fishers' preference for large crabs may facilitate the removal of large females from the population prior to winter, resulting in a greater proportion of small second-year spawners in winter. Second, mature female blue crabs are generally larger in Maryland (upper Bay, Miller et al. 2011) than in Virginia (lower Bay) due to a combination of lower salinity in Maryland waters (Van Engel 1958) and higher selective fishing pressure on females in Virginia waters (Lipcius & Stockhausen 2002). Maryland blue crabs migrate from the upper Bay to the spawning grounds in fall and do not reach the spawning grounds during the spawning season prior to the onset of winter (Turner et al. 2003, Aguilar et al. 2005). Crabs from Virginia migrate to the spawning grounds continuously throughout the year and have a greater likelihood of spawning prior to winter. Third, crabs in warmer conditions tend to be smaller than crabs in cooler environments, both over wide geographic ranges (Hirose et al. 2013, Olson et al. 2018, Johnson et al. 2019), and within local areas with seasonal temperature changes (Fisher 1999, Graham et al. 2012). Warmer temperatures shorten the intermolt period of crustaceans (Cadman & Weinstein 1988, Kuhn & Darnell 2019) and subsequently reduce growth per molt, resulting in smaller crabs per instar (Kuhn & Darnell 2019) and size at maturity (Dawe et al. 2012, Azra et al. 2020). Consequently, crabs that molt to maturity in summer are smaller than crabs that molt to maturity in spring and fall (Fisher 1999, Darnell et al. 2009, Dawe et al. 2012), and are able to reproduce before winter; these females are likely to be categorized as second-year spawners. Crabs that molt to maturity in spring, however, are more likely to be culled by the fishery before winter (Lipcius & Stockhausen 2002). Taken together with previous work (Darnell et al. 2009, Graham et al. 2012), we suggest that all three mechanisms collectively drive the inverse relationship between blue crab size and spawning history.

Contrary to our hypothesis that probability of being a second-year spawner would be inversely related to GSI, the probability increased with GSI. This may be due to the length of time a female spends in the spawning grounds. Mature females who migrate early enough in the year to produce a clutch would have sufficient time to regrow their ovaries before winter dormancy as second-year spawners. First-year spawners are likely those mature females that reached the spawning grounds in fall after the spawning season, and preferentially allocated energy stores to muscle development and hepatopancreas accumulation before building ovarian tissue (Turner et al. 2003).

4.5. Implications for reproductive potential

The probability of being a first-year or second-year spawner relative to crab size or GSI has significant implications for female reproductive potential given that fecundity is directly related to a female’s carapace width (Prager et al. 1990), and a female’s ovary enlarges as she approaches spawning (Hard 1942). Given that (i) relatively larger first-year spawners produce bigger clutches than relatively smaller second-year spawners; (ii) the first brood is the largest brood; and (iii) the first brood produces eggs with higher viability, we suggest that first-year spawners produce disproportionately more eggs per clutch than second-year spawners. Moreover, first-year spawners comprised 81 to 92% of the spawning stock from 2020 through 2022 in the lower Bay. Consequently, protection of first-year spawning females in spring, prior to the spawning season when females are protected in the spawning sanctuary, is vital for persistence of the spawning stock. Currently, female blue crabs on the spawning grounds are at risk of harvest between March 17th, when the fishing season begins, and mid-May or June, when the spawning sanctuary regulation takes effect (Va. Admin. Code § 20-270-10). Unfortunately, harvest in spring has intensified since the closure of the winter dredge fishery in 2008 (P. Geer, Virginia Marine Resources Commission, pers. comm.), such that protection of female crabs in spring should be bolstered to maintain high population-level reproductive potential.

Spawning stock size per se is an insufficient proxy of egg production for Chesapeake Bay blue crabs because smaller second-year spawners produce fewer eggs per clutch after winter dormancy. We therefore caution that the increased proportion of second-year spawners in the 2020s compared with the 1990s does not equate with greater production of eggs or recruitment in the 2020s. Equating egg production rates of first and second-year spawners could produce inflated estimates of egg production in stock assessment. Moreover, size of mature female blue crabs is positively related to abundance (Lipcius & Stockhausen 2002). We thus recommend an age- and size-based approach to estimating egg production in blue crabs, using the proportion of first- and second-year spawners with size-specific reproductive potential to inform the spawner-egg model.

Wintertime monitoring of the proportion of second-year spawners of female decapods provides a unique snapshot of spawning stock characteristics after the spawning season as well as a precursor of spawning stock composition before the upcoming spawning season. This should therefore be continued for the Chesapeake Bay blue crab and considered for blue crabs in other populations along its range.

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Table 1. Variables used in generalized linear models of the probability of a mature, female crab being a second-year spawner for both the two-year and four-year model sets. Two-year model set includes observations from 2020 and 2021, whereas the four-year models include observations from 1992, 1993, 2020, and 2021. Crabs were identified as second-year spawners on the basis of the presence of *Carcinonemertes carcinophila* on their gills or carapace.

Predictors	Description	Variable type	Two-year models	Four-year models
Carapace Width (CW)	Tip to tip distance of the lateral spines (mm)	Continuous	✓	✓
Year	Survey year: 1992, 1993, 2020, & 2021 (GSI models); 2020 & 2021 (contemporary models)	Factor	✓	✓
Distance (Dist)	Distance from tow location to Chesapeake Bay mouth (km)	Continuous	✓	✓
Distance × Year (Dist × Year)	Interaction term of year and distance	Factor	✓	✓
Salinity (Sal)	Bottom salinity at tow	Continuous	✓	✓
GSI	Gonadosomatic index [Ovary weight (g)/Individual weight (g)]	Continuous	✓	✓
Maximum barnacle size (Barn)	Maximum size of *Chelonibia spp* on female's carapace (mm)	Continuous	✓	
Carapace Condition (CC)	Condition of female carapace (white, yellow, brown)	Factor	✓	
Spermathecae wet weight (Swt)	Wet weight of a female's spermathecae (g)	Continuous	✓	

Table 2. Generalized linear models analyzing the probability of a mature, female crab being a second-year spawner with a logit link tested in the four-year model set, represented by C_i, and corrected Akaike's Information Criterion (AICc). Details on model predictors are presented in Table 1. k = number of parameters in the model including the intercept and model variance. Δ_i = difference between AICc of a given model and the model with the lowest AICc. w_i = probability of a model being the best in the set. Model C_1, the global model, was selected for interpretation, and includes observations from 1992, 1993, 2020, and 2021.

Model	Model Structure	k	AICc	Δ_i	w_i
C_1	**CW + Year + Dist + (Dist × Year) + Sal + GSI**	**11**	**540**	**0**	**0.997**
C_2	CW + Year + Dist + (Dist × Year) + GSI	10	551	11	0.003

Table 3. Generalized linear models analyzing the probability of a mature, female crab being a second-year spawner with a complementary log-log link tested in the two-year model set, represented by T_i and corrected Akaike's Information Criterion (AICc). Details on model predictors are presented in Table 1. k = number of parameters in the model including the intercept and model variance. Δ_i = difference between AICc of a given model and the model with the lowest AICc. w_i = probability of a model being the best in the set. Model T_3 (in bold) was chosen for interpretation and includes observations from 2020 and 2021.

Model	Model Structure	k	AICc	Δ_i	w_i
T_1	CW + Year + Dist + (Dist × Year) + Sal + GSI + Barn + CC + Swt	11	115	7	0.02
T_2	CW + Year + Dist + (Dist × Year) + GSI + Barn + CC + Swt	10	113	5	0.04
T_3	**CW + Year + Dist + (Dist × Year) + Sal + GSI + Barn**	**8**	**110**	**2**	**0.25**
T_4	CW + Year + Dist + (Dist × Year) + GSI + Barn	7	108	0	0.70

Table 4. Parameter estimates for the generalized linear models exploring the probability of a mature, female crab being a second-year spawner chosen for inference for the four-year (C_1, Table 2.) and two-year (T_3, Table 3.) model sets. Two-year models included observations from 2020 and 2021 and used a complementary log-log link. Four-year models included observations from 1992, 1993, 2020, and 2021, and used a logit link. SE = standard error, Z = Z statistic, p = p value for model estimates.

	Four-year model: C_1				Two-year model: T_3			
Parameter	Estimate	SE	Z	p	Estimate	SE	Z	p
Intercept	-2.64	0.25	-10.78	< 0.01	-2.15	0.41	-5.29	< 0.01
CW	-1.10	0.25	-4.42	< 0.01	-1.37	0.41	-3.32	< 0.01
$Year_{1993}$	-0.15	0.33	-0.45	< 0.01	-	-	-	-
$Year_{2020}$	1.11	0.42	2.61	< 0.01	-	-	-	-
$Year_{2021}$	-1.09	0.53	-2.06	< 0.01	-2.66	0.75	-3.55	< 0.01
Dist	-0.72	0.42	-1.69	< 0.01	-0.29	0.69	-0.42	0.67
Dist × $Year_{1993}$	-1.03	0.57	-1.81	< 0.01	-	-	-	-
Dist × $Year_{2020}$	-0.64	0.83	-0.77	< 0.01	-	-	-	-
Dist × $Year_{2021}$	-2.26	0.88	-2.59	< 0.01	-3.12	1.12	-2.78	< 0.01
Sal	0.91	0.26	3.58	< 0.01	-0.017	0.46	-0.044	0.96
GSI	1.58	0.23	6.82	< 0.01	2.32	0.46	5.015	< 0.01
Barn	-	-	-	-	2.60	0.59	4.37	< 0.01

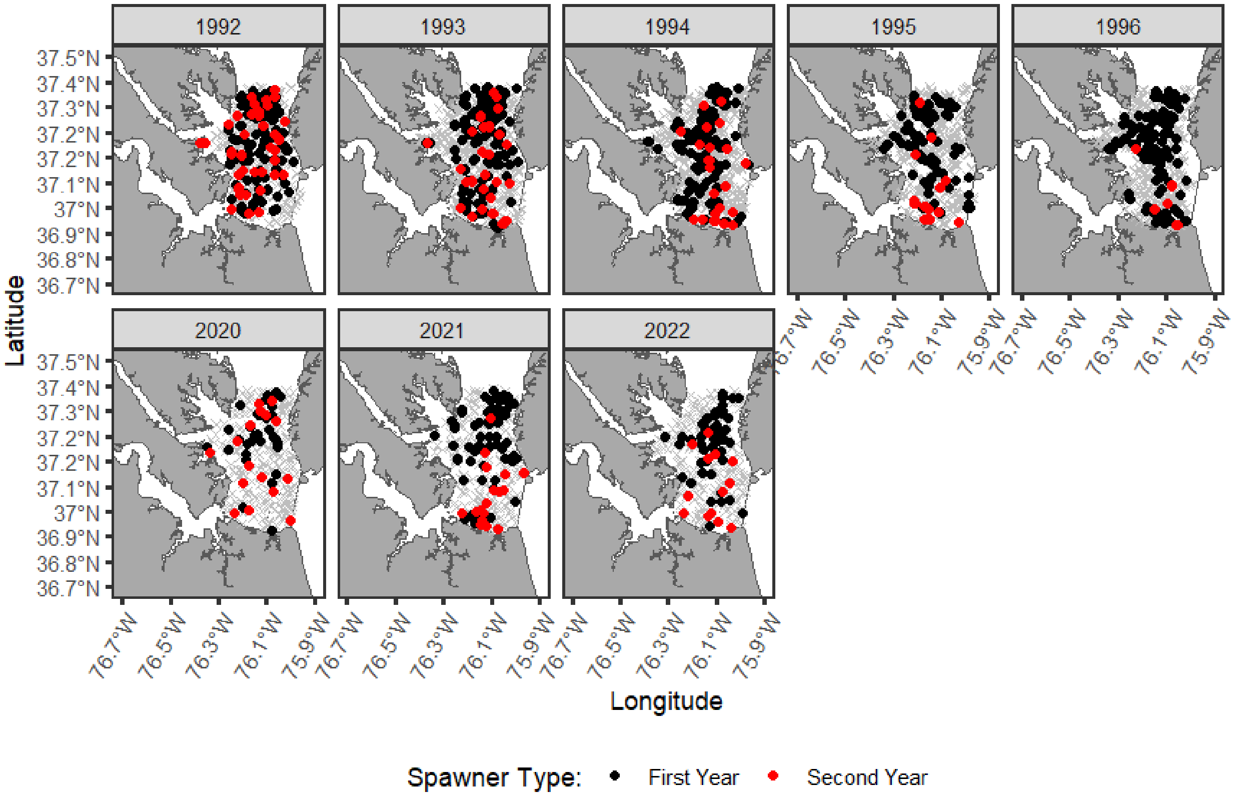

Figure 1. Location of VIMS Winter Dredge Survey tows where adult female crabs were collected and assessed for spawning history from 1992-1996 and 2020-2022. Gray x: dredge tows in which no female crabs were caught.

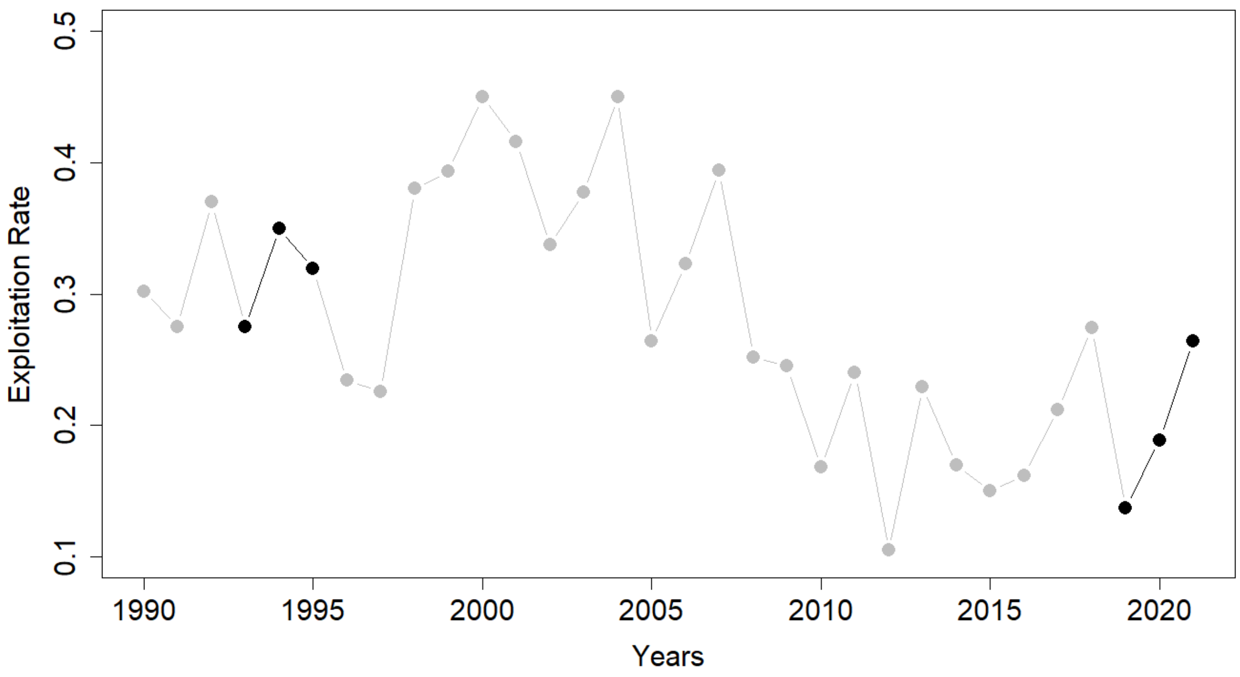

Figure 2. Exploitation rates of female blue crabs in Chesapeake Bay from 1990-2021 (G. Davis per. comm.). Black circles indicate years when spawning status was assessed. Stricter management actions were implemented in 2008 to protect the spawning stock.

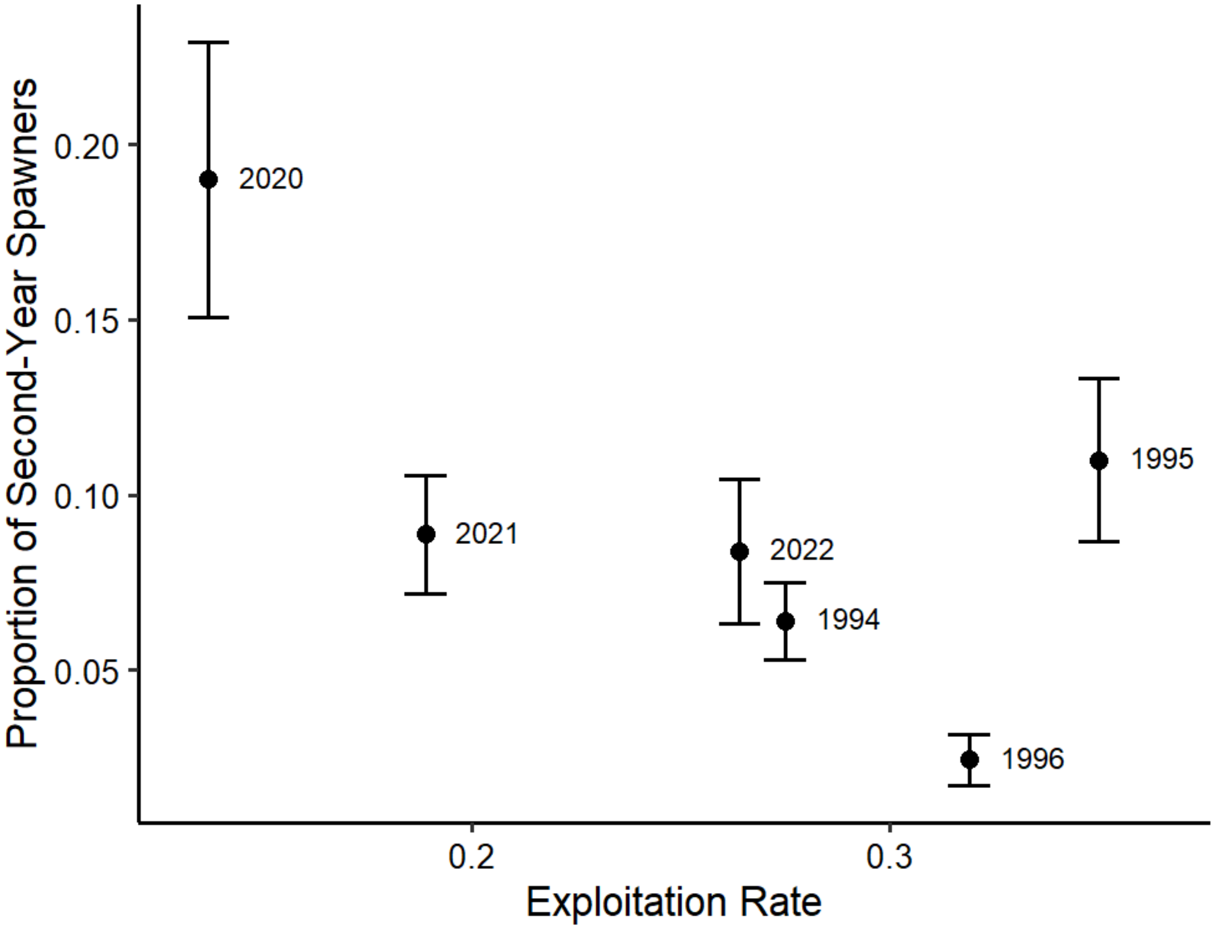

Figure 3. Relationship between exploitation rates of female blue crabs and the proportion of second-year spawners. Due to the dredge survey occurring from December through March, the exploitation rates represent exploitation during the previous year's crabbing season (March-November). The sample sizes in 1994, 1995, 1996, 2020, 2021 and 2022 were 500, 182, 452, 100, 282, and 179 mature female crabs, respectively.

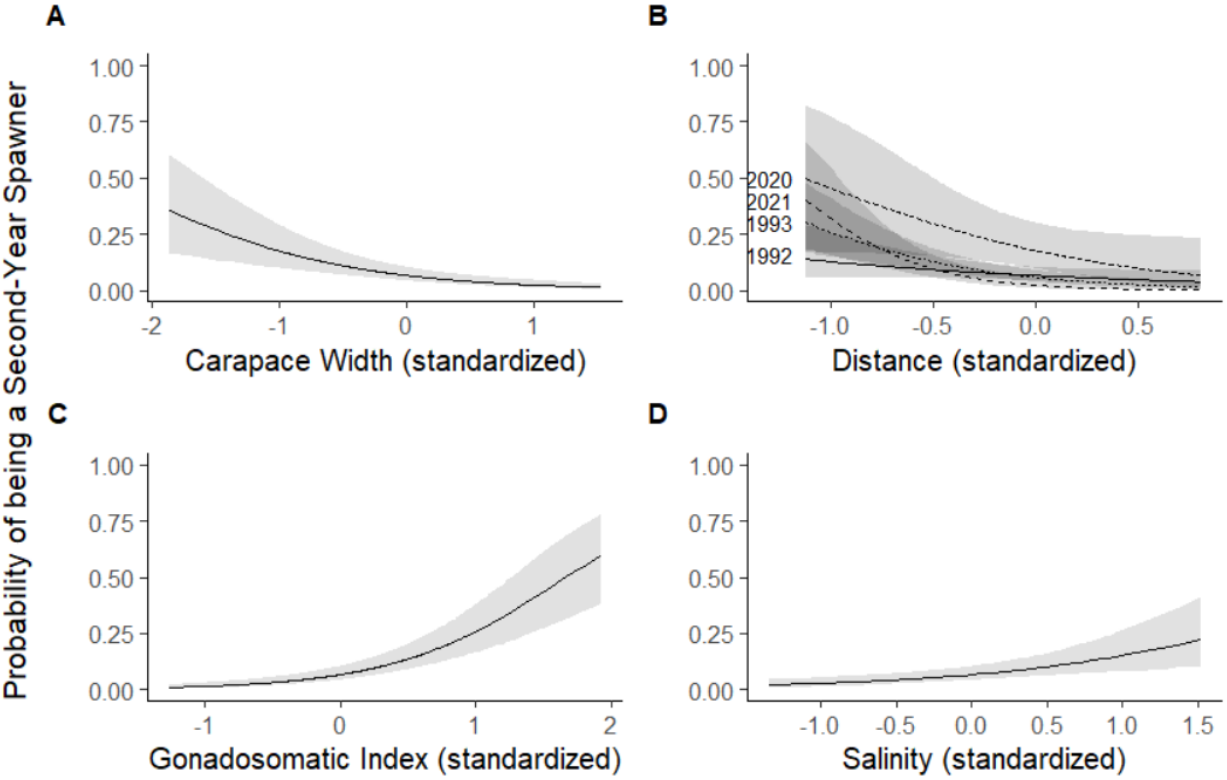

Figure 4. The effect of (A) carapace width, (B) distance and year, (C) gonadosomatic index and (D) salinity on the probability of a female being a second-year spawner based on the model chosen for inference from the four-year model set (see Table 2, C1). Note that the independent variables have been standardized for comparison. Gray bands are the 95% confidence interval.

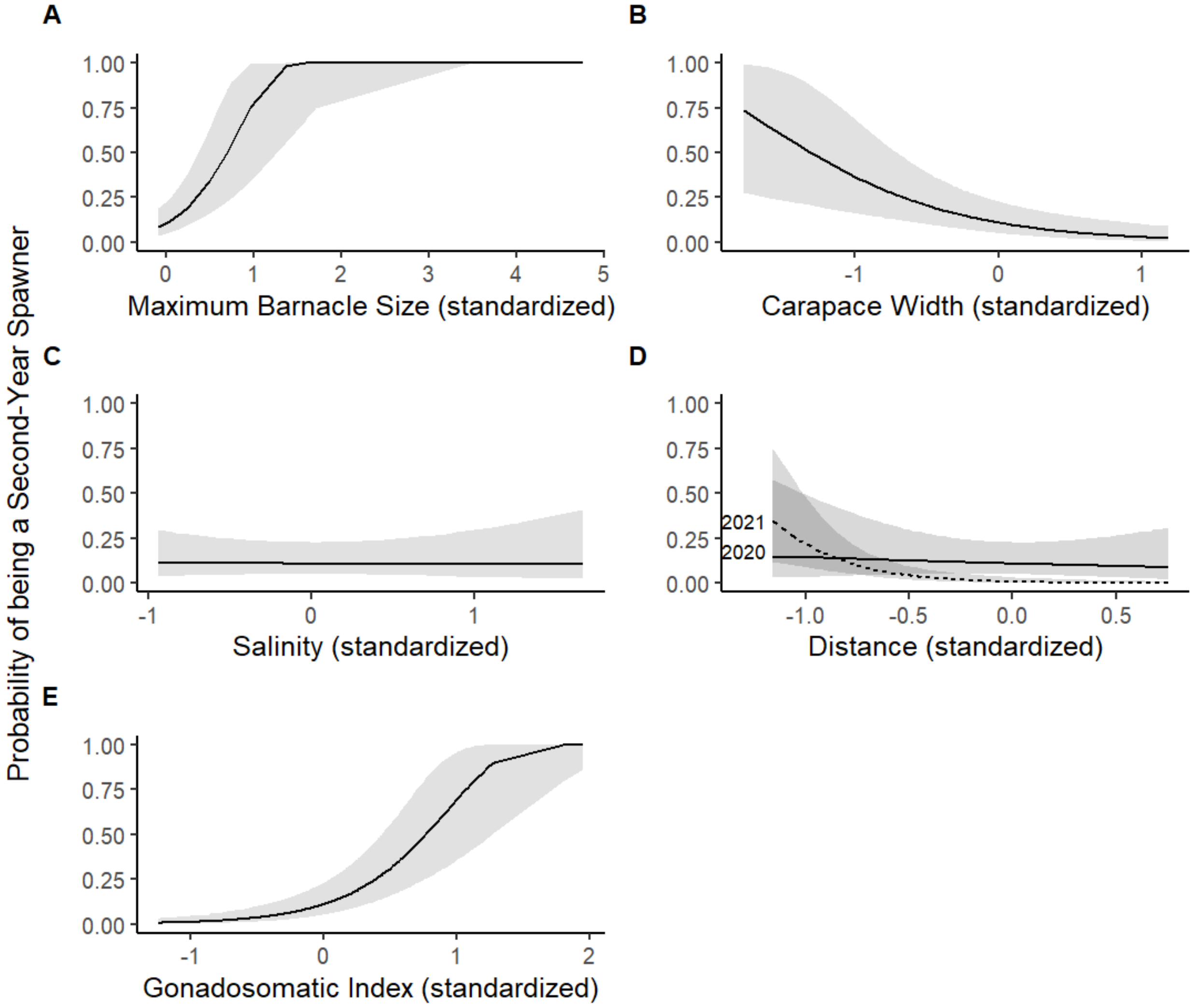

Figure 5. The effect of (A) maximum barnacle size, (B) crab carapace width, (C) salinity, (D) distance and year, and (E) gonadosomatic index on the probability of a female being a second-year spawner based on the model chosen for inference from the two-year model set (see Table 3, T_3). Note that the independent variables have been standardized for comparisons. Gray bands represent the 95% confidence interval.

CHAPTER 2: Reproductive phenology of the Chesapeake Bay blue crab population in a changing climate

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Abstract

Global temperatures are rising across marine ecosystems in response to climate change. Marine and estuarine-dependent species including the blue crab, *Callinectes sapidus*, may adapt to warming temperatures phenologically, by shifting the seasonal timing of biological events, such as reproduction. In Chesapeake Bay, average water temperatures have risen by an average 0.02°C per year since the 1980s. Extension of the blue crab spawning season, through earlier onset and later conclusion, may augment annual brood production and alter the efficacy of management strategies. The duration of the potential spawning season from 1985 to 2019 was assessed using degree days, and the observed spawning season from 1995 to 2019 was assessed using the occurrence of ovigerous crabs from the Virginia Institute of Marine Science Trawl Survey in the James River and in the mainstem of lower Chesapeake Bay. Spawning degree days (SDD) and reproductive degree days (RDD) were defined using minimum temperatures of 19°C and 12°C, respectively. The mean duration of the potential spawning season increased by 25% in SDD and 10% in RDD between 1985 and 2019 in the James River and lower Chesapeake Bay, respectively. This progressive expansion of the potential spawning season was not, however, reflected in the observed spawning season. Rather, the onset, conclusion, and duration of the observed spawning season were variable over the time series. The observed month of onset was driven by RDD in spring, whereby spawning began earlier during warmer springs. The spawning conclusion date was driven by the onset of spawning, rather than Fall temperature, such that the duration of the observed spawning season and, therefore, annual brood production did not change over time. In Chesapeake Bay, the spawning stock is protected by a sanctuary that is closed to fishing from mid-May to mid-September during the putative spawning season. An earlier start to the spawning season during warmer springs, as seen in recent years, is expected to reduce the efficacy of the spawning sanctuary and intensify exploitation of the spawning stock, without enhancing brood production, thereby reducing reproductive output of the blue crab population in Chesapeake Bay.

Keywords: degree days$_1$, reproduction$_2$, crustaceans$_3$, climate change$_4$, *Callinectes sapidus*$_5$.

1. Introduction

Global temperatures are rising across ecosystems in response to climate change (Burrows et al., 2011; Pörtner et al., 2022). Increases in temperature alter the thermal regimes to which species are adapted and may modify their physiological responses, life history, and demographic rates (Doney et al., 2012). For example, increased temperatures raise metabolic rates (Atkinson, 1994; Brown et al., 2004), and potentially accelerate growth rates and reduce size at maturity. Moreover, as temperature regimes become stressful to species, individuals must either adapt or face local extirpation (Parmesan, 2006). Population-level adaptations to climate change include changes in abundance, altered spatial distributions, and shifts in phenology (Doney et al., 2012; Anderson et al., 2013; Poloczanska et al., 2016). Phenology is the study of seasonality in biological phenomena (Leith, 1974) such as spawning or migration. In contrast to changes in abundance and altered spatial distributions, which have been well documented across biomes and taxa (Huntley et al., 2006; Elith and Leathwick, 2009; Nye et al., 2009; Last et al., 2011; Johnston et al., 2012; Franke et al., 2022), shifts in phenology are more variable and not as well understood, particularly for marine organisms (Poloczanska et al., 2016; Tang et al., 2016; Piao et al., 2019).

Phenological shifts in response to climate change have potential ecological and economic consequences (Tang et al., 2016). Ecologically, phenological shifts can create trophic mismatches between predators and prey, disrupting ecosystem function (Edwards and Richardson, 2004; Damien and Tougeron, 2019; Visser and Gienapp, 2019). Economically, shifts in phenology can impact the time of catch and the volume landed in commercial fisheries (Mills et al., 2013). At the species level, shifts in reproductive phenology have potential consequences for reproductive success and thus the stability of a population (Dickey et al., 2008; Linton and Macdonald, 2018; Reséndiz-Infante et al., 2020). Overall, shifts in reproductive phenology may define the reproductive output of a species in the context of climate change and thus need to be understood to assess population vulnerability.

Shifts in reproductive phenology are especially important to quantify in marine decapods because of their complex reproductive patterns and importance to commercial fisheries. Moreover, shifts in the phenology of decapod crustaceans are understudied compared with other marine taxa, likely due to data availability (Brown et al., 2016; Poloczanska et al., 2016). Marine decapods commonly have a planktonic larval phase, and recruitment success from larval to juvenile stages may be impacted by climatic forces that shift spawning time (Cushing, 1990; Wieland et al., 2000; McGeady et al., 2020). The reproductive strategies of decapods also involve trade-offs between molting and reproduction (Hartnoll, 1985; Raviv et al., 2008). Valuable decapod fisheries are often managed by protecting egg-bearing females, e.g., American lobster *Homarus americanus* (Atlantic States Marine Fisheries Commission, 2020), Dungeness crab *Cancer magister* (Oregon Department of Fish and Wildlife, 2022), Alaskan king crab *Paralithodes camtschaticus* (Alaska Department of Fish and Game, 2021), and blue crab *Callinectes sapidus* (Lipcius et al., 2003; Fogarty and Lipcius, 2007; Miller et al., 2011).

The blue crab is an economically important decapod crustacean that occupies a wide native range along tropical, subtropical, and temperate ecosystems in the Western Atlantic Ocean and Gulf of Mexico (Williams, 2007). The length of the blue crab spawning season increases as a function of water temperature, lasting about four months in Chesapeake Bay, six months in North Carolina, nine months in Florida, and year-round in southeast Brazil (Van Engel, 1958; Hines et al., 2011; Severino-Rodrigues et al., 2013; Hart et al., 2021). A longer spawning season allows production of additional broods per year because blue crabs are multiparous. For example, females in Chesapeake Bay produce one to three broods per season, whereas females in Florida produce six to eight (Hines et al., 2011). Differences in reproductive timing between tropical, subtropical, and temperate populations of blue crab hint at potential effects of warming on the length of the spawning season, yet changes in the duration of the spawning season due to climate change within geographic locations have not been explored for this species.

Chesapeake Bay is an ideal location to assess shifts in blue crab reproductive phenology because a key blue crab management strategy is to protect egg-bearing females during their putative spawning season. In the early 2000s, a 654,246-ha marine protected area and corridor (i.e., spawning sanctuary) were established (Lipcius et al., 2003); these areas are closed to commercial crabbing from mid-May to mid-September (Va. Admin. Code § 20-252-10). The duration of the blue crab spawning season may have expanded in recent years in response to rising water temperatures in Chesapeake Bay, where temperatures increased an average of 0.02°C per year during the past three decades (Hinson et al., 2021). An expanded spawning season could be advantageous by increasing reproductive output (Hines et al., 2011). However, an extension of the spawning season could be disadvantageous if such a change renders ovigerous crabs (i.e., egg-bearing crabs) vulnerable to fishing prior to, or after, the closure of the spawning sanctuary. The effect of climate change on the onset, duration, and conclusion of the spawning season is critical to predicting long-term responses of the blue crab population in Chesapeake Bay.

Analyses that investigate responses to climate change require robust and informative temperature data. Degree days are a useful temperature metric because they represent the accumulation of heat in a system over time and can be defined in relation to biological processes. Degree days are calculated by summing the difference between the observed temperature and a minimum temperature threshold (T_{min}), for those days of the year when temperatures exceed the T_{min}. The value of T_{min} represents a temperature threshold below which the accumulation of heat is uninformative to the biological process of interest, such as reproduction and spawning of blue crabs, and therefore those days do not contribute to the total degree days. Degree days account for spatial and temporal variation in temperature, which is useful in climate-change studies because long-term changes in temperature, especially as they relate to biological processes, are non-stationary (Grigorieva et al., 2010). Degree days can also be used to compare the duration of biological process, such as reproduction, across regions and time frames (Trudgill et al., 2005). Within a region, interannual comparisons of degree days indicate rates of warming in physiological time, while cross-regional comparisons of degree days, such as comparison of annual degree days along the latitudinal range of the blue crab, may aid predictions of future spawning season duration. Lastly, degree days have been used in studies on blue crab growth (Brylawski and Miller, 2006), reproduction (Darnell et al., 2009), survival (Glandon et al., 2019), and catch (Weiss and Downs, 2020) and can reliably predict phenology (Cayton et al., 2015).

Our objectives were to 1) investigate changes in the timing and duration of the potential spawning season using degree days to measure cumulative temperature effects; 2) identify the onset, conclusion, and duration of the observed spawning season using fishery-independent observations of ovigerous female crabs; 3) determine the relationships between temperature and spawning season onset, conclusion, and duration; and 4) compare differences in the potential spawning season duration across the native latitudinal range of the blue crab in the US. We hypothesized that the onset of the spawning season would occur earlier in the more recent years of the time series due to warming waters in Chesapeake Bay. Similarly, we hypothesized the conclusion of the spawning season would be later and the duration of the spawning season would be longer in more recent years. We anticipated these trends to be present in both the analyses of degree days and fishery-independent observations of ovigerous crabs. Lastly, we hypothesized that the duration of the spawning season would be longer in low latitudes than in high latitudes because of the increased duration of high temperatures.

2. Material and Methods

2.1. Potential spawning season

For annual degree days, two values of T_{min} were used: 12°C representing reproductive degree days (RDD), and 19°C representing spawning degree days (SDD). A derived mean temperature when crab feeding begins, 12°C (Darnell et al., 2009), represents the minimum temperature at which females can begin to allocate energy to reproduction, and is herein referred to as reproductive degree days (RDD). The minimum optimal spawning temperature for Chesapeake Bay blue crabs is 19°C (Bembe et al., 2017) and represents the ideal temperature required for spawning; herein, we refer to these degree days as spawning degree days (SDD). Including only days when the mean daily water temperature was greater than or equal to T_{min}, RDD and SDD were calculated as:

$$RDD = \sum_{k}^{n} (mean\ daily\ temperature - 12)$$

$$SDD = \sum_{k}^{n} (mean\ daily\ temperature - 19)$$

where k represents the first day and n represents the total number of days for each calculation of degree days for years 1985 to 2019. Annual RDD and SDD summed mean daily temperature over the entire calendar year (i.e., k =1, n = 365). We also calculated spring and fall degree days for each year. Spring RDD and SDD were calculated using temperatures from January 1 to April 30 and fall SDD and RDD were calculated using temperatures from September 1 to December 31.

Annual estimates of RDD and SDD were calculated using model-based estimates of water temperature from a three-dimensional numerical simulation of daily Chesapeake Bay conditions (Hinson et al., 2021). The numerical model is an implementation of the Regional Ocean Modeling System (Shchepetkin and McWilliams, 2005) for Chesapeake Bay (ChesROMS; Xu et al., 2012) with an average horizontal grid cell resolution of 1 to 2 km over a 100 by 150 curvilinear grid. Model inputs include atmospheric forcings from a re-analysis product, ocean boundary forcings derived from observations offshore, and riverine inputs from the Chesapeake Bay Program’s Phase 6 Watershed Model (Chesapeake Bay Program, 2020; Hood et al., 2021).

For calculations of RDD, the spatial extent of the temperature data was limited to bottom temperatures in the lower James River and Virginia portion of mainstem Chesapeake Bay to correspond to available fishery-independent observations of female blue crabs (Figure 1, see section 2.2). For calculations of SDD, the area was additionally restricted to grid cells in which bottom salinities were greater than 15 for more than 50% of the time series between April 1 and October 31 (Figure 1). This ensures that SDD are considered only in areas where salinity conditions are conducive for blue crab embryogenesis (Sandoz and Rogers, 1944).

RDD and SDD were calculated for each grid cell in the model; these values were then averaged over the relevant spatial extents in the James River and Chesapeake Bay. Averaging over regions was appropriate for inferences on blue crab spawning because adult females are highly mobile foragers and undergo migrations throughout Chesapeake Bay (Aguilar et al., 2005; Lambert et al., 2006a). To quantify trends in the potential spawning season, annual RDD and SDD estimates for each of the James River and the Virginia portion of the mainstem of the Chesapeake Bay (herein Chesapeake Bay) were modeled as a function of year and region (James or Chesapeake Bay) using weighted linear regression. Weights were defined as the inverse variance of the mean RDD and SDD estimates; a first-order autoregressive correlation structure was used to account for temporal autocorrelation across the time series. Model assumptions were assessed visually using normalized residuals, which satisfied assumptions of normality and homoskedasticity.

2.2. Observed spawning season

Onset, conclusion, and duration of the blue crab spawning season were calculated annually from 1995 to 2019 using counts of ovigerous females from the Virginia Institute of Marine Science Trawl Survey, herein trawl survey (Tuckey and Fabrizio, 2022). The presence of egg-bearing crabs was noted by the trawl survey scientists starting in 1995. From 1995 to 2015, the gear consisted of 9.1-m headline, 4-seam trawl net with a 38.1-mm stretch-mesh body and a 6.4-mm mesh cod liner. Since 2016, the net has had a 5.8-m headline, a 40-mm stretch-mesh body and a 6.4-mm liner. Counts of ovigerous female crabs were adjusted to account for changes in gear (Fabrizio and Tuckey, 2016). The trawl survey is a stratified (by depth and region) random survey, with 5-min tows performed monthly at 22 stations in the James River and 39 to 45 stations in the Virginia portion of the Chesapeake Bay (Figure 1). The trawl survey also samples the York and Rappahannock rivers, however, ovigerous crabs are not reliably encountered in these two rivers, likely due to lower salinities in these regions. Therefore, these regions were excluded from analyses.

Trawl survey sampling occurred monthly, year-round, except for January and March in the Chesapeake Bay. All female crabs captured by the trawl survey were counted, classified as mature or immature based on abdomen shape (Van Engel, 1958), and egg-bearing females were noted. Only catches from February, and April through November were used in the analysis to maintain consistency between sampling months in the James River and the Chesapeake Bay. December was excluded due to concerns about catchability of blue crabs during winter when blue crabs may not be vulnerable to the gear as a result of their burying behavior. Methods for imputation of missing data due to vessel issues or weather conditions are provided in Supplementary Materials (SM) section 1.

Counts of ovigerous female crabs were fit using generalized linear models (GLM) with a negative binomial distribution and log-link, adapted from Edwards and Crone (2021). The GLM was specified as:

$$\mathbf{Counts\ of\ ovigerous\ crabs} \sim \mathbf{NB}(\boldsymbol{\lambda_{ij}}, \boldsymbol{k})$$

$$\mathbf{log}(\boldsymbol{\lambda_{ij}}) = \boldsymbol{\beta_0} + \boldsymbol{\beta_1 year_j} + \boldsymbol{\beta_2}(\boldsymbol{month_i} \times \boldsymbol{year_j}) + \boldsymbol{\beta_3}(\boldsymbol{month_i^2} \times \boldsymbol{year_j})$$

Where k is the overdispersion parameter for the negative binomial distribution, λ_{ij}represents the mean count of egg-bearing female crabs in $month_i$ and $year_j$, β_0 is the intercept and set to 0, β_1 is the estimate for the effect of year j as a categorical variable, β_2 is the estimate for the interaction effect of $month_i \times year_j$ where month is a continuous variable, and β_3 is the partial regression coefficient for the interaction effect of $month_i^2 \times year_j$. Within the model, month acts as the independent variable while year functions as a blocking factor. This model formulation allows the slope and quadratic term to parameterize a Gaussian curve. To obtain a bell-shaped curve, β_3 must be negative (see Edwards and Crone, 2021 for full methodological details). This method assumes that the spawning season is unimodal, which is appropriate for blue crabs in Chesapeake Bay (SM section 2). Model fit was evaluated through visual inspection of residuals as well as the ratio of model deviance to degrees of freedom, which is expected to equal 1 for negative binomial GLMs that fit the data well.

Given that the trawl survey sampling effort has been consistent over the study time frame, using count data in lieu of catch per unit effort was appropriate. To ensure this assumption was reasonable, we compared model estimates for a negative binomial model with and without effort as an offset and found no statistically significant differences in estimates of phenology metrics (SM section 3).

The parameter estimates from the GLM were used to estimate phenological metrics of the observed spawning season: onset, conclusion and duration of spawning. The months at which 10% and 90% of ovigerous crabs were collected by the survey were considered the spawning onset and spawning conclusion, respectively. Duration was calculated as the time between onset and conclusion. All estimates are presented in months to stay consistent with the trawl survey sampling design. Confidence intervals for the estimates of the phenological metrics were calculated via parametric bootstrapping in which the model variance-covariance matrix was used to estimate a distribution for each model coefficient. The distribution of each model coefficient was sampled 10,000 times for each year and phenological estimates were recalculated from the bootstrap replicates. The variance, 95% confidence interval, and standard error were calculated from the resulting 10,000 phenological estimates. Two statistical models were constructed: one model used counts of ovigerous females from the James River, and the other used counts from Chesapeake Bay. The two areas were evaluated separately to avoid confounding space and time given the sampling design of the trawl survey. Within a given month, the trawl survey does not sample the Chesapeake Bay and James River simultaneously, and the Chesapeake Bay was sampled prior to the James River in most (76%) months sampled in this study.

2.3. Drivers of the observed spawning season

Weighted linear regressions were used to examine the effect of SDD and RDD on spawning onset, conclusion and duration, with the weight equal to the inverse variance of the phenology metric to account for uncertainty in the modeled estimates. The variance of each phenology metric was estimated from the phenological metrics derived from parametric bootstrapping. An additional model of spawning conclusion was constructed using spawning onset as the independent variable. Spring SDD and RDD were used in onset models and were calculated using temperatures from January 1 to April 30. Fall SDD and RDD were used in conclusion models and calculated using temperatures from September 1 to December 31. Annual SDD and RDD were used in duration models and used temperatures from the entire calendar year. Models of the same phenology metric (i.e., onset, conclusion or duration) and region but using SDD or RDD as the independent variable were compared using Akaike's Information Criterion (AIC, Anderson, 2008).

Linear model performance was evaluated using the deviance explained. Assumptions of normality and homogeneity of variance were assessed visually using normalized residuals. Temporal dependence among phenology metrics was investigated using an autocorrelation function plot. All models used for inference met the assumptions of general linear models.

2.4. Latitudinal differences in potential spawning season

Temperature data from coastal waters in Florida to Maine were retrieved from the National Estuarine Research Reserve System (NERRS). Thirty-two water-quality monitoring buoys spanning 8 states along the native range of the blue crab were selected: Florida, North

Carolina, South Carolina, Delaware, New Jersey, Rhode Island, New Hampshire, and Maine (SM section 4). These states represent areas with NERRS monitoring buoys and either reported distribution shifts of blue crabs (New Hampshire and Maine: Johnson, 2015; Stasse et al., 2023) or areas with considerable research on blue crab spawning (Florida, North Carolina, Chesapeake Bay), as well as outermost states of the east coast of the United States portion of the latitudinal range (Florida and Maine). Monitoring buoys record temperature every 15 minutes. Temperatures from 2015 to 2019 were used in this analysis; temperature observations from two stations in 2015 were omitted due to implausible temperature values (SM section 4). Daily temperature was calculated by taking the mean of the ~96 temperature readings recorded during each 24-hour period, and the SDD and RDD were calculated for each year and monitoring station based on the average daily temperature. Within a monitoring station, annual degree days for years 2015 to 2019 were averaged to a single estimate. Degree days for the James River and Chesapeake Bay were calculated as described in section 2.1, and the annual degree days from 2015 to 2019 were similarly averaged. The relationship between degree days and latitude was modeled using a simple linear regression. Model estimates of RDD and SDD were compared between North Carolina and the Chesapeake Bay because North Carolina borders Virginia to the south and future Chesapeake Bay conditions are often predicted based on current North Carolina conditions. For example, in 2100, the duration and extent of lethal winter temperatures for blue crabs in Chesapeake Bay are expected to be similar to present day North Carolina temperature regimes (Glandon et al., 2019). Moreover, RDD and spawning activity are positively correlated in North Carolina, allowing for comparisons of reproductive activity across regions (Darnell et al., 2009).

3. Results

3.1. Potential spawning season

The duration of the potential spawning season lengthened significantly from 1985 to 2019 in the James River and Chesapeake Bay (Figure 2, Table 1). Spawning degree days (SDD) increased by 3.6 degree-days y^{-1} (Table 1), while reproductive degree days (RDD) increased by 5.0 degree-days y^{-1} (Table 1) in the James River and Chesapeake Bay. Moreover, the duration of the potential spawning season was significantly longer in the James River than in Chesapeake Bay. The James River had 392.9 more SDD (Table 1) and 663.3 more RDD than Chesapeake Bay (Table 1).

3.2. Observed spawning season

From 1995 to 2019, the trawl survey captured 3,662 ovigerous blue crabs in Chesapeake Bay and 1,705 ovigerous blue crabs in the James River. The negative binomial GLMs visually fit the data well, and our data supported the assumption of a unimodal spawning season (SM section 2). Over the 25 years, onset of the spawning season occurred earlier in the James River (mean ± SE: 5.13 ± 0.13 months after Jan. 1, which corresponds to early May) than in Chesapeake Bay (mean ± SE: 5.96 ± 0.09 months after Jan. 1, which corresponds to late May to early June, Figure 3). The spawning season also concluded earlier in the James River than in Chesapeake Bay, in mid-July (mean ± SE: 7.58 ± 0.11 months after Jan. 1) and early August (mean ± SE: 8.31 ± 0.11 months after January 1), respectively (Figure 3). Despite differences in onset and conclusion, the duration of the spawning season was about 2.4 months for both the

James River and Chesapeake Bay (mean ± SE: 2.44 ± 0.12 and 2.35 ± 0.08), respectively (Figure 3), which reflected a difference of only 3 days.

3.3. Drivers of the observed spawning season

Model comparisons of spawning phenology for the James River and Chesapeake Bay were similar across areas based on AIC. Month of spawning onset was best predicted by spring RDD and spawning conclusion was best predicted by spawning onset (Table 2). In both the James River and Chesapeake Bay, month of spawning onset was earlier in years with greater spring RDD (Table 3, Figure 4), and month of spawning conclusion occurred earlier in the year when the month of spawning onset was earlier (Table 4, Figure 5). In the James River, spawning conclusion was also later in the year when fall SDD and RDD were high, neither of which was significantly related to spawning season conclusion in Chesapeake Bay (SM section 5). In Chesapeake Bay, the best predictor of spawning duration was annual RDD (Table 2), although years with increased RDD had shorter spawning durations (Table 5, Figure 6). In the James River, annual RDD and SDD were poor predictors of spawning duration (SM section 5).

3.4. Latitudinal differences in potential spawning season

As hypothesized, RDD and SDD were strongly linearly related with latitude (linear model: $r^2 = 0.95$ and $r^2 = 0.93$, respectively; Figure 7; Supplementary materials 6). Based on the slope parameters, SDD decreased by 125.6 degree days and RDD decreased by 223.7 degree days per unit increase in latitude (Figure 7, SM section 6). North Carolina had 383 more SDD and 683 more RDD than Chesapeake Bay. Given our estimates of the rates of change for RDD and SDD in Chesapeake Bay (Table 1), the Bay region will reach the RDD and SDD for North

Carolina in 137 y and 106 y, respectively, assuming rates of temperature change remain constant.

4. Discussion

From 1985 to 2019, the duration of the potential spawning season, measured with degree days, increased, although the duration of the observed spawning season had no temporal trend. Rather the observed month of spawning onset was driven by RDD in spring, whereby a greater accumulation of RDD in the beginning of the year led to an earlier spawning onset. We found that the conclusion of spawning was positively related to the onset of spawning, such that the duration of the observed spawning season did not change for the blue crab in Chesapeake Bay or the James River. Increasing trends in RDD and SDD reflect the warming of Chesapeake Bay and an expansion of the potential spawning season. From 1985 to 2019, degree days increased by about 25% SDD and 10% RDD, but these temporal trends were not reflected in the fishery-independent observations of blue crab spawning phenology. In this study, we demonstrated that the spawning season currently lasts approximately 2.4 months, but spawning begins and concludes earlier in years with warmer springs. Notably, in these warmer springs, spawning onset can occur before the blue crab spawning sanctuary is in effect. Intense female harvest in spring may reduce reproductive output of female crabs in the Chesapeake Bay by removing females before they have the opportunity to spawn. As warming continues, female spawners may become more vulnerable to fishing during warm springs, prior to the onset of the spawning season and the closure of the spawning sanctuary.

4.1 Implications for blue crab reproduction

Temperature regimes differed substantially between North Carolina and Chesapeake Bay, as reflected in a longer spawning season and greater brood production in North Carolina (Dickinson et al., 2006; Darnell et al., 2009). Considerable warming is required before Chesapeake Bay females can produce broods at the annual rate currently observed in North Carolina. In North Carolina, females produce their first egg mass within 747 RDD of mating and have an average brood production interval of 263 RDD per brood, giving them the potential to produce eight broods per spawning season (Dickinson et al., 2006; Darnell et al., 2009). The average annual RDD in Chesapeake Bay from 2015 to 2019 was about 1,800 RDD (Figure 7, Supplementary Table 5), which would allow Chesapeake Bay females to produce up to four broods per spawning season, assuming their brood production per RDD is equivalent to females in North Carolina (Darnell et al., 2009). This is a slightly higher estimate than the two to three broods currently observed. Since 1958, females in the Chesapeake Bay have been assumed to spawn one to three times per year (Van Engel, 1958). In North Carolina the average RDD from 2015 to 2019 was about 3,000, suggesting that females could produce up to eight broods, which is greater than the observed maximum of seven broods per female over one to two spawning seasons (Dickinson et al., 2006; Darnell et al., 2009). Therefore, estimates of brood production using degree days appear to overestimate annual brood production. Moreover, reproductive timing alone may not dictate the number of sponges, which may be affected by additional factors such as sperm limitation and lifespan (Hines et al., 2003; Darnell et al., 2009). Additional field studies are needed to quantify the number of broods produced by female blue crabs in Chesapeake Bay and how increases in temperature may affect brood production.

4.2. Spawning season trends

The lack of temporal trends in the observed phenological metrics (i.e., onset, conclusion and duration of spawning) was contrary to what we hypothesized for blue crabs in Chesapeake Bay. Our results, however, indicate that spawning season onset was significantly advanced by warmer spring temperatures, and since temperatures are rising, future warming will likely produce consistently early spawning onset and possibly a longer spawning duration. Phenological shifts have occurred in other species in Chesapeake Bay, such as cobia *Rachycentron canadum* (Crear et al., 2020), and in other decapod species, such as American lobster *Homarus americanus* in the Gulf of St. Lawrence (Haarr et al., 2020) and northern shrimp *Pandalus borealis* in the Gulf of Maine (Richards, 2012). Moreover, we expect blue crabs, being a short-lived, r-selected species, to respond rapidly to shifts in temperature (Perry et al., 2005). Our results indicate that a unidirectional phenological shift in blue crab reproduction in mid-latitude systems may not be apparent over a 25-year time period with gradual increases in ambient temperature. Our observation is consistent with Poloczanska et al. (2016) who reported phenological shifts in mid-latitudes are slower than phenological shifts at high and low latitudes. Responses to climate change have been documented for the blue crab at higher latitudes, such as range expansions into regions that historically were too cold to maintain permanent or reproducing populations (Johnson, 2015; Stasse et al., 2023).

The lack of an observed unidirectional temporal trend in the blue crab spawning season in Chesapeake Bay may simply reflect the abridged time series that we analyzed (1995 to 2019). Additional years of trawl survey data may be needed to observe a temporal pattern, because the length of the time series is a significant predictor in detecting phenological shifts (Bush et al., 2018). Moreover, the relationship between RDD and year is subtle (5 RDD per year), and the trawl survey sampling design may be too temporally coarse to detect slow changes in the onset or conclusion of the spawning season in Chesapeake Bay. In addition, the percent increase in temperature rise was greater for SDD than RDD, which aligns with a higher rate of warming in summer than the remainder of the year (Hinson et al., 2021). RDD was a clearer predictor of phenology metrics than SDD; therefore, spring and fall warming may be more important in altering blue crab spawning phenology than higher summer temperatures. Temperature is a major driver of female blue crab spawning frequency (Bembe et al., 2017), such that expansion of spawning season duration may become more pronounced as warming continues.

The onset and conclusion of the spawning season differed notably between the James River and Chesapeake Bay. The spawning season began and ended three to four weeks earlier in the James River than in Chesapeake Bay, likely due to earlier warming and cooling in the James River. The James River is shallower than Chesapeake Bay and is therefore more strongly influenced by air temperature (Hinson et al., 2021). Moreover, Chesapeake Bay receives a greater influx of cooler ocean water than the James River throughout the year. The earlier spawning season conclusion in the James River than in Chesapeake Bay may also have been related to air temperature, because the James River cools more quickly than Chesapeake Bay in fall. This is supported by the positive, significant relationship between SDD or RDD and spawning conclusion in the James River. Additionally, there may be a delayed conclusion of the spawning season in the James River because the ovigerous crabs from the James River are assumed to migrate to the mouth of the Chesapeake Bay to hatch their eggs after spawning in the lower James River. However, mature females on the spawning grounds return to the lower

James River to feed in the shallow high salinity areas between broods (Lambert et al., 2006a), and therefore a unidirectional movement of mature or egg-bearing females out of the Chesapeake Bay tributaries may not characterize the James River.

The earlier onset and conclusion of the spawning season in the James River may also have been influenced by the sampling design of the trawl survey. On average, Chesapeake Bay is sampled 5.7 d earlier than the James River. In spring, sampling in the Chesapeake Bay may occur prior to the onset of spawning, whereas sampling the James River later in the same month increases the odds of encountering an ovigerous crab in any given month. A similar phenomenon may occur in the fall: the later sampling in the James River could decrease the probability of encountering an ovigerous female, leading to an earlier estimate of spawning season conclusion. Conversely, earlier sampling in Chesapeake Bay could cause estimates in the Bay to be earlier if spawning begins concurrently in Chesapeake Bay and the James River. Unfortunately, we were unable to test these potential biases with the available data. We believe that the magnitude of difference between spawning metrics (3-4 weeks) in the James River and Chesapeake Bay compared to the average difference in sampling time (5.7 d) reduces the likelihood that the sampling design is a major driver in the regional differences between phenological estimates.

The James River had greater uncertainty in phenology metrics than Chesapeake Bay, likely due to the lower number of ovigerous crabs encountered in the James River. Specifically, the variances of the onset estimates were greater for the James River (mean var = 1.1) and lower for the Chesapeake Bay (mean var = 0.1); uncertainty estimates for other phenology metrics exhibited the same pattern. The lower catches of ovigerous crabs in the James River are likely related to the smaller area of the James River, the declining salinities in upriver sections, and the fewer trawl tows performed in the James River. Catches of egg-bearing crabs in Chesapeake Bay between 1995 and 2019 were more than double those in the James River. Years with the lowest catches in the James River, such as 1995 (n = 4), 2000 (n = 19) and 2005 (n = 21), had high uncertainty in the estimates of onset and conclusion. Years with low total counts were also more influenced by observations of one or two egg-bearing crabs in early and late spawning months, such as November. This may have contributed to differences in the effect sizes between the James River and Chesapeake Bay.

4.3. Fishery implications

Female crabs in the James River are vulnerable to fishing during the entire commercial crabbing season, while females in the spawning sanctuary in the Chesapeake Bay are protected from harvest from mid-May to mid-September. Females in the James River will molt to maturity, mate, and migrate to high salinity areas from spring through fall. After their migration to the lower Chesapeake Bay and between broods, adult females forage in shallow, high salinity areas, including the lower James River (Lambert et al., 2006a), making them vulnerable to fishing. Within Chesapeake Bay, the onset of the observed spawning season now begins prior to the sanctuary closure dates (May 16 for the majority of the sanctuary) in at least 20% of the years examined. When we used a lower quantile to estimate spawning onset (i.e., 2.5% quantile instead of the 10% quantile described in section 2.2), the spawning season was estimated to begin before the sanctuary was closed to fishing in 72% of years. This implies that a sizable portion of the female spawners in any given year will be vulnerable to harvest prior to the close of fishing in the sanctuary. Most mature females in spring have not yet spawned and will begin their first spawning season (Schneider et al., 2023) by producing their largest and most viable egg clutch (Darnell et al., 2009; Graham et al., 2012). High fishing mortality rates on these females (primiparous, first-year spawners) during spring may thus decrease population-level reproductive output substantially (Schneider et al., 2023).

Our results justify further protection of female crabs in April and May to ensure the highest level of egg production prior to their harvest. As warming continues and spawners become more active earlier in spring, phenological shifts in reproduction will become more pronounced. Shifts in species phenology or distribution in response to climate change can decrease the efficacy of marine sanctuaries (Van Keeken et al., 2007), such as the blue crab spawning sanctuary (Lipcius et al., 2003; Lambert et al., 2006b) and increase the risk of exploitation, which may be the case here. The lack of expansion of the duration of the observed spawning season suggests that warming has not progressed enough in Chesapeake Bay to allow for additional broods to be produced by females later in the year. Globally, our study informs how warming is impacting the timing of reproduction of an economically important decapod species. Locally, our study allows managers to consider the effects of spring warming on the efficacy of the spawning sanctuary. A greater fraction of the spawning stock could be protected by earlier closure to fishing in the spawning sanctuary, or by reduction of fishing effort in the spring before the sanctuary closes.

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Table 1. Parameter estimates for weighted linear regression models of spawning degree days (SDD) or reproductive degree days (RDD) as a function of year and region from 1985 to 2019 for Chesapeake Bay and the James River (SDD T_{min} = 19°C, RDD T_{min} = 12°C).

Response	Parameter	Effect	Estimate	Standard Error	t	p
SDD	β_0	Intercept	505.0	14.5	34.9	< 0.001
	β_1	Year	3.6	0.7	5.5	< 0.001
	α_{JA}	James River	392.9	15.2	25.8	< 0.001
RDD	β_0	Intercept	1752.6	21.9	80.2	< 0.001
	β_1	Year	5.0	1.0	5.0	< 0.001
	α_{JA}	James River	663.3	23.8	27.8	< 0.001

Table 2. Hypothesized onset models and Akaike's Information Criteria (AIC), for the Chesapeake Bay mainstem (Bay) and James River (ΔAIC represents the difference in AIC values between a given model and the model with the lowest AIC within model groupings). k is the number of parameters in the model including the intercept and variance. SDD = spawning degree days and RDD = reproductive degree days. Onsets are regressed as a function of spring degree days (Jan. 1 – April 30), conclusions are regressed as a function of fall degree days (Sept. 1 – Dec. 31), and durations are regressed as a function of annual degree days. The top performing model, based on AIC, is in bold font.

Model	Predictors	k	Bay		James	
			AIC	ΔAIC	AIC	ΔAIC
Onset model 1	SDD_{spring}	3	47	8	56	5
Onset model 2	RDD_{spring}	3	39	0	51	0
Conclusion model 1	SDD_{fall}	3	57	23	41	1
Conclusion model 2	RDD_{fall}	3	56	22	47	7
Conclusion model 3	$Onset$	3	34	0	40	0
Duration model 1	SDD_{year}	3	33	4	47	0
Duration model 2	RDD_{year}	3	29	0	47	0

Table 3. Parameter estimates from weighted linear regression models of spawning season onset in Chesapeake Bay ($r^2 = 0.28$) and the James River ($r^2 = 0.15$) as a function of spring reproductive degree days (RDD, calculated from Jan. 1 – April 30).

		Chesapeake Bay				James River			
Parameter	Effect	Estimate	Standard Error	*t*	*p*	Estimate	Standard Error	*t*	*p*
β_0	Intercept	7.34	0.48	15.19	< 0.001	6.85	0.80	8.52	< 0.001
β_1	RDD	-0.0077	0.0026	-2.99	< 0.01	-0.0039	0.0019	-2.029	0.054

Table 4. Parameter estimates from weighted linear regression models of spawning season conclusion in Chesapeake Bay ($r^2 = 0.60$) and the James River ($r^2 = 0.38$) as a function of spawning season onset.

		Chesapeake Bay				James River			
Parameter	Effect	Estimate	Standard Error	*t*	*p*	Estimate	Standard Error	*t*	*p*
β_0	Intercept	2.84	0.92	3.09	< 0.01	4.83	0.69	7.043	< 0.001
β_1	Onset	0.91	0.16	5.85	< 0.0001	0.50	0.13	3.77	0.001

Table 5. Parameter estimates from weighted linear regression models of spawning season duration in Chesapeake Bay ($r^2 = 0.21$) as a function of annual reproductive degree day (RDD, calculated from Jan. 1 – Dec. 31).

		Chesapeake Bay			
Parameter	Effect	Estimate	Standard Error	t	p
β_0	Intercept	5.88	1.46	4.029	< 0.001
β_1	RDD	-0.0019	0.00077	-2.48	0.021

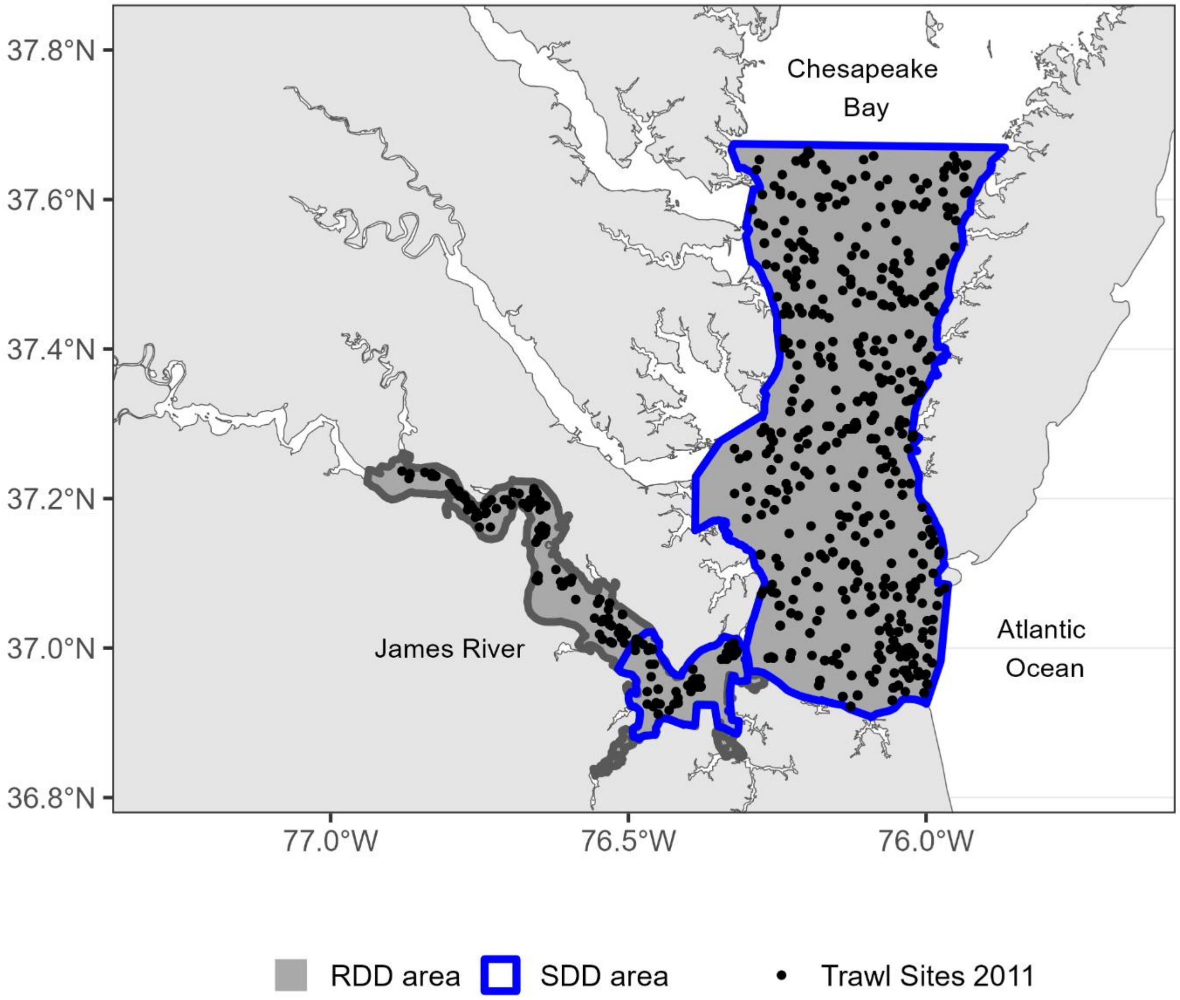

Figure 1. Sampling locations of the Virginia Institute of Marine Science Juvenile Fish Trawl Survey in 2011 for the James River and mainstem of lower Chesapeake Bay in February and April to November. The year 2011 is as an example of the spatial coverage of the trawl survey across months: February, April, May, June, July, August, September, October, and November. Dark gray polygons represent the areas where reproductive degree days (RDD) were calculated. Polygons outlined in blue represent the areas where spawning degree days (SDD) were calculated.

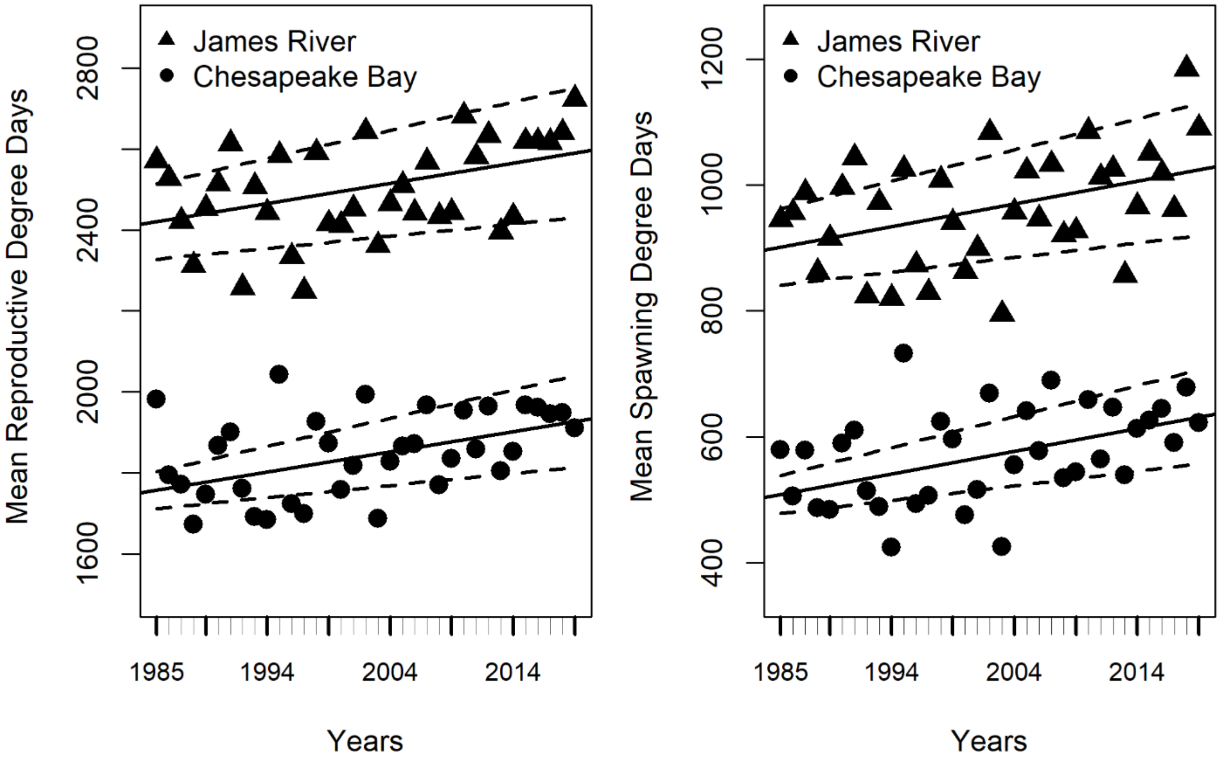

Figure 2. Mean annual reproductive degree days (RDD, left) and spawning degree days (SDD, right) as a function of region and years (1985 to 2019). The James River is represented by triangles and Chesapeake Bay is represented by circles. Black lines represent weighted linear regressions, dashed lines are 95% confidence intervals. Model results are presented in Table 1.

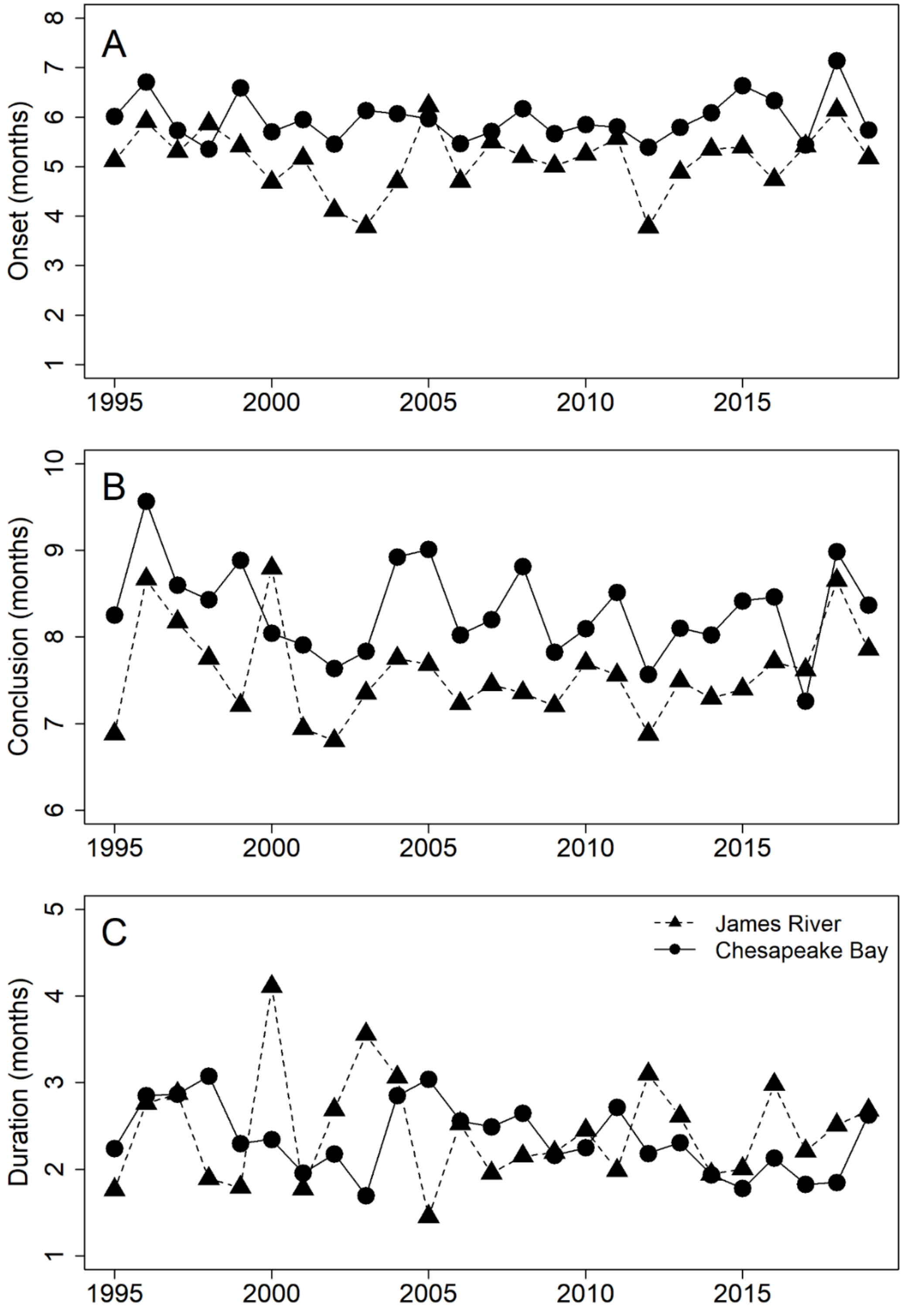

Figure 3. Estimates of the observed spawning season (A) onset, (B) conclusion, and (C) duration in months since January 1 from 1995 to 2019. The James River is represented by triangles and the Chesapeake Bay is represented by circles.

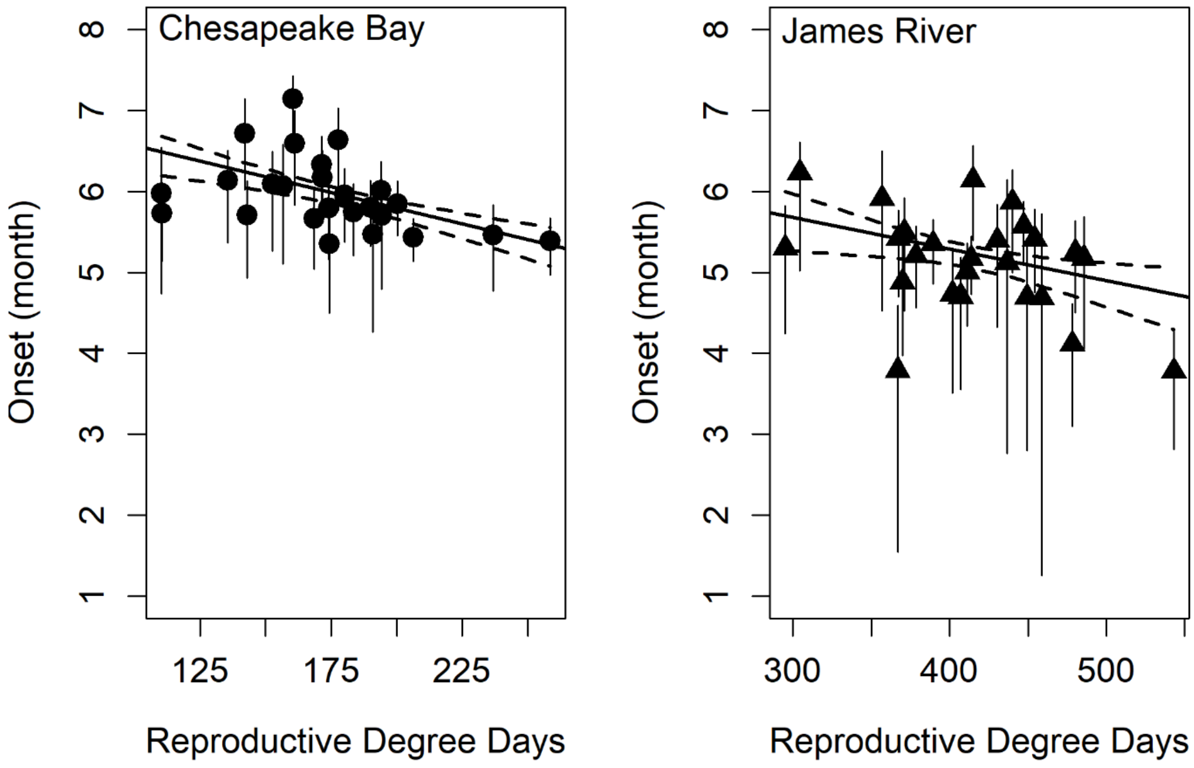

Figure 4. The effect of reproductive degree days on spawning onset in Chesapeake Bay (left) and James River (right). Chesapeake Bay is represented by circles and the James River is represented by triangles. Dashed lines are the 95% confidence interval for the linear model (black regression line, $r^2_{Bay} = 0.28$ and $r^2_{James} = 0.15$) and vertical error bars represent 95% confidence intervals in the estimate of the phenology metric.

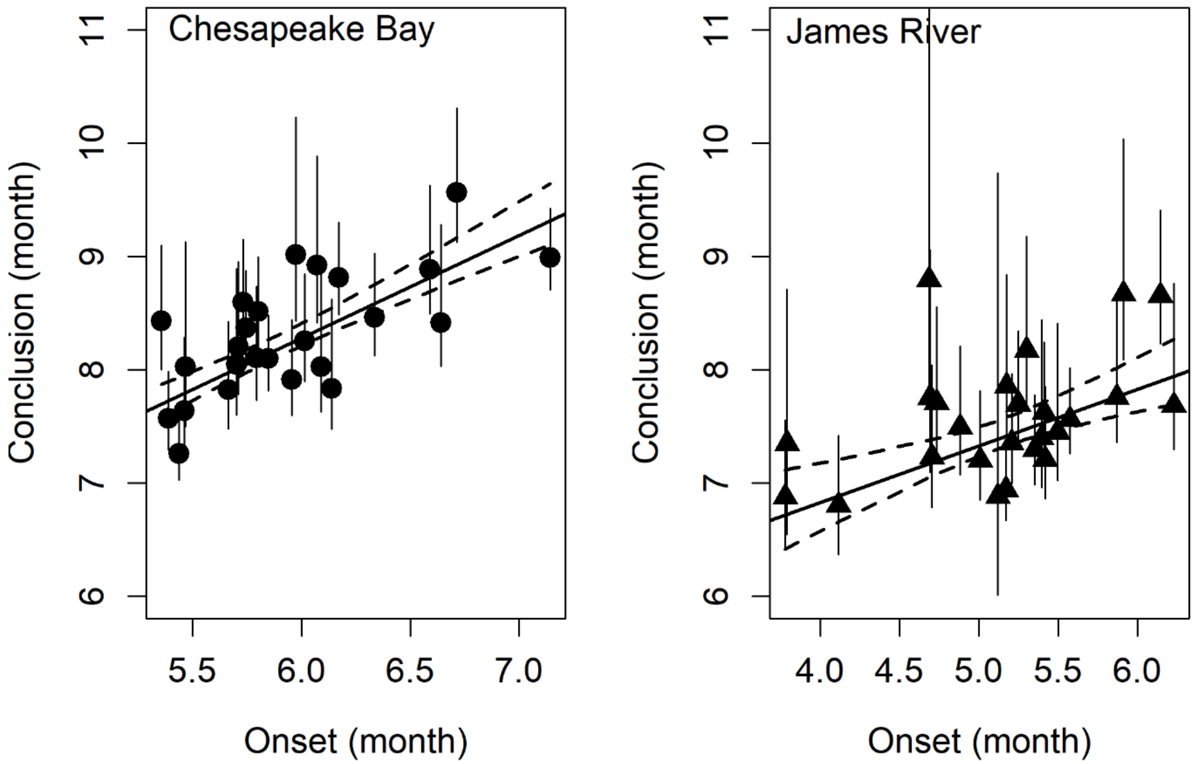

Figure 5. The effect of spawning onset on spawning conclusion in Chesapeake Bay (left) and James River (right). Dashed lines are the 95% confidence interval for the linear model (black regression line, $r^2_{Bay} = 0.60$ and $r^2_{James} = 0.38$) and vertical error bars represent 95% confidence intervals in the estimate of the phenology metric.

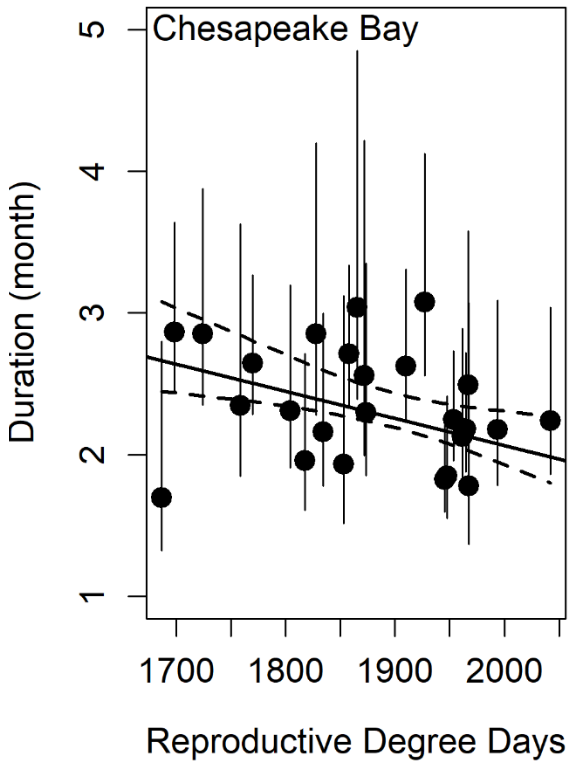

Figure 6. The effect of reproductive degree days on spawning duration in Chesapeake Bay. Dashed lines are the 95% confidence interval for the linear model (black regression line, r^2 = 0.21) and vertical error bars represent 95% confidence intervals in the estimate of the phenology metric.

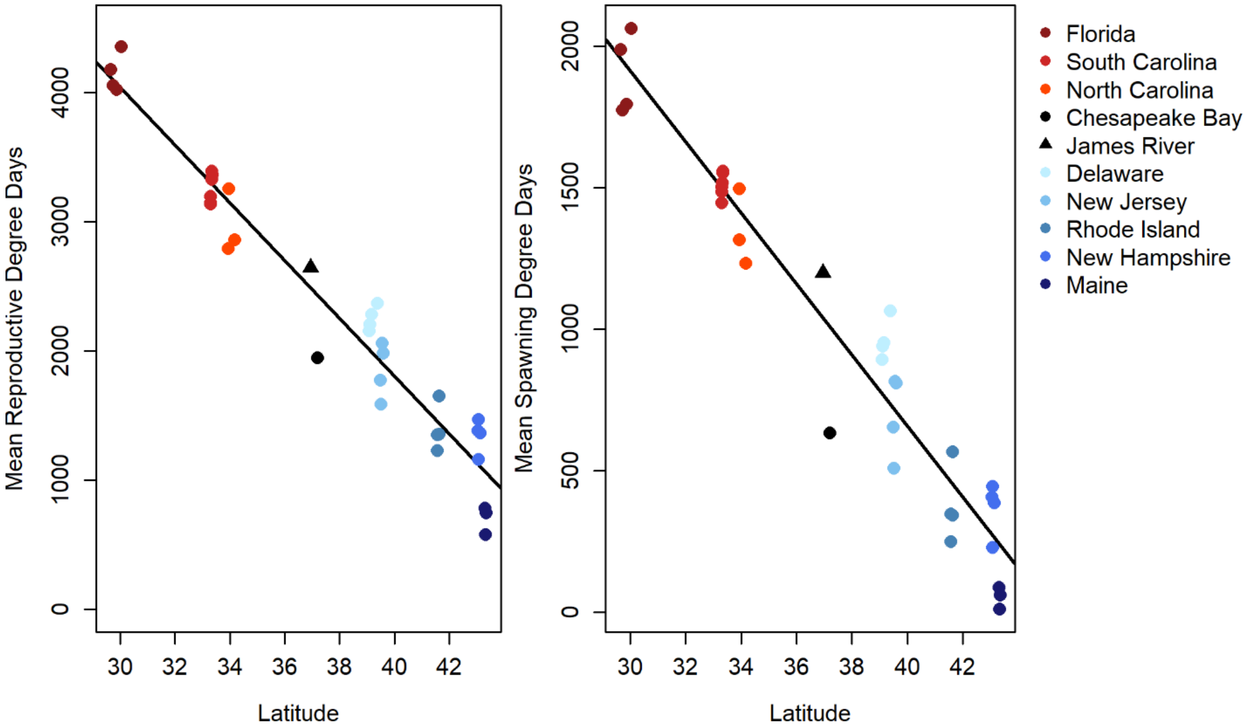

Figure 7. Mean reproductive degree days (RDD, left) and mean spawning degree days (SDD, right) estimated from temperature data collected by monitoring buoys in coastal waters along the East Coast of the U.S. Means represent annual degree days averaged from 2015 to 2019. All temperature data were retrieved from the National Estuarine Research Reserve System (SM section 4), except Chesapeake Bay and James River data which were calculated as described in section 2.1. Black lines are simple linear regressions of degree days as a function of latitude (RDD = 10743.5 – 223.7 × Lat, $r^2_{RDD} = 0.95$; and SDD = 5674.3 – 125.6 × Lat, $r^2_{SDD} = 0.93$).

CHAPTER 3: Spawning history, fecundity, and potential sperm limitation of female blue crabs in Chesapeake Bay

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Highlights:

Blue crab reproductive potential in Chesapeake Bay was assessed

Females in June, early in the spawning season, had the highest reproductive potential

Fecundity was higher in primiparous than multiparous females

Size-specific fecundity has not changed appreciably between four decades

Individual reproductive potential is high and population sperm limitation is unlikely

Abstract

The blue crab (*Callinectes sapidus*) is an ecologically and economically important species in estuaries of the Western Atlantic Ocean and Gulf of Mexico. Given the importance of reproductive output and spawner demography on population dynamics, blue crab management may be improved if individual-based changes in egg production are identified and incorporated into management advice. We determined the spawning history, batch fecundity, and stored sperm quantities of 126 ovigerous blue crabs in 2022 to estimate the reproductive potential of female blue crabs in Chesapeake Bay. Our mean estimate of fecundity, 2.17 million eggs/female, is lower than one (4.0 million eggs/female in 1987) of two historical estimates but similar to a second (2.6 million eggs/female in 1986). The 1987 estimate was likely biased due to methodological differences; hence, we conclude that size-specific fecundity has not changed over the last four decades. Moreover, fecundity was reduced by 0.28 million eggs in multiparous females (those that produced at least one egg mass prior) compared with primiparous females (those that produced their first egg mass). Most females captured in June were primiparous; these females had significantly higher quantities of stored sperm and thus higher reproductive potential than primiparous or multiparous females in July and August, although females in July and August had substantially more eggs per brood than those in June. Our study is the first to pair individual fecundity and stored sperm quantity for blue crabs, which allows for a robust assessment of their reproductive potential. Generally, the reproductive potential of blue crabs is high at the individual level and sperm limitation is unlikely at the population level. Population-level production may be increased by protecting primiparous spawners as these crabs have the highest capacity to contribute offspring to the population. Furthermore, fisheries management may be improved by using our updated estimate of size-specific fecundity (Fecundity = $268{,}337 \times e^{0.015CW}$) and incorporating spawn month or spawner history in models of stock production.

Keywords**:** Decapoda, spawners, multiparous, primiparous, reproductive potential; reproduction

1. Introduction

Effective fisheries management relies on biological data to characterize population dynamics in stock assessment models, which are used to inform management decisions. Biological data on the reproductive potential of a population are critical for sustaining exploitation because such potential is an indicator of the production of recruits and affects the rate at which a population may recover from disturbance or overexploitation. Stock assessments and management decisions often incorporate aspects of reproduction such as spawning stock biomass and average fecundity; however, assessment models and decisions can be improved by incorporating reproductive potential and individual spawner demographics (Trippel, 1999; Lambert, 2008; Kell et al., 2016). This is especially so for species with complex reproductive dynamics like Atlantic blue crabs (Fitzhugh et al., 2012).

Reproductive potential and spawner demography are difficult to assess for decapods. Reproduction in decapods is tightly associated with molting, which results in a range of specialized strategies for reproduction, such as determinate molting, mating restricted to specific stages of the molt cycle, and female sperm storage (Hartnoll, 1985; Raviv et al., 2008). Decapods are also difficult to age due to variations in growth rate between successive molts and the length of the inter-molt period, which is compounded by step-wise growth and a lack of retained hard parts, which are lost at molting (Vogt, 2012; Crowley et al., 2014; Becker et al., 2018; Gnanalingam et al., 2019). These can hinder the assessment of age at maturity, which is a critical parameter in population models. In addition, fecundity can vary throughout an animal's lifetime, and selective fishing can truncate the age structure of the population (Hixon et al., 2014; Beyer et al., 2015; Ohlberger et al., 2022). Despite these difficulties, understanding the reproductive potential and spawner demography of decapods is essential because many species support valuable fisheries, and many of these species are managed by protecting female spawners (Orensanz et al., 1998; Phillips and Melville-Smith, 2005; Rasmuson, 2013; Wahle et al., 2020; National Marine Fisheries Service NOAA Fisheries, 2022).

Although female blue crabs (*Callinectes sapidus*) in Chesapeake Bay are protected from high levels of commercial exploitation during reproductive periods, the spawning stock is fished, and annual abundances are variable (Chesapeake Bay Stock Assessment Committee, 2023). In Chesapeake Bay, management actions that conserve spawners were implemented between 2000 and 2008 in response to an 81% decline in spawning stock abundance from 1992 to 2000 (Lipcius and Stockhausen, 2002) and due to the significant spawning stock-recruitment relationship (Tang, 1985; Lipcius and Van Engel, 1990; Lipcius and Stockhausen, 2002; Fogarty and Lipcius, 2007). In Virginia, the winter dredge fishery, which mostly harvested females from the spawning grounds prior to the spawning season, was closed; the historic spawning sanctuary was expanded to protect 50% of the spawning stock (Lipcius et al., 2003) in 2000; and the harvest of females with dark egg clutches, which hatch within days, was prohibited. In Maryland, access to the female fishery was restricted and female bushel limits were lowered (CBSAC, 2023). Female blue crab fecundity has not been evaluated since these management actions took effect, despite concerns about intense male exploitation that could lead to sperm limitation and about declines in female reproductive success (Ogburn et al., 2014, 2019; Schneider et al., 2023a). An updated, robust analysis of fecundity is, therefore, needed to understand the reproductive output of blue crabs in Chesapeake Bay since the implementation of the aforementioned management actions.

Recent concerns about sperm limitation and lowered reproductive success are related to the interaction between the reproductive strategy of blue crabs and intense fishing pressure. Adult blue crabs mate in mesohaline waters immediately following the terminal molt to maturity of the female (Van Engel, 1958), which is the only opportunity for females to mate (Jivoff, 1997; Jivoff et al., 2007). Females store sperm in specialized organs, spermathecae, and use the sperm reserve to produce multiple broods over their lifetime (Hines et al., 2003; Darnell et al., 2009). If females receive a low quantity of sperm from their mate, reproduction can become sperm limited, and reproductive output may decline (Ogburn, 2019). Intense harvest on males, resulting in uneven sex ratios, is associated with lowered quantities of stored sperm in females (Kendall et al., 2002; Ogburn et al., 2014). After mating, females migrate to polyhaline waters, i.e., spawning grounds, where they will stay for the remainder of their life (Lambert et al., 2006b, Gelpi et al., 2013). These movements are known to fishers, who target prepubertal females during their terminal molt for the soft-shell crab industry (Van Engel, 1984; Kennedy et al., 2007) and adult females during their migration to the spawning grounds (Aguilar et al., 2008). These exploitation patterns preferentially exploit females before they are able to reproduce, threatening the reproductive output of the population.

In this study, we seek to reassess blue crab fecundity, elucidate drivers of fecundity and stored sperm quantity, and evaluate the reproductive potential of Chesapeake Bay blue crabs. Specifically, the objectives of this study were to 1) quantify the proportion of primiparous and multiparous spawners during the 2022 spawning season; 2) estimate fecundity relative to female size, spawning history, time of year, and egg stage; 3) compare estimates of fecundity in 2022 with historical estimates of fecundity; 4) determine the quantity of stored sperm in ovigerous females relative to female size, spawning history, and time of year; and 5) estimate reproductive potential based on individual batch fecundity and quantity of stored sperm over the life of mature females. The hypotheses supporting the predictors for fecundity and stored sperm quantity are presented in Section S1 (supplementary materials).

High variation in stored sperm quantity and fecundity (Prager et al., 1990; Graham et al., 2012; Ogburn et al., 2014; Rains et al., 2016; Ogburn et al., 2019) highlights the need to examine reproductive potential using observations at the individual level. To estimate reproductive potential, defined here as the potential number of broods a female can produce in her lifetime, we paired fecundity and stored sperm quantity with spawning history. Spawning history refers to the number of times a female has produced eggs and is used as a proxy for reproductive age. Female spawning history -- whether a female is primiparous (produced first egg mass) or multiparous (produced at least two egg masses) -- can be classified using the presence of egg predators in the gills of female blue crabs (Hopkins 1947, Schneider et al. 2023a, 2023b). These classifications can be used to improve our understanding of the distribution of reproductive ages, i.e., spawning stock demography, as well as lifetime reproductive potential. Current projections of reproductive potential in Chesapeake Bay rely on average fecundity and average stored-sperm quantities of individual crabs and must account for sperm loss prior to fertilization (Ogburn et al., 2019). Fecundity and stored sperm quantity vary greatly among individuals and the rate at which sperm are lost between mating and fertilization remains unresolved and difficult to assess. Estimates of reproductive potential, therefore, can be improved by pairing fecundity and stored sperm quantity from individual ovigerous females with known spawning histories.

2. Methods

2.1. Animal collection and processing

Ovigerous blue crabs were collected from the Virginia portion of the mainstem of Chesapeake Bay by the Virginia Institute of Marine Science Trawl Survey, herein trawl survey (Tuckey and Fabrizio, 2023). This survey uses a randomly stratified design to conduct 5-min trawl tows each month at 39-45 stations in the mainstem of Chesapeake Bay (Fig. 1). Sampling occurred from April to October 2022, to encompass the entire blue crab spawning season (Lipcius et al., 2003; Schneider et al., 2024); however, no egg-bearing crabs were encountered in April or October, therefore, subsequent analyses include ovigerous crabs from May to September. All ovigerous crabs captured were returned to the lab on ice and refrigerated until processed. Lab processing occurred within 72 h of collection.

Females were measured for carapace width (CW), from epibranchial lateral spine to lateral spine, to 0.1 mm with Vernier calipers, and weighed to the nearest 0.01 g. The carapace was then removed and the spermathecae dissected whole, weighed, and preserved in 70% ethanol for later assessment of sperm quantity. Egg stage, based on egg color, was recorded as early development (orange eggs), mid-development (brown eggs), and late development (black eggs; Van Engel, 1958).

Spawning history was determined by the presence of the nemertean worm, *Carcinomertes carcinophila*, in a female blue crab's gills and egg mass (Hopkins, 1947; Schneider et al., 2023b). These nemerteans are egg predators that reach maturity upon consumption of crab eggs. If a female blue crab has pink or red worms within her gills, she has spawned at least once; if she has white or no worms within her gills, she has not yet spawned (Hopkins, 1947; Wickham et al., 1984). Therefore, ovigerous females with mature (pink or red) worms in their gills are considered multiparous (produced at least one prior egg mass), whereas ovigerous females without mature worms in their gills are considered primiparous (produced their first egg mass, Schneider et al., 2023b).

2.2. Fecundity calculations

To estimate fecundity, eggs were mechanically removed from the pleopods, and weighed to the nearest 0.001 g. A sample of 0.1% to 3.0% of the eggs (or about 800 eggs on average) was subsequently weighed and preserved in 5% formalin in seawater. The remaining eggs were dried at 50°C to the nearest 0.001 g. The total egg mass dry weight was estimated by multiplying the dried weight by the proportion preserved. A subsample of the preserved eggs was weighed, counted under a dissecting microscope (Nikon C-DSS15), and dried at 50°C to the nearest 0.0001 g. Estimated fecundity, herein fecundity, was expressed as the number of eggs per female and calculated as: Fecundity = total egg mass dry weight × (number of eggs in subsample/dry weight of subsample).

2.3. Sperm quantity estimation

Preserved spermathecae were blotted dry and weighed to the nearest 0.0001 g. To estimate stored sperm quantity, the preserved spermathecae were opened, the sperm packets were removed, and the spermathecal walls were scraped with forceps. The empty spermathecae were weighed to the nearest 0.001 g and subsequently rinsed with deionized (DI) water, and the rinsate and spermathecal contents were homogenized for 1 min in a 15 ml

Dounce tissue grinder. Samples were then sonicated with a microtip probe (Branson 450 digital sonifier) at 20% amplitude for 20 s to ensure that sperm cells were isolated and homogeneously suspended in solution. The homogenate was then diluted with DI water and the dilution factor noted. Two 500 µl aliquots of the diluted homogenate were stained with 250 µl of 0.3% trypan blue (w:v in water) to aid in sperm cell identification. Two counts from each pair of spermatheca were performed with a hemocytometer (Neubauer Brightline) at 400x using the center counting grid at each corner square and the central square (n = 5 squares per count). Counts were averaged to estimate the total sperm count. Stored sperm quantity was then calculated by multiplying the total sperm count by the dilution factor, total volume of the homogenate and the counting chamber correction.

2.4. Statistical analyses

Multiple linear regression was employed to model mean fecundity using CW (continuous), month (categorical), egg stage (categorical), and spawning history (i.e., female parity, categorical) as predictors. The interaction between month and parity was examined and ultimately excluded from the regression analysis due to a high degree of influence from one observation (Section S2). An additional interaction between CW and egg stage was explored graphically, deemed inconsequential, and was not considered in the multiple linear regression. Three models were formulated and compared: a global model, a management model, and a comparative model. The global model included all hypothesized predictors of fecundity as fixed effects. The management model included CW, month, and egg stage as fixed effects. These variables are currently used to inform management strategies in Chesapeake Bay. Specifically, blue crab fisheries are size selective and have month-specific restrictions pertaining to catch limits and closed areas. Moreover, in Virginia, ovigerous females with dark eggs (i.e., those about to hatch) cannot be landed (Va. Admin. Code § 20-270). Lastly, the comparative model included CW as a sole predictor and this allowed us to compare our findings with previously published studies on blue crab fecundity. A random effect of tow was not considered because 55% of the tows with ovigerous crabs captured only one ovigerous crab, and within tows the intra-class correlation was low (ICC = 0.13), indicating low dependence among crabs captured within the same tow.

Fecundity was $\log_e$ transformed, herein log; model predictions were back-transformed from log space for plotting with a log-normal bias correction (Sprugel, 1983). Model predictions in log space are presented in Section S3. The three linear regression models of log fecundity were evaluated within an information theoretic framework (Burnham and Anderson, 2007) to identify predictors that were important in explaining variation in female fecundity. Akaike's Information Criterion corrected for small sample sizes (AICc) and weighted model probabilities (w_i) based on Δ_i values were used to determine the probability that a particular model (i) was the best performing model within the set (Anderson, 2008). Models within two Δ_i points were considered equally plausible. Models of mean fecundity were analyzed using the `lm` function in the `stats` package in R (R Core Team, 2022). All fecundity models met assumptions of normality and homogeneity of variance using log-transformed fecundity data.

To assess potential differences in fecundity across years, an analysis of covariance (ANCOVA) was formulated for mean fecundity in 2022 and two prior years using CW as the covariate. Fecundity and size data for 1986 and 1987 were retrieved from Prager et al. (1990) using the `digitize` package in R (Poisot, 2011). As before, fecundity was $\log_e$ transformed. The interaction between year and CW was examined but was considered uninformative and excluded because models with and without the interaction term had less than a 0.5 Δ_i difference (Section S4). Due to an observed difference in the distribution of CW among the three years, an analysis of variance was conducted on CW from 1986, 1987, and 2022.

Stored sperm quantity was modeled as a function of CW, parity, and month using generalized least squares regression with the `nlme` package in R (Pinheiro and Bates, 2022, 2000). Initial model runs for stored-sperm quantity indicated heterogeneity in variance, so we applied an exponential variance function to model sperm quantity. We did not include an interaction between month and parity because only one multiparous female was captured in June. Consequently, we created a month-parity variable to examine differences in mean sperm counts among unique month-parity groups (Primiparous-June, Primiparous-July, Multiparous-July, Primiparous-August, Multiparous-August).

The estimates of stored sperm quantity and fecundity of each female were used to determine reproductive potential. For blue crabs, the sperm-to-egg ratio needed for successful fertilization has not been empirically derived. Therefore, in our estimates of reproductive potential, we examined multiple, theoretical sperm-to-egg ratios of 1:1, 4:1, 10:1 and 25:1. Hypothesized sperm-to-egg ratios range between 4:1 and 10:1 (Ogburn et al., 2019), but 1:1 and 25:1 sperm-to-egg ratios were included here to examine more extreme conditions. Reproductive potential, the potential number of broods a female can produce in her lifetime, was then augmented to account for the brood at the time of capture and previous broods: primiparous females were assumed to have produced their first egg mass at the time of capture, whereas multiparous females were assumed to have produced the egg mass at the time of capture as well as one additional egg mass. We note that multiparous females may have produced more than one egg mass previously, however, the exact number is not known, so we chose to use a conservative estimate (i.e., one additional egg mass). The potential number of broods produced by each female was averaged to estimate reproductive potential under each sperm-to-egg ratio.

3. Results

For the 2022 spawning season, fecundity and stored-sperm quantity were quantified from 126 ovigerous females, ranging from 52.3 mm to 183.1 mm CW, of which 44.4% were multiparous. The percentage of multiparous females increased from 0.0% in May to 64% in August (Fig. 2), and then declined in September to 25%, but sample size in September was small (n = 4). Of all females collected, the mean fecundity was 2.17 million eggs and the mean number of eggs per mm of CW was 15,643.

Diagnostic plots for the fecundity models indicated notable outliers within the data set. Crabs in May (n = 1) and September (n = 4) were excluded from fecundity models because of low sample sizes and because the resulting model was overparametrized. One crab captured in July was considered an outlier due to its extremely small size (CW = 52.3 mm) and high influence as determined by Cook's distance; observations from this crab were excluded from the models of fecundity.

The top-performing model of fecundity was the global model with a w_i of 0.89, followed by the management and comparative models (Table 1). The comparative model was the least informative, however, it may be the most useful in scenarios in which CW is the only available predictor of fecundity. As such the model equation was parameterized as:

$$\text{Fecundity} = 268{,}337 \times e^{0.015\text{CW}}$$

The global model accounted for 54% of the variation in log fecundity ($r^2 = 0.54$), and with the exception of egg stage, all predictors were informative (Table 2). As expected, CW had a strong, positive effect on mean fecundity (Fig. 3). Based on model least square means, primiparous females had about 0.28 million more eggs on average than multiparous crabs, albeit a relatively small difference considering the mean fecundity for all blue crabs was 2.17 million eggs. Females in July and August had a greater mean fecundity than females in June (Table 2, Fig. 3). Parameter estimates from the management and comparative models aligned with the results of the global model (Section S5).

The ANCOVA using data from three years (1986, 1987, 2022) accounted for 49% of the variation in mean fecundity and indicated substantial differences in mean fecundity among years ($r^2 = 0.49$). The effect of CW on mean fecundity in all three years was similar to that of the global fecundity model for 2022 (Table 2, 3). Mean fecundity in 1986 did not differ from that in 2022 (Table 3); however, fecundity in 1987 was considerably higher compared with that in 1986 and 2022 (Fig. 4A). Mean CW also varied substantially across years: the least squares means (± SE) of CW in 1986 and 1987 were 146 ± 2.0 and 148 ± 2.2 mm, respectively, whereas the least squares mean CW in 2022 was significantly smaller: 138 ± 1.6 mm (Fig. 4B). Size-frequency histograms of primiparous and multiparous females from 2022 are presented in Section S6.

Similar to the fecundity models, crabs from May and September and the 52.3 mm CW crab were excluded from models of stored-sperm quantity. Models of mean stored-sperm quantity indicated CW, the month-parity predictor, and the interaction between the two were important predictors of sperm quantity (Table 4). Mean stored-sperm quantity increased with CW of female blue crabs, with the exception of primiparous females in July (Fig. 5). There were no clear patterns in mean sperm quantity between multiparous females and primiparous females across months; as expected, primiparous females in June had the highest quantity of stored sperm (Fig. 5).

The degree to which sperm limitation impacts brood production depended on the sperm-to-egg ratio and month (Table 5, 6). The estimated mean brood production was substantially higher for females in June, compared with females in July and August. For all months, the proportion of females unable to fertilize additional broods was negligible under a 1:1 or 4:1 sperm-to-egg ratio. Using a 10:1 sperm-to-egg ratio, lifetime brood production for primiparous and multiparous females ranged from 5 to 19 egg masses and the proportion unable to fertilize an additional egg mass ranged from 0.04 to 0.24. The proportion of primiparous and multiparous females unable to produce additional egg masses increased greatly at a sperm-to-egg ratio of 25:1. Under high sperm-to-egg ratios (i.e., 25:1), multiparous females are more likely to become sperm limited, with a greater proportion unable to fertilize additional egg masses (Table 6).

4. Discussion

We estimated reproductive output of female blue crabs in Chesapeake Bay by examining individual spawning history, fecundity, and stored-sperm quantity. Spawners in June were mainly primiparous and had the highest quantities of stored sperm (June mean: 289 million sperm cells; July & August combined mean: 95 million sperm cells), whereas about 50% of spawners in July and August were multiparous. Overall, primiparous crabs had a higher mean fecundity than multiparous crabs, with primiparous females in August exhibiting the highest mean fecundity (mean = 2.7 million eggs). Our study adds to previous research by pairing fecundity and stored-sperm quantity data for blue crabs, which provides a more realistic assessment of individual reproductive potential. Generally, the reproductive potential of blue crabs is high at the individual level and sperm limitation is unlikely at the population level. Population-level production may be enhanced by increasing protection of primiparous blue crabs, particularly in June, July, and August when they are more susceptible to fishing mortality and exhibit high reproductive capacity. Moreover, the efficacy of management decisions may be improved by using our updated estimate of mean fecundity, and by accounting for individual or temporal differences in egg production.

4.1. Insights on female blue crab reproductive output

Fecundity in 1987 was significantly higher than in 1986, resulting in a combined average for 1986 and 1987 (Prager et al. 1990) that was more than 1 million eggs higher than the estimated mean individual fecundity in 2022. However, the 1986-1987 average fecundity was based on methods that differed; in 1987 a volumetric approach was used, whereas proportional dry weights were used in 1986. We estimated fecundity using proportional dry weights in 2022; hence our results could be compared more directly with the 1986 results of Prager et al. (1990). Differences in fecundity among years likely reflect methodological differences, rather than a true population-level decline in fecundity at size. The volumetric approach likely biased fecundity estimates high due to the difficulty in removing setae and pleopods from the eggs, inability to remove interstitial water and materials (e.g., sand grains, mud, vegetation) from egg masses, and the assumption that all eggs are spherical (Prager et al., 1990). The use of two-year (1986, 1987) mean fecundity estimates from Prager et al. (1990) has resulted in overestimation of sperm limitation in brood production models (Ogburn et al., 2014; Rains et al., 2016) and overestimation of population production in stock assessment models (Miller et al., 2011) as well as underestimation of brood mortality due to egg predators (Schneider et al., 2023b). Future model estimates of blue crab production should be improved with our updated fecundity estimates, which do not differ from the 1986 results of Prager et al. (1990). Moreover, our estimates of fecundity were generated from a fishery-independent stratified random survey of the spawning stock in the spawning grounds (Lipcius et al., 2003) and are thus representative of the population in Chesapeake Bay. Conversely, fecundity estimates from Prager et al. (1990) may have been biased because sampling in those years was in only about 50% of the spawning grounds; compare sampling area for 1986 and 1987 in Fig. 1 of Jones et al. (1990) with the full spawning ground area in Fig. 6 of Lipcius et al. (2003), which represents the area sampled in 2022.

We conclude that there has not been a population-level decline in fecundity at size between the 1980s and 2022. However, the smaller mean size of female crabs in 2022 may have reduced population-level reproductive output, although the estimated larger sizes in 1986 and 1987 may also have been biased due to sampling extent, as described above. Given the positive, exponential relationship between CW and fecundity, the loss of large, highly fecund females from the population suggests a reduction in population-level production of the Chesapeake Bay spawning stock, as observed in other commercially exploited species (Ohlberger et al., 2020). As such, changes in mean size highlight the importance of assessing population-level reproduction in the context of size structure or biomass, rather than abundance. Larger female blue crabs were more prevalent in Chesapeake Bay prior to the population decline in the 1990s (Lipcius and Stockhausen, 2002). Although the mean size of females in 2022 (138 mm CW) was smaller than that in 1986 and 1987, it was larger than mean size during the population decline in the 1990s and early 2000s, which ranged from 130 to 135 mm CW (Lipcius and Stockhausen, 2002). Additional analyses of female blue crab size in the Bay are needed to confirm if smaller average sizes persisted since the early 2000s.

Primiparous crabs had more eggs per brood than multiparous crabs. In contrast, fecundity of blue crab females in the Gulf of Mexico did not differ between primiparous and multiparous crabs (Graham et al., 2012). This may be due to differences in reproductive physiology between spawners in the Gulf of Mexico and Chesapeake Bay, but may also reflect differences in methods used to assign parity (see Schneider et al., 2023b). With our assignment method, we were unable to differentiate between multiparous females that are on their second, third, or fourth broods; however, fecundity of blue crabs in monitored enclosures declined with successive broods (Darnell et al., 2009). As such, the difference in fecundity between primiparous and multiparous females should be more pronounced if later broods are included in estimates of fecundity for multiparous females.

Month had a substantial effect on female fecundity; spawners in July and August produced more eggs per brood than females in June. Across months, primiparous females produced greater quantities of eggs than multiparous females. Within the spawning grounds, abundance of egg-bearing crabs varies by month (Lipcius et al., 2003, Schneider et al., 2024), indicating that annual egg production may fluctuate substantially as a result of interannual fluctuations in abundance and perhaps fishing pressure. A lower fecundity in June may be related to the high proportion of primiparous females because first-year spawners have a lower gonadosomatic index prior to the start of the spawning season (Schneider et al., 2023a). Additional research is needed to assess fecundity at the beginning and end of the spawning season (i.e., May and September) and to examine monthly patterns in fecundity across years.

Notably, we did not detect an effect of egg stage on fecundity, suggesting that blue crabs lost a negligible portion of their eggs during embryogenesis, which is 10-14 d (Jivoff et al., 2007). Decapods with longer embryogenesis times, such as the American lobster (*Homarus americanus*) lose a large portion of eggs from early to late stages of egg development (Goldstein et al. 2022). Blue crabs can mutilate up to 50% of their egg mass (Dickinson et al., 2006) when conditions are stressful. Indeed, a loss of eggs was observed for blue crabs collected from commercial crab pots only (Graham et al. 2012, Schneider unpublished data). Females in our study were collected by trawl, which does not cause as much prolonged stress as being confined in a trap with conspecifics. We hypothesize that egg loss in the commercial pot fishery reflects a stress response by spawners with egg masses that are in late development.

Our models of fecundity are the first to evaluate the effect of multiple predictors on blue crab fecundity in Chesapeake Bay. The global and management model outperformed the comparative model substantially, indicating CW is not the sole driver of blue crab fecundity. The global model, which includes parity designations as predictors, requires sacrificing egg-bearing females. The management model (including CW, month, and egg stage) outperformed the comparative model and included only non-lethal predictors. Therefore, the management model may be the most practical model of fecundity, especially for long-term monitoring. Both the global and management model explained about half the variation in mean fecundity, indicating additional predictors (e.g., brood number) influence fecundity.

The stored-sperm quantities we observed in 2022 are consistent with previously reported means and variation in stored-sperm quantities (Ogburn et al., 2014; Rains et al., 2016; Ogburn, 2019). Our hypotheses that stored-sperm quantity in multiparous females would decline with increases in CW and that stored-sperm quantity of primiparous females is greater than that of multiparous females were not supported by our data. Rather, the relationship between stored-sperm quantity and CW was variable across months and female parity. For most month-parity combinations, stored-sperm quantity increased with CW, supporting findings that larger females receive more sperm from mates than smaller females (Carver et al., 2005; Jivoff, 1997). Much of the variation in stored-sperm quantity depends on quality of the mate (e.g., mate size, mate nutrition, and mating frequency) and on the location and timing of mating, which cannot be assessed for wild-captured females (Kendall et al., 2002; Carver et al., 2005; Ogburn et al., 2014, 2019). Despite a high level of variation in stored-sperm quantity, females generally had a high complement of sperm in our study.

Blue crab reproductive output is high and sperm limitation likely does not affect the majority of mature female blue crabs in Chesapeake Bay. Under all sperm-to-egg ratios examined, the average female could produce at least three egg masses in her lifetime. Using the recent 4:1 estimate of sperm-to-egg ratio for Chesapeake Bay blue crabs (Ogburn et al. 2019), only 3% of primiparous females and 5% of multiparous females would be sperm limited and unable to produce an additional brood. With the 4:1 sperm-to-egg ratio, three broods per lifetime, and the individual fecundity and stored sperm quantities, population egg production would be reduced by 1.9% due to sperm limitation. Female blue crabs in Chesapeake Bay experience a 6% annual survival rate (Lambert et al., 2006), and their short lifespan suggests that sperm limitation is likely not reducing the reproductive output of blue crabs, unless the sperm-to-egg ratio exceeds 10:1. If females were to live long enough to produce six broods in their lifetime, population egg production would be reduced by 7.7%, under the 4:1 ratio. Based on our values of mean brood production coupled with estimates of annual brood production (Van Engel, 1958; Hines et al., 2003; Darnell et al., 2009), our data support a ratio between 4:1 and 10:1. This aligns well with previous estimates for blue crabs (Ogburn et al., 2019) and other decapods, such as *Chionoecetes opilio* (Sainte-Marie and Lovrich, 1994). Conclusions about sperm limitation and total brood production remain uncertain due to lack of conclusive evidence of the sperm-to-egg ratio required for successful brood production, as well as uncertainty related to declines in fecundity with each subsequent brood produced.

4.2. Fishery implications

Population-level reproductive output may be enhanced by conserving females with the greatest capacity for reproduction and reducing the total pot capture of ovigerous crabs. Overall, primiparous crabs had the greatest capacity for reproduction; primiparous females in June had the highest reproductive potential, whereas primiparous females in August had the highest fecundity. Primiparous females are likely to be those that recently migrated to the spawning grounds. Migrating females experience high exploitation rates along their migratory routes (Aguilar et al., 2008) until they reach the spawning sanctuary. Females in June are particularly vulnerable because the northern extent of the spawning sanctuary does not protect blue crabs until early-June when crabbing is banned (Va. Admin. Code § 20-270). Egg-bearing females are vulnerable to handling and trap mortality especially in July and August due to temperature stress (R.N. Lipcius, unpublished data); hence, we encourage management actions to reduce fishing of ovigerous females June through August. Reproductive potential is also severely limited by the low annual survival of adult blue crabs (6% survival, Lambert et al., 2006a); by winter, only 8-19 % of the spawning stock is comprised of females entering their second year of spawning (Schneider et al., 2023a). Therefore, protecting females until they are able to reproduce is critical. Additional research on the reproductive potential of blue crabs will improve our ability to accurately model production and conserve spawners. We suggest that robust management actions be implemented to protect mature females along their migratory routes and June through August to increase population-level reproductive output.

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Table 1. Linear regression models and corrected Akaike Information Criterion (AICc) for examining fecundity in Chesapeake Bay blue crabs in 2022; CW = carapace width, parity = primiparous or multiparous, egg stage = early, mid, or late development stage. Fecundity was $\log_e$ transformed for all models; k = number of parameters in the model including the intercept and variance; Δ_i = difference in AICc values between a given model and the model with the lowest AICc; w_i = weighted probability of a model being the best in the set. The model with the lowest AICc and highest w_i is in bold. The global model represents all hypothesized predictors of fecundity. The management model includes only those predictors currently used in blue crab management in Chesapeake Bay. The comparative model allows comparison between this study and previous studies. The hypotheses supporting the predictors for fecundity are presented in Section S1 (supplementary materials).

Model	Predictors	k	AICc	Δ_i	w_i
Global	**CW + egg stage + month + parity**	**8**	**28**	**0**	**0.89**
Management	CW + egg stage + month	7	32	4	0.11
Comparative	CW	3	53	25	0.0

Table 2. Parameter estimates in $\log_e$ space for the global model of $\log_e$ fecundity. CW = carapace width; SE = standard error; t = t statistic; p = probability of observing an equal or more extreme value under the null hypothesis. The intercept represents the base condition with CW = 0, Egg $\text{Stage}_{\text{early}}$, $\text{Parity}_{\text{Multiparous}}$ and $\text{Month}_{\text{June}}$.

Variable	Estimate	SE	t	p
Intercept	12.09	0.24	51.1	< 0.0001
CW	0.015	0.0016	9.7	< 0.0001
$\text{Parity}_{\text{Primiparous}}$	0.14	0.06	2.51	0.013
Egg $\text{Stage}_{\text{mid}}$	-0.057	0.06	-0.96	0.34
Egg $\text{Stage}_{\text{late}}$	0.080	0.06	1.26	0.21
$\text{Month}_{\text{July}}$	0.32	0.07	4.54	< 0.0001
$\text{Month}_{\text{August}}$	0.41	0.07	5.94	< 0.0001

Table 3. Parameter estimates for the ANCOVA model of $\log_e$ fecundity as a function of carapace width (CW) and year (1986, 1987, and 2022); estimates are in $\log_e$ space. SE = standard error; t = t statistic; p = p probability of observing an equal or more extreme value under the null hypothesis. The intercept represents the base condition with CW = 0 and Year_{1986}.

Variable	Estimate	SE	t	p
Intercept	12.51	0.20	63.1	< 0.0001
CW	0.014	0.001	10.79	< 0.0001
Year_{1987}	0.52	0.06	8.43	< 0.0001
Year_{2022}	0.07	0.05	1.25	0.212

Table 4. Parameter estimates for the generalized least-squares regression of stored sperm quantity as a function of carapace width (CW), month and parity of a female, and the interaction between CW, month and parity. SE = standard error; t = t statistic; p = probability of observing an equal or more extreme value under the null hypothesis. The intercept represents the base condition of CW = 0 and Primiparous-June.

Variable	Estimate	SE	t	p
Intercept	-490,467,507	101,905,742	-4.81	< 0.0001
CW	5,566,983	877,798	6.34	< 0.0001
Multiparous-July	206,756,995	142,653,617	1.45	0.15
Primiparous-July	681,353,519	202,225,794	3.37	0.001
Multiparous-August	253,127,780	122,552,877	2.065	0.041
Primiparous-August	309,112,807	183,795,074	1.68	0.096
CW × Multiparous-July	-2,806,298	1,170,311	-2.40	0.018
CW × Primiparous-July	-6,258,959	1,624,931	-3.85	0.0002
CW × Multiparous-August	-3,291,287	1,029,400	-3.20	0.0018
CW × Primiparous-August	-3,266,514	1,531,381	-2.13	0.035

Table 5. Estimated number of broods a mature blue crab can produce in her lifetime using four sperm-to-egg ratios across months of the spawning season and combined for all three months, for both primiparous and multiparous females collected by the VIMS Trawl Survey from Chesapeake Bay in 2022. n = sample size of female blue crabs for each month. Primiparous females were assumed to have produced one egg mass, whereas multiparous females were assumed to have produced two egg masses.

		Sperm-to-egg ratios			
Primiparous	n	1:1	4:1	10:1	25:1
June	27	158	27	17	7
July	18	43	18	5	3
August	19	49	19	6	3
Combined	64	93	24	10	5
Multiparous					
June	1	176	45	19	9
July	20	48	13	7	4
August	34	34	10	5	3
Combined	55	42	12	6	3

Table 6. Estimated proportion of females that would be unable to produce an additional egg mass using four sperm-to-egg ratios across months of the spawning season and combined for all three months for both primiparous and multiparous females collected by the VIMS Trawl Survey from Chesapeake Bay in 2022. n = sample size of female blue crabs in each month.

		Sperm-to-egg ratios			
Primiparous	n	1:1	4:1	10:1	25:1
June	27	0	0	0.04	0.07
July	18	0	0.06	0.22	0.33
August	19	0	0.05	0.11	0.37
Combined	64	0	0.03	0.11	0.23
Multiparous					
June	1	0	0	0	0
July	20	0	0	0	0.30
August	34	0.03	0.09	0.24	0.50
Combined	55	0.02	0.05	0.15	0.42

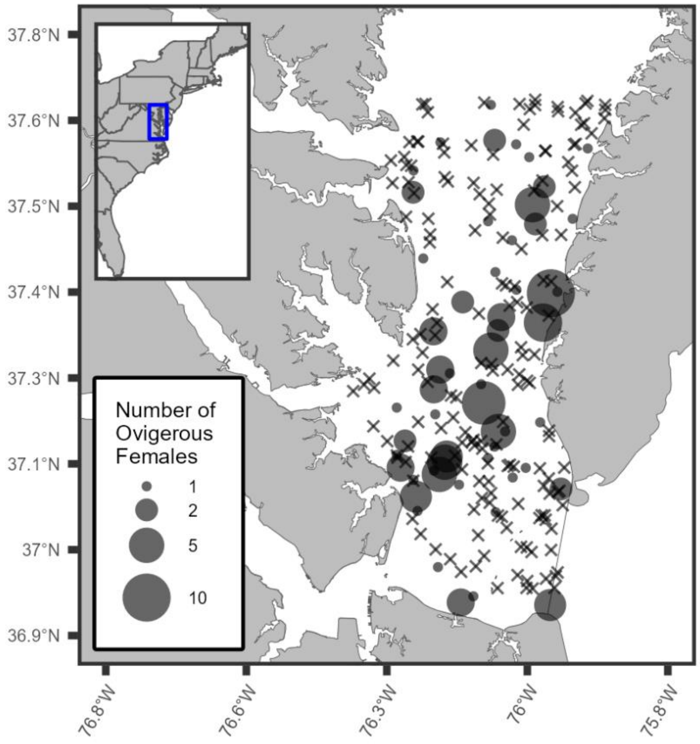

Figure 1. Locations of the VIMS Trawl Survey sampling sites from May to September 2022. Dark circles represent locations where ovigerous blue crabs were captured, with the size of the circle representing the number of ovigerous crabs captured. x = locations that were sampled but no ovigerous crabs were found.

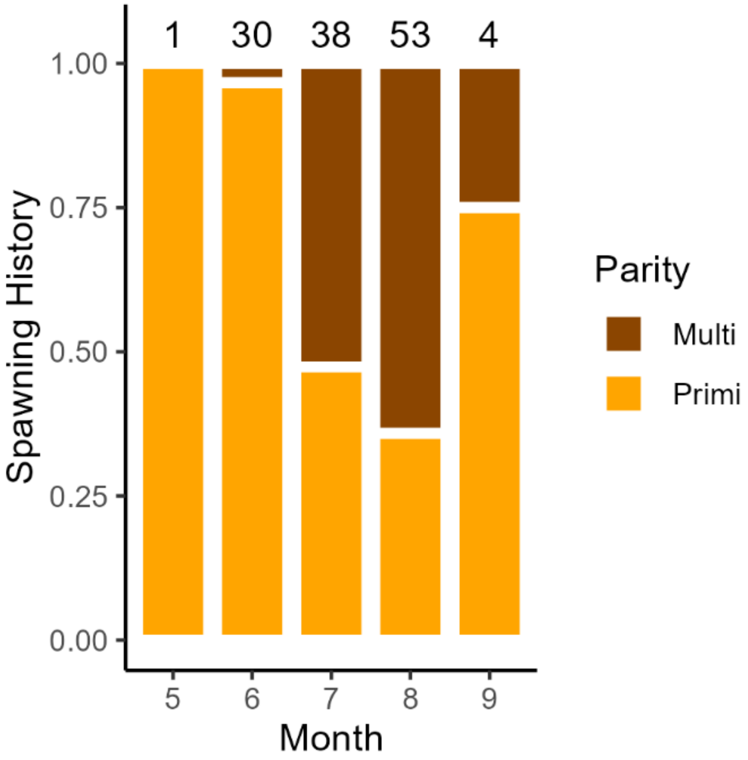

Figure 2. The proportion of multiparous (brown) and primiparous (light orange) female blue crabs across months during the 2022 spawning season in Chesapeake Bay. Month 5 corresponds to May, 6 to June, and so forth. Numbers at the top of the bars represent sample sizes.

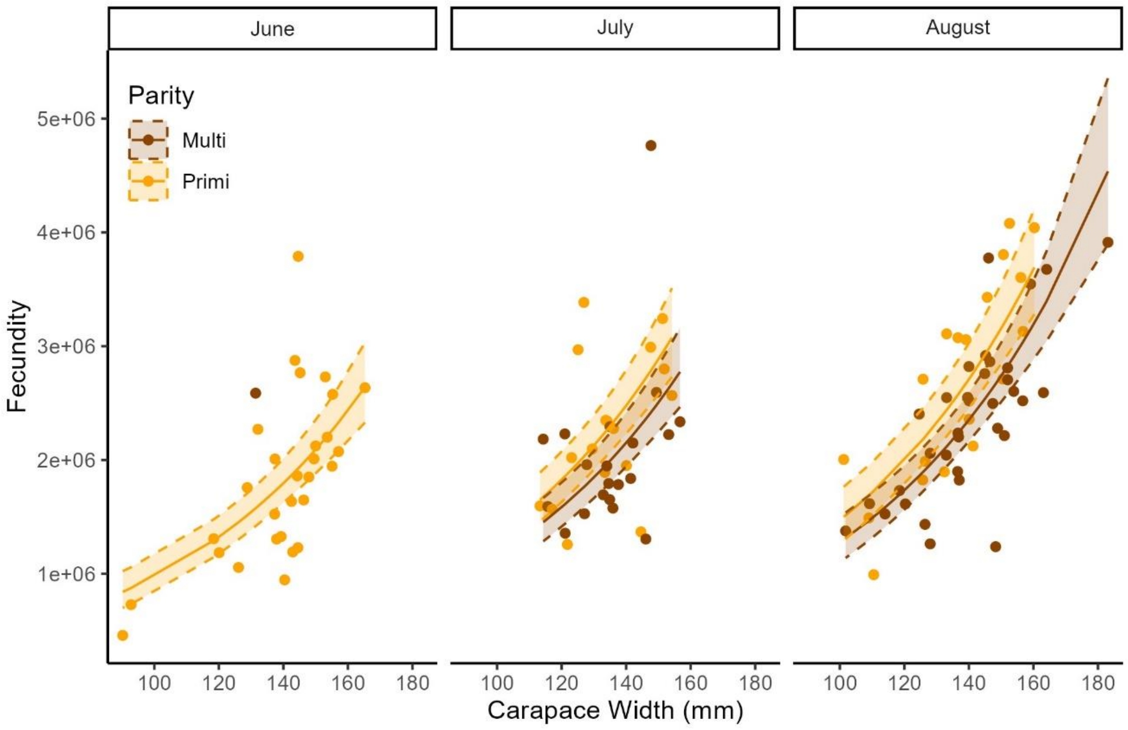

Figure 3. Relationship between fecundity (number of eggs) and carapace width (mm) by female parity and month for blue crabs from Chesapeake Bay in 2022. The solid lines represent the predicted values from the global model (Table 2), with egg stage held constant at early development. The shaded regions denote the 95% confidence intervals of the regression. Model predictions were back-transformed from log space using a bias correction.

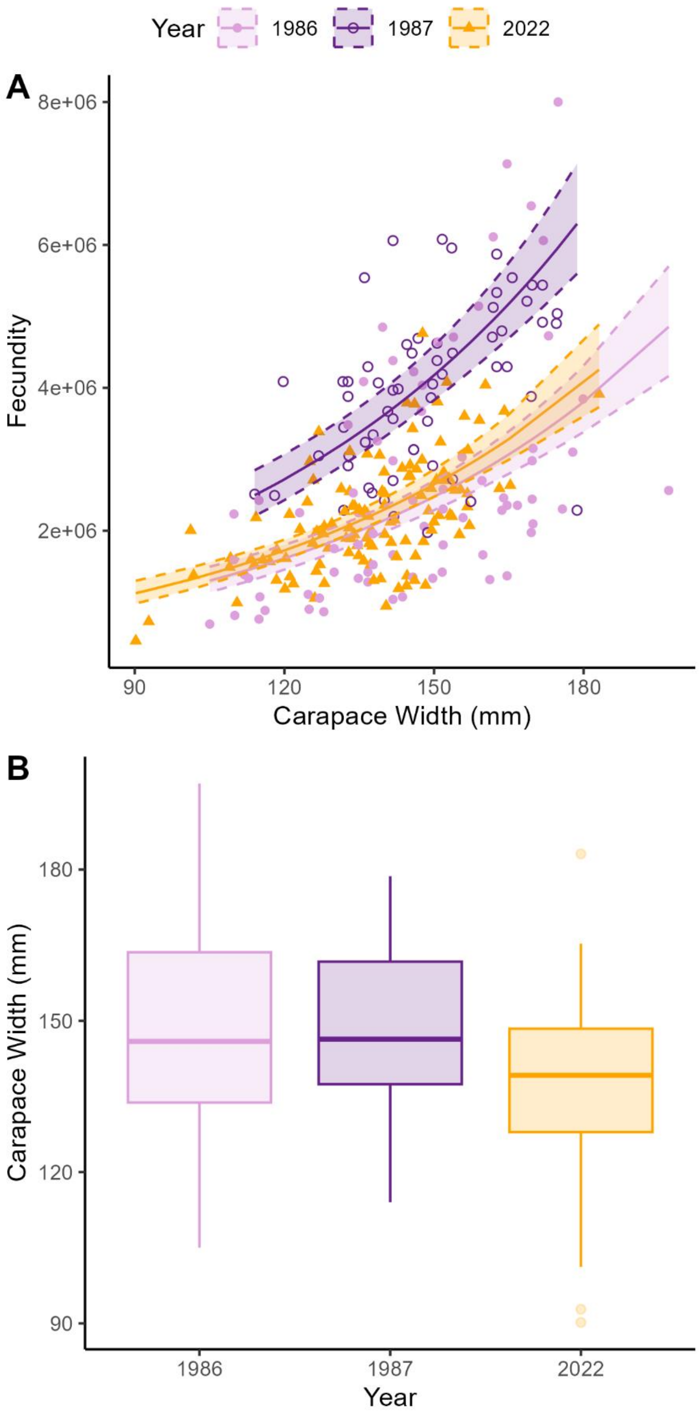

Figure 4. (A) The relationship between carapace width (mm) and year (1986, 1987 and 2022) on blue crab fecundity in Chesapeake Bay. Solid lines represent back-transformed linear regressions, and the shaded regions denote the 95% confidence intervals of the regression (Table 3). (B) Boxplots of carapace width (mm) for females used in fecundity models in 1986, 1987, and 2022. Fecundity and carapace width data from 1986 and 1987 were retrieved from Prager et al. (1990). Individual dots in 2022 are outliers.

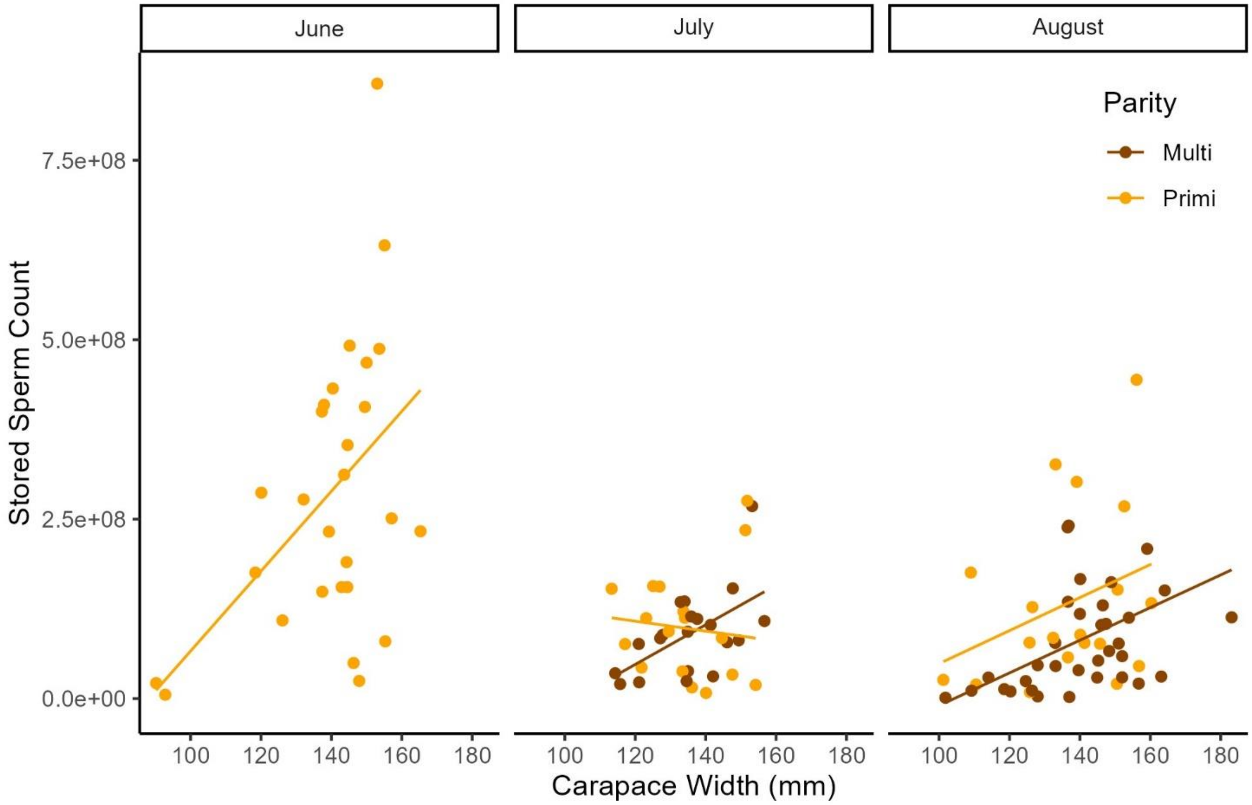

Figure 5. Stored sperm quantity in ovigerous blue crabs from Chesapeake Bay in 2022 as a function of carapace width, female parity, and month. Solid lines represent predictions from generalized least-squares regression (Table 4).

CHAPTER 4: Long-term trends in female blue crab abundance and size: Consequences for total egg production and fishery stability

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Abstract

The blue crab population in Chesapeake Bay, which supports the most valuable fishery in the region, has experienced high variability from the late 1980s through the 2020s. After a period of high productivity, the population declined dramatically in the early 1990s and low abundance persisted throughout the early 2000s (depressed regime), until multiple management actions were implemented in 2008 (recovery regime). The depression in abundance coincided with a reduction in the mean size of mature female blue crabs in the spawning grounds. The extent to which spawning stock abundance and mean size during the spawning season recovered after 2008 is unknown. Similarly, the extent to which declines in size at maturity may impact reproductive output of the population has not been explored. We assessed trends in spawning stock relative abundance, mean size at maturity, and total egg production from 1988 to 2023 using observations from the Virginia Institute of Marine Science Trawl Survey which samples blue crabs from their spawning grounds monthly. We examined mean size at maturity, rather than the commonly reported 50% size at maturity because female blue crabs have a terminal pubertal molt. Given previous declines in size at maturity, we also quantified the relative importance of using size-specific fecundity versus a population-level average fecundity to estimate total egg production for the stock. Spawning stock metrics generally improved since 2008, but in most cases these improvements failed to reach the levels observed during the pre-decline regime (1988 to 1992), indicating a partial recovery of the spawning stock. Mean size at maturity increased after 2008, with subsequent increases in total egg production during the recovery regime. Since 2016, relative abundance, mean size at maturity, and total egg production have varied markedly among years with no apparent pattern, highlighting the need for precautionary fisheries management for this species.

Keywords: Decapod, Exploitation, Fisheries management, Size at maturity, timeseries

1. Introduction

Fisheries management generally aims to sustain healthy populations of exploited species to ensure continued support of ecosystem, economic, and societal needs (Food and Agricultural Organization, 1995; International Council for the Exploration of the Seas, 2019; 16 U.S.C. §§ 1801 et seq). Unfortunately, many fisheries are threatened worldwide due to overfishing, habitat destruction, and the consequences of climate change (Jackson *et al.*, 2001; Möllmann and Diekmann, 2012; Link and Watson, 2019). Decapod fisheries are particularly vulnerable to these factors; various high-value exploited species, such as American Lobster (*Homarus americanus*), snow crab (*Chionoecetes opilio*), and Atlantic blue crab (*Callinectes sapidus*) have experienced significant declines in abundance followed by slow or limited recovery, highlighting the need for more robust evaluations of stock health (Miller *et al.*, 2011; Atlantic States Marine Fisheries Commision, 2020; Szuwalski *et al.*, 2023).

Evaluations of stock health may be improved by assessing multiple indicators of stock status, especially if management strategies aim to be precautionary and holistic (Mullowney and Baker, 2023). Common indicators used to assess stock health are abundance, landings or catch data, and exploitation rates; however, inclusion of additional metrics, such as recruitment indices, size at maturity, age at maturity, population age structure, sex-ratio, egg production, and body condition factors (e.g., Fulton's K, gonadosomatic indices), can inform and improve fisheries management (Hilborn, 2002; Shin *et al.*, 2005; Probst *et al.*, 2013; Lloret *et al.*, 2014; Morgan, 2018). For decapod fisheries, indicators of spawning stock health and size at maturity are especially important because management strategies for these fisheries focus on minimum landing sizes and protection of mature females (Miller *et al.*, 2011; Penn *et al.*, 2019).

Size-at-maturity (SAM) data are used to inform minimum landing sizes for many commercially exploited decapods and to estimate reproductive output of populations. Minimum landing sizes that are greater than SAM help prevent recruitment overfishing by reducing harvest mortality of individuals that have not yet matured or reproduced (Froese *et al.*, 2008). Size at maturity is also used to monitor stock health because this indicator responds quickly to intense fishing pressure (Pollock, 1995; Trippel, 1995; De Roos *et al.*, 2006). For organisms with continuous growth, such as American lobster or blue swimming crab (*Portunus pelagicus*), the size at which 50% of the population is mature is typically used as an indicator of the onset of maturity (Pollock, 1995; de Lestang *et al.*, 2003; Le Bris *et al.,* 2017; Waiho *et al.,* 2017; Mullowney and Baker, 2021; Waller *et al.,* 2021). Maturity indicators for decapods with determinate growth are better represented by the mean size at maturity (Somerton, 1981; Hines, 1989; Corgos and Freire, 2006; Orensanz *et al.,* 2007; Zheng, 2008). Size has a well-established relationship with fecundity for decapods (Hines, 1982) and a reduction in female SAM can reduce the reproductive output of a population (Ohlberger *et al.*, 2020). Moreover, a reduction in SAM may diminish the value of harvested individuals and encourage commercial fishers to increase harvest rates to maintain the average biomass of their catch. Unaccounted-for shifts in SAM, and thus changes to reproductive output, may reduce the efficacy of fishing regulations and jeopardize population health.

The Atlantic blue crab is a commercially important decapod that is subject to high exploitation in Chesapeake Bay. Currently, annual decisions about blue crab population and fishery status are based on the absolute abundance of spawning capable (mature or imminently maturing) female crabs and their exploitation rate, while also considering socio-economic impacts of management options and the abundance of male and juvenile cabs (Sharov *et al.*, 2003; Miller *et al.*, 2011). Absolute abundance of mature females is estimated by a bay-wide Blue Crab Winter Dredge Survey (hereafter, Winter Dredge Survey), cooperatively run by the Virginia Institute of Marine Science (VIMS) and Maryland Department of Natural Resources (Sharov *et al.*, 2003). Annual estimates of mature female abundance have fluctuated dramatically since 1990, ranging from approximately 50 to 250 million mature female crabs during winter; annual harvest has also varied, ranging from 57 to 220 million female crabs (Chesapeake Bay Stock Assessment Committee, 2023).

Harvest regulations for the Chesapeake Bay blue crab fishery changed in response to abundance trajectories of mature females. An 81% reduction in female abundance between 1992 to 2000 (Lipcius and Stockhausen, 2002), and persistent low abundances through 2008, prompted the implementation of strict management regulations aimed at protecting female crabs. In Chesapeake Bay, blue crabs exhibit a significant stock-recruit relationship, and as such, an increase in the number of mature females is expected to increase recruitment (Lipcius and Van Engel, 1990; Lipcius and Stockhausen, 2002). Following a series of management actions, including expansion of the historic spawning sanctuary by 535% in 2000 to 2002 and the closure of the commercial dredge fishery in 2008, harvest of females was lowered by 34% (Lipcius *et* *al.*, 2001, 2003; Seitz *et al.*, 2001; Miller *et al.*, 2011). In response to management actions, the average abundance of females increased significantly (Chesapeake Bay Stock Assessment Committee, 2023). In most years, however, annual female abundance remains variable and consistently below the abundance target identified in the 2011 stock assessment (Miller *et al.*, 2011), even though exploitation rate has generally been below the target (Chesapeake Bay Stock Assessment Committee, 2023), suggesting that effective protection of female blue crabs has not been achieved in recent years under the current set of management regulations. Moreover, the juvenile segment of the population reached a record low abundance in 2021 and the entire population reached a record low abundance in 2022 (Chesapeake Bay Stock Assessment Committee, 2023).

The high variability in annual abundance prompts evaluation of the female segment of the population during the spawning season, to complement the currently used approach that relies on winter sampling of the population. Stock indicators that are assessed on the spawning grounds during the spawning season may be more representative of the health and productivity of the spawning stock compared with estimates derived from winter survey results. After winter, when temperatures rise, female blue crabs that are not yet on the spawning grounds will migrate up to 250 km to high-salinity spawning areas (Turner *et al.,* 2003; Aguilar *et al.*, 2005; Lambert *et al.*, 2006b). Migration patterns of mature females are unidirectional and known by fishers who target migrating females (Aguilar *et al.*, 2008). Female blue crabs on the spawning grounds in late winter through spring, when temperatures begin to rise, are also subject to fishing mortality until the spawning sanctuary goes into effect in late spring and early summer (Lipcius *et al.*, 2003; Schneider *et al.,* 2023b; Virginia. Admin. Code § 20-270-40). Therefore, many of the females tallied during the winter survey may not survive to spawn. In addition, newly molted and mated females may join the spawning stock during spring; these females would also not have been tallied during the winter survey. Spawning stock indicators during the spawning season are thus more likely to reflect actual egg production by the spawning stock than indicators derived during winter.

Indicators of stock health, such as total egg production (TEP), must also account for variation in reproductive capacity by size, because mean SAM of blue crabs can fluctuate by 20 mm among years (Lipcius and Stockhausen, 2002). The loss of large, highly fecund females from the population implies a loss of reproductive output, which may be captured only by assessing size-specific egg production. Positive associations between relative abundance and female SAM were previously identified from 1988 to 2000 in Chesapeake Bay (Lipcius and Stockhausen, 2002). At low spawning stock abundance, mean size was 8% smaller than at high spawning stock abundance, implying a disproportionately higher loss of reproductive output with low population sizes (Lipcius and Stockhausen, 2002). The fishery in Chesapeake Bay is size-selective and depensatory, thereby removing a greater fraction of large females at low population sizes and reducing the population’s capacity to recover from low abundance levels (Miller *et al.,* 2011). Moreover, the SAM for a female remains constant through her mature life because of her terminal molt to maturity (Smith and Chang, 2007), precluding increased egg production with growth.

In this study, we assessed indicators of spawning stock health during the spawning season and across three temporal regimes within the blue crab fishery: pre-decline (1988 to 1992), depressed (1993 to 2007), and recovery (2008 to 2023). The indicators of spawning stock health that we considered were relative abundance, mean SAM, and TEP. We hypothesized that 1) relative abundance and TEP would be greatest during the pre-decline regime, followed by the recovery regime, and the depressed regime, based on trends of bay-wide abundance of the spawning stock in winter (Chesapeake Bay Stock Assessment Committee, 2023). We also hypothesized that 2) SAM would positively covary with relative abundance. Our specific objectives were to 1) assess patterns in spawning stock health from 1988 to 2023 and quantify differences in indicators among the three temporal fishery regimes for blue crabs, 2) investigate covariation between mean SAM and relative abundance, and 3) quantify the impact of different measures of fecundity (i.e., size-specific or population average) on TEP.

2. Methods

2.1 Data sources

Blue crab abundance and size data were obtained from the VIMS Trawl Survey, a stratified random survey that samples the Virginia portion of Chesapeake Bay. We used 1988 as the first year in our time series because sampling in the Bay mainstem was inconsistent prior to 1988. Each month, 45 stations within 12 depth-defined strata in the mainstem were sampled. At each station, a 9.1-m headline, 4-seam trawl net with a 38.1-mm stretch-mesh body and a 6.4-mm mesh cod liner was towed for 5 min. Starting mid-2015, the gear consisted of a 5.8-m headline semi-balloon otter trawl with a 40-mm stretch-mesh body and a 6.4-mm liner and tickler chain. The number of blue crabs was calibrated to account for changes in gear throughout the time series (Fabrizio and Tuckey, 2016).

All mature females captured in the mainstem of the Bay in June, July, and August from 1988 to 2023 were considered because this is the primary spawning area for females in the Bay and because the majority of spawning occurs between June and August (Schneider *et al.*, 2024). Females encountered by the trawl survey were enumerated, measured, and assigned as mature based on the rounded abdomen shape characteristic of mature female blue crabs (Van Engel, 1958). Size was measured as carapace width (CW) in mm, from lateral spine to lateral spine.

2.2 Spawning stock indicators

A random stratified index (RSI) of relative abundance was calculated annually from the number of mature females captured by the Trawl Survey, following Tuckey and Fabrizio (2023). The RSI was calculated using design-based estimates and a delta-lognormal model of stratum-specific abundances because the time series included a high proportion of trawl tows that captured zero mature females. This resulted in RSI_{delta} for abundance, which was calculated as

$$\mu_k = \frac{\sum_{x > 0}^{n_k} (\ln x_i)}{n_k} \quad (1)$$

$$P_k = \left(\frac{n_{k,\ x=0}}{n_k}\right) \quad (2)$$

$$\Delta_k = e^{\left(\mu_k + \ \ln P_k + \frac{s_k^2}{2}\right)} \quad (3)$$

$$RA = \frac{\sum w_k * \Delta_k}{\sum w_k} \quad (4)$$

where within each k^{th} stratum, the $\log_e$ mean (μ) count of mature females (x) was calculated for all tows (n) with a positive catch (eq. 1). The probability (P) that a tow would encounter zero mature females was also calculated (eq. 2). Within each stratum, the mean, logged probability, and half of the variance in blue crabs among tows (s^2) were summed and exponentiated out of $\log_e$ space (eq. 3) to estimate a delta mean per stratum, Δ_k (Fletcher, 2008; Tuckey and Fabrizio, 2023). Variance was calculated according to Fletcher (2008). A Bay-wide relative abundance (RSI_{delta}) was calculated by weighting the stratum means (Δ_k) with the spatial area of each stratum, w_k (eq.4). The RSI_{delta} value thus represents an expected number of crabs per tow, accounting for the spatial distribution of tows and probability of zero encounters. The RSI_{delta} calculation for abundance was performed in SAS 9.4, and is herein referred to as relative abundance.

We also estimated an RSI_{delta} of TEP using size-specific fecundity (herein, TEP_{size}). Size-specific fecundity was calculated using the CW of each female captured and the allometric relationship between fecundity and CW , fecundity = 268,337 × $e^{0.015 \times CW}$; fecundity was multiplied with a bias correction factor of 1.045 to account for transformations to and from log space (Schneider et al., *In review*). We assumed all females produced one brood. Females in Chesapeake Bay are assumed to produce one to three broods in a season, however, we chose a conservative value of brood production because these values and the predictors of multiple brood production (e.g., CW; Dickinson *et al.*, 2006) have not been empirically derived within Chesapeake Bay and differ regionally (Hines *et al.*, 2011). This resulted in an estimate of the potential number of eggs produced by each female captured by each tow. Number of eggs was summed across females in the tow to estimate potential egg production per tow. Egg production per tow was then used to calculate a relative index of TEP_{size} each year using the delta-lognormal method, as described previously.

Mean SAM was used rather than the commonly reported 50% SAM, which is the size at which an individual has a 50% chance of being mature. The 50% SAM indicator is often relied on for species that have continuous growth to indicate the size at which maturation begins. Robust 50% SAM metrics for blue crabs in the spawning grounds are difficult to estimate because of sex-specific habitat partitioning between immature females and mature females (Hines *et al.*, 1987; Hines, 2007). However, because female blue crabs have a terminal molt, the average size of the blue crabs on the spawning grounds during the spawning season represents the mean SAM of the spawning stock (Hines, 1989). Therefore, the CW of all females was averaged arithmetically to estimate the annual SAM. SAM allowed us to infer the relative importance of female blue crab size on egg production. Relative abundance, TEP_{size}, and mean SAM were normalized, to allow for comparisons of these metrics on the same scale. Metrics were normalized by subtracting the index mean and dividing by the index standard deviation.

2.3 Evaluating indicators across regimes

We assessed annual indices of relative abundance and TEP_{size} during each temporal regime to evaluate changes in spawning stock abundance and egg production over time. Each time series was analyzed with autoregressive moving average models using the auto.arima function in the `forecast` package in R (Hyndman and Khandakar, 2008; Hyndman *et al.,* 2024).

Estimates of the autocorrelation parameters (p, q, and d) were zero for models of relative abundance and TEP_{size}; therefore, generalized least squares regressions were performed in R using the `nlme` package (Pinheiro and Bates, 2000, 2022). The assumption of normality was assessed using visualizations of normalized residuals, and no substantial deviations from normality were detected. Due to heteroskedasticity among groups, regressions of relative abundance and TEP_{size}, were fit using parameters for unequal variances among the regimes.

Annual mean size was regressed as a function of relative abundance to explore the potential covariation between mean size and abundance and to examine if this relationship persisted in Chesapeake Bay since 2000 (Lipcius and Stockhausen, 2002). We used a weighted linear regression with the inverse variance of the annual CWs as weights. The model residuals met the assumptions of normality and independence; however, due to nonstationary heteroskedasticity among temporal regimes, we added regime as a categorical variable to the weighted linear regression model. The resulting multiple linear regression model with relative abundance and regime met the assumptions of linear models, including no collinearity between predictors and no heteroskedastic errors. With the addition of regime to the model, we explored including an interaction between regime and abundance but ultimately excluded said interaction because it was an unimportant predictor.

2.4 Differences in TEP

To investigate the importance of blue crab size when assessing TEP, we compared relative indices of egg production per year calculated from the size-specific fecundity (TEP_{size}, described in section 2.2) of females and two estimates of fecundity that do not account for size.

First, a constant of 2.17 million eggs per female, estimated in 2022 (Schneider *et al., In review)*, was used to represent an average fecundity (TEP_{2022}). Second, a constant of 3.0 million eggs per female, estimated in 1986 and 1987 (Prager *et al.,* 1990), was used as an alternative mean fecundity (TEP_{1980s}). Variation between TEP indices was evaluated by calculating the difference between TEP_{size} and mean TEP calculations, as TEP_{size} – TEP_{2022} (= TEP_{diff22}) and TEP_{size} – TEP_{1980s} (= $TEP_{diff80s}$). A t-test, implemented in package `stats` in R (R Core Team, 2022), was used to identify if TEP_{diff22} and $TEP_{diff80s}$ were significantly different from zero. TEP differences were modeled using generalized least squares as a function of relative abundance, regime, and an interaction between the two. An interaction was hypothesized given differences in TEP_{size} with abundance. The variance for each regime was modeled individually due to heteroskedasticity. The models met assumptions of normality and independence and were fit using the `nlme` package in R (Pinheiro and Bates, 2000, 2022.

3. Results

From 1988 to 2023, 5,978 mature female blue crabs were captured in 4,410 tows (Figure 1). More than 100 mature females were encountered annually in most years (56%); fewer than 50 mature females were encountered in 2003, 2004, 2005, 2015, and 2021. Over the 36 years considered, the average percent of tows that encountered mature female blue crabs was 37.9% (n = ~ 135 tows yr^{-1}). The highest percentage of encounters occurred in 1991 at 71.4 % and the lowest percentage of encounters occurred in 2015 at 17.1% (Figure 2).

3.1. Survey indices

The long-term, mean relative abundance (RSI_{delta}) was 2.47 mature female blue crabs per tow (Figure 3A). Regime (pre-decline, depressed, recovery) was a significant predictor of relative abundance (Table 1, Figure 4A). Female abundance was about seven-fold higher during the pre-decline regime than during the depressed regime (Table 1). Relative abundance in the recovery regime was more than twice as high as that during the depressed regime, suggesting a modest recovery (Table 1). The least squares mean (± SE) of relative abundance was 7.1 ± 2.7 crabs per tow during the pre-decline regime, 0.98 ± 0.14 crabs per tow during the depressed regime, and 2.42 ± 0.77 crabs per tow during the recovery regime (Figure 4A).

The pattern in TEP_{size} across years was similar to that of relative abundance (Figures 3B, 4B). The average TEP_{size} was 4.1 million eggs per tow (Figure 3B). Estimated values of TEP_{size} for the pre-decline regime (9.7 ± 1.8 million eggs per tow) and for the recovery regime (4.3 ± 1.1 million eggs per tow) were substantially greater than that of the depressed regime (1.9 ± 0.21 million eggs per tow; Table 2). The least squares mean of TEP_{size} for the recovery regime was less than half the estimated TEP_{size} in the pre-decline regime, but over twice that of the depressed regime (Figure 4B).

3.2. Mean size at maturity

Size (CW) of mature females captured during the spawning season ranged from 48 mm to 197 mm, with a mean ± SE of 141.3 ± 0.2 mm. Across years, the largest mean SAM was 147.1 ± 1.6 mm CW in 2007; the lowest mean SAM was 131.1 ± 1.6 mm CW in 1994 (Figure 5).

Regime was an important predictor of mean SAM, whereas the relative abundance of mature females was an uninformative predictor (Table 3). Overall, the weighted linear regression model accounted for a moderate amount of variation in mean SAM, with $r^2 = 0.39$. The least squares mean for SAM decreased by about 5% from the pre-decline regime (144.0 ± 1.9 mm CW) to the depressed regime (137.0 ± 0.98 mm CW) and rebounded during the recovery regime (141.5 ± 1.0 mm CW) to a value that was 98.3% of the pre-decline regime mean (Figure 4C). The variance in mean SAM was almost three times higher, at 20.0, when relative abundance was less than the long-term mean (2.47 crabs per tow). When relative abundance was greater than the long term mean; the variance was 7.0, suggesting consistently large size with high relative abundance (Figure 6).

3.3. Trends in stock indicators

The normalized spawning stock indicators, relative abundance, TEP_{size}, and mean SAM of females, exhibited a similar pattern over time (Figure 7), as did the percentage of trawl tows that encountered a mature female during the spawning period (Figure 2). These patterns were characterized by high values in the early part of the time series, followed by a prolonged decline and a subsequent increase after management actions. Mean SAM declined after and recovered earlier than relative abundance and TEP_{size}, with relative abundance and TEP_{size} having almost identical trends. The main difference between the two occurred at low abundances: TEP_{size} suggested worse stock health than relative abundance when the scaled metrics were at values less than their long-term mean. In contrast, TEP_{size} suggested that the stock was in better health than did relative abundance when the scaled metrics were greater than their long-term mean (Figure 7).

3.4. Differences in TEP

Estimates of TEP_{size}, TEP_{2022}, and TEP_{1980s} differed substantially (Figure 8). TEP_{1980s} produced higher estimates than TEP_{size} and TEP_{2022} in all years; TEP_{2022} and TEP_{size} were similar though TEP_{2022} was less than TEP_{size} in 83% of years (Figure 8). In absolute numbers, the average TEP_{diff22} ($TEP_{size} – TEP_{2022}$) was 0.40 million eggs per tow and $TEP_{diff80s}$ ($TEP_{size} – TEP_{1980s}$) was 1.4 million eggs per tow. Both were statistically different than 0 (*t*-test TEP_{diff22}: $t = 4.1$, $p < 0.001$, *t*-test $TEP_{diff80s}$: $t = -6.8$, $p < 0.0001$). The smallest TEP_{diff22} was 7,380 eggs per tow in 2003 and the largest was 2.0 million eggs per tow in 2017. The smallest $TEP_{diff80s}$ occurred in 2021, 0.24 million eggs per tow, and the greatest occurred in 2017, 6.2 million eggs per tow.

Regime, relative abundance, and their interaction were important predictors of $TEP_{diff80s}$ and TEP_{diff22} (Tables 4, 5). While the parameter estimates for the interaction terms were only marginally different than 0 for the TEP_{diff22} model, we retained the interaction in the TEP_{diff22} model to be consistent with the $TEP_{diff80s}$ model. Generally, TEP_{diff22} increased with relative abundance for the pre-decline and recovery regimes, but was unrelated to relative abundance in the depressed regime. Moreover, the estimated difference in total egg production was greatest for the pre-decline regime and lowest for the depressed regime (Figure 9A). For $TEP_{diff80s,}$ relative abundance in all regimes had a negative effect, but greater differences in TEP generally occurred at higher abundances (Figure 9B).

4. Discussion

Indicators of spawning stock health generally improved after the new management regulations were implemented in 2008; however, in all cases, values of these annual indicators remained lower than those observed during the pre-decline regime. Moreover, indicators during the recovery regime were characterized by extreme variability, with rapid year-to-year changes. This pattern was especially true for mean size at maturity (SAM), which varied markedly from 2016 to 2023, changing by about 10 mm from year to year. Egg production (TEP), and thus larval supply, were disproportionately reduced in years when low relative abundance and a smaller SAM co-occurred. In some years of low relative abundance, however, mean SAM was average or high, thereby buffering egg production to some extent. This highlights the need to account for blue crab body size when estimating TEP for models. Based on our results, we caution against using average fecundity when calculating TEP and instead recommend using size-specific fecundity, especially because the historical and commonly used average fecundity from the 1980s overestimated TEP in all years. This is the value of fecundity currently used in the stock assessment and as such, recruitment predictions from the assessment are biased high and lead to overly optimistic projections of stock productivity. High variability in stock indicators suggest that this population responds quickly to perturbations. Variability and rapid change make fisheries management more difficult, and recent instability in stock estimates requires more precautionary fishery management. We recommend evaluating stock health indicators during the spawning season as we did here, to better assess spawning stock health.

4.1 Changes in size at maturity (SAM) & consequences for total egg production (TEP)

Changes in mean SAM may reflect a rapid response to management interventions. For example, the progressive expansion of the spawning sanctuary in 2000 and 2002 (Lipcius *et al.*, 2003; Lambert *et al.*, 2006b) may have promoted larger female sizes in 2003 and 2004. Mean SAM varied with temporal regime likely due in part to the depensatory nature of the commercial fishery and a high exploitation of large females during periods of high exploitation (Lipcius and Stockhausen, 2002; Miller *et al.*, 2011).

Our model explained 39% of the variation in mean SAM, indicating that additional factors impact mature female size. Environmental conditions during molting affect blue crab growth and thus SAM. Blue crab growth is temperature dependent; warmer temperatures decrease growth per molt, leading to smaller individuals per instar (Kuhn and Darnell, 2019). As a result, female SAM is negatively correlated with water temperature and varies with season (Darnell *et al.*, 2009; Hines *et al.*, 2011; Graham *et al.*, 2012). Smaller sizes at the terminal molt are also associated with high salinity (Fisher, 1999). In addition, mean SAM can vary substantially across geographic locations (Miller *et al.,* 2011). We were unable to account for these predictors in our study because environmental conditions at the location of the pubertal molt are unknown for mature blue crabs captured by the trawl. Given that females on the spawning grounds grow and molt to maturity within various subestuaries throughout Chesapeake Bay, the location that females on the spawning grounds migrated from and the relative contribution of each tributary to the spawning stock remains unknown.

Blue crabs, and brachyuran crabs generally, have a positive, hyper-allometric relationship between the number of eggs per brood and body size (Hines, 1982; Prager *et al.*, 1990; Medina Mantelatto and Fransozo, 1997; Graham *et al.*, 2012; Severino-Rodrigues *et al.*, 2013). Thus, larger individuals contribute disproportionately more offspring per brood to the population than smaller individuals, and negative shifts in the size distribution of mature females result in a significant loss of reproductive potential. When high mean SAM is preserved, however, minor reductions in relative abundance may be less concerning because population-level reproductive capacity is buffered by greater egg production per crab. For example, between the pre-decline regime and depressed regime, TEP_{size} decreased by 80% while relative abundance declined by 86%. Moreover, mean SAM declined after observed declines in relative abundance and recovered before relative abundance, thereby buffering some reductions in stock health.

Smaller females may produce more broods than larger females, as in North Carolina (Dickinson *et al.*, 2006), thereby compensating for the reduced number of eggs per brood and minimizing the impact of reduced size on reproductive output. Females in North Carolina are exposed to temperatures warmer than those in Chesapeake Bay and thus produce more broods per season than females in Chesapeake Bay (Hines *et al.,* 2011). The number of broods produced per season is assumed to range from 1 to 3 in Chesapeake Bay, but has not been quantified. The period of time between each brood and whether brood production varies by size are also unknown for Chesapeake Bay. Therefore, we conservatively assumed all females produce one brood. We also assumed 100% fertilization success based on the low probability of egg predation and sperm limitation *(*Schneider *et al.*, 2023a, Schneider *et al*., *In review*).

Given the high annual variation in mean SAM and the positive relationship between fecundity and size, we caution against using time-invariant fecundity estimates and instead recommend using TEP_{size} for estimates of total egg production. If this is not feasible, then we recommend calculating the mean size of mature female blue crabs in a given year and estimating the fecundity for a female at the mean size given established fecundity and size relationships (Section 2.2). Differences between TEP_{size} and TEP estimated using mean fecundities are likely associated with annual differences in the observed size distribution of female blue crabs. When mean SAM was close to the CW associated with the average fecundity, the differences in TEP were lower, although the number of crabs dampened this effect at high abundances. The average differences between TEP_{size} and TEP_{2022} or TEP_{1980s} were notable. At maximum differences, TEP_{diff22} was the equivalent of removing approximately 1 crab per tow as compared to estimates of TEP_{size} and $TEP_{diff80s}$ was the equivalent of adding about 2.5 to 3 additional crabs per tow; these are substantial changes given that the average number of female blue crabs per tow was 2.47.

The difference between the average fecundity per female estimated in the 1980s (3.0 million eggs; Prager *et al.,* 1990) and that estimated in 2022, and subsequently used to calculate TEP in this study (2.17 million eggs), was likely due to methodological differences between studies rather than biological differences between timepoints (Schneider et al. *In review*). The average fecundity value from the 1980s, which has historically been used in stock assessments for blue crab in Chesapeake Bay, and to estimate brood production and brood mortality rates (Miller *et al.*, 2011; Ogburn *et al.*, 2019; Schneider *et al.*, 2023a), produced an overestimate of annual egg production. Therefore, we recommend using updated fecundity values for future production models.

4.2 Indicators of stock health

We observed high synchrony between our stock health indicators, which was unsurprising for relative abundance and TEP_{size} because they were based on observations from crabs collected by the same survey and similar estimation methods (RSI_{delta}). Compared to relative abundance, TEP_{size} provided a more optimistic view of spawning stock health when the normalized indicators were above zero, and a less optimistic view of spawning stock health when said indicators where below zero, suggesting that relative abundance alone may not capture the dynamics of the spawning stock, especially as it pertains to reproductive potential. Patterns in relative abundance and TEP_{size} also generally tracked spawning stock abundance estimates from the Blue Crab Winter Dredge Survey, despite differences in survey timeframes and design (Chesapeake Bay Stock Assessment Committee, 2023). The Winter Dredge Survey results indicate a higher degree of recovery of the spawning stock than the TEP_{size} and relative abundance estimated in this study. Since 2008, relative abundance in the Trawl Survey was greater than the time-series mean (2.47 crabs per tow) in 25% of years, and TEP_{size} was greater than the long-term average (4.1 million eggs per tow) in 38% of years. Since 2008, however, female blue crab abundance from the Winter Dredge Survey was greater than the long-term mean in 69% of years (Chesapeake Bay Stock Assessment Committee, 2023).

Similar trajectories in the indicators of spawning stock health (relative abundance, TEP, mean SAM), with dramatic variability from 2016 to 2023, were also observed in the proportion of trawl tows that encountered female crabs. While the proportion of tows that encountered mature female blue crabs is not a recognized stock health indicator, the low proportion observed between 1993 and 2007, and in select years after 2012, suggests that this may be a useful indicator of spawning stock health. Although trawls can have low efficiency at capturing crabs (Homer *et al.,* 1980), trawl catches are considered less biased for crab sex and size, compared with seines and pots, and are generally recommended for sampling crabs (Smith *et al.,* 2004; Bellchambers and De Lestang, 2005). As such, trawl surveys are a primary monitoring and collecting program for blue crabs (Jones *et al.*, 1990; Fisher, 1999; Seitz *et al.*, 2001; Lipcius and Stockhausen, 2002; Lipcius *et al.*, 2003; Kahn and Helser, 2005; Ogburn and Habegger, 2015; Weiss and Downs, 2020; Kemberling and Darnell, 2020; Taylor and Fehon, 2021; Schneider *et al.*, 2024) and other exploited crab species (Somerton, 1981; Dew and McConnaughey, 2005; Zheng, 2008; Swiney *et al.*, 2012; Marks *et al.*, 2021; Mullowney and Baker, 2021; Murphy, 2021; Szuwalski *et al.*, 2023). Surveys with larger vessels and longer tow times, compared with the VIMS Trawl Survey, such as those used by the Chesapeake Bay Multispecies Monitoring and Assessment Program (CHESMMAP), can encounter mature female crabs at low rates as well (G. Ralph pers. comm.). The proportion of encounters observed by the VIMS Trawl Survey was much higher prior to the population decline, around 70%. This may indicate that the survey effectively sampled the spawning stock and that the proportion of encounters during the spawning season and on the spawning grounds are indicative of current low spawning stock abundance.

4.3 Fishery stability and management considerations

High exploitation rates often increase population variability (Beddington and May, 1977), as selective and intensive fishing can truncate size or age structure of the population (Pollock, 1995). This truncation alters demographic parameters such as SAM and reduces population resilience (Anderson *et al.*, 2008). We found evidence of increased variability among all stock health indicators during the recovery regime. Differences in variability were also evident across regimes and may have resulted in the lack of significant correlation across years in models of relative abundance and $\mathrm{TEP}_{\mathrm{size}}$. Periods of high abundance were associated with larger SAM and lower variability in SAM; therefore, management actions that preserve high relative abundance on the spawning grounds may reduce variability and help stabilize the population.

Management actions implemented in 2008 appeared to have improved the health of the spawning stock and maintained some resilience. Relative abundance, $\mathrm{TEP}_{\mathrm{size}}$, and mean SAM increased during the recovery regime, but did not reach the levels observed during the pre-decline regime. $\mathrm{TEP}_{\mathrm{size}}$ remained 55% lower in the recovery regime compared with values observed during the pre-decline regime. Presently, low annual survival implies that the population primarily relies on a single annual cohort of females for egg production (Lambert *et al.*, 2006a; Ogburn *et al.*, 2019; Schneider *et al.*, 2023b), thereby decreasing the population's capacity to buffer perturbations such as those due to harvest mortality. Predation pressure, hypoxia, global warming, changes in food availability, disease, and habitat degradation (Bromilow *et al.*, 2022) are additional threats to the health of the population. Warming, in particular, may decrease mean SAM of female blue crabs (Hines *et al.,* 2011) and increase the likelihood they are harvested prior to reproducing in Chesapeake Bay (Schneider *et al.,* 2024). For many collapsed fisheries, reducing fishing pressure alone does not result in population recovery, especially to the pre-collapse conditions (Hutchings and Reynolds, 2004).

The VIMS Trawl Survey is an important resource for monitoring the population of blue crabs in Chesapeake Bay due to its specific spatial and temporal coverage of the spawning stock during the spawning season. It is the only fishery-independent survey that comprehensively samples the blue crab spawning grounds during the spawning season. Maryland fishery-independent surveys do not sample high-salinity spawning grounds and other Virginia surveys do not sample in all months of the spawning season (Chesapeake Bay Stock Assessment Committee, 2023; Latour *et al.*, 2023). Since 2008, the blue crab management framework in Virginia has focused on protecting female crabs, with the goal of increasing egg and thus larval production (Chesapeake Bay Stock Assessment Committee, 2023), because of the significant stock-recruit relationship for this species (Tang, 1985; Lipcius and Van Engel, 1990; Lipcius and Stockhausen, 2002). Thus, spawning stock indicators estimated during the reproductive season can inform decisions because such indicators are representative of the realized rather than the potential spawning stock (Hutchings and Reynolds, 2004).

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Table 1. Parameter estimates for the generalized least squares regression of relative abundance as a function of blue crab regime: 1988 to 1992 as the pre-decline, 1993 to 2007 as the depressed, and 2008 to 2023 as the recovery regime. SE = standard error; t = t statistic; p = probability of observing an equal or more extreme value under the null hypothesis. The intercept represents the depressed regime.

Variable	Estimate	SE	*t*	*p*
Intercept	0.98	0.14	6.9	< 0.0001
Pre-Decline	6.1	2.7	2.2	0.03
Recovery	1.4	0.8	1.8	0.08

Table 2. Parameter estimates for the generalized least squares regression of size-specific total egg production as a function of blue crab regime: 1988 to 1992 as the pre-decline, 1993 to 2007 as the depressed, and 2008 to 2023 as the recovery regime. SE = standard error; t = t statistic; p = probability of observing an equal or more extreme value under the null hypothesis. The intercept represents the depressed regime.

Variable	Estimate	SE	*t*	*p*
Intercept	1,923,429	213,386.4	9.0	< 0.0001
Pre-Decline	7,761,889	1,797,274.3	4.3	0.0001
Recovery	2,421,252	1,107,650.6	2.2	0.04

Table 3. Parameter estimates for the weighted linear regression of mean size at maturity as a function of relative abundance and blue crab regime: 1988 to 1992 as the pre-decline, 1993 to 2007 as the depressed, and 2008 to 2023 as the recovery regime. SE = standard error; t = t statistic; p = probability of observing an equal or more extreme value under the null hypothesis. The intercept represents the depressed regime.

Variable	Estimate	SE	*t*	*p*
Intercept	136.8	1.0	143.6	< 0.0001
Abundance	0.08	0.2	0.4	0.7
Pre-Decline	6.9	2.2	3.1	< 0.01
Recovery	4.4	1.4	3.1	< 0.01

Table 4. Parameter estimates for the generalized least squares regression of the difference in size specific total egg production and the 2022 mean fecundity total egg production (TEP_{diff22}) as a function of blue crab regime, relative abundance, and an interaction between the two. Blue crab regimes are 1988 to 1992 as the pre-decline, 1993 to 2007 as the depressed, and 2008 to 2023 as the recovery regime. SE = standard error; t = t statistic; p = probability of observing an equal or more extreme value under the null hypothesis. The intercept represents the depressed regime.

Variable	Estimate	SE	*t*	*p*
Intercept	87,812.7	117,155.7	0.7	0.5
Abundance	-33,556.3	104,550.7	-0.3	0.8
Pre-Decline	582,056.1	198,005.2	2.9	<0.01
Recovery	-27,098.9	136,400.0	-0.2	0.8
Abundance x Pre-Decline	115,320.0	106,060.7	1.1	0.3
Abundance x Recovery	183,591.4	106,116.9	1.7	0.1

Table 5. Parameter estimates for the generalized least squares regression of the difference in size specific total egg production and the 1980s mean fecundity total egg production ($TEP_{diff80s}$) as a function of blue crab regime, relative abundance, and an interaction between the two. Blue crab regimes are 1988 to 1992 as the pre-decline, 1993 to 2007 as the depressed, and 2008 to 2023 as the recovery regime. SE = standard error; t = t statistic; p = probability of observing an equal or more extreme value under the null hypothesis. The intercept represents the depressed regime.

Variable	Estimate	SE	*t*	*p*
Intercept	-121,346.0	195,616.0	-0.6	0.5
Abundance	-722,356.4	174,569.3	-4.1	< 0.001
Pre-Decline	-1,534,541.4	330,611.0	-4.6	< 0.001
Recovery	-245,640.9	227,748.4	-1.1	0.3
Abundance x Pre-Decline	568,016.6	177,090.5	3.2	< 0.01
Abundance x Recovery	280,396.7	177,184.4	1.6	0.1

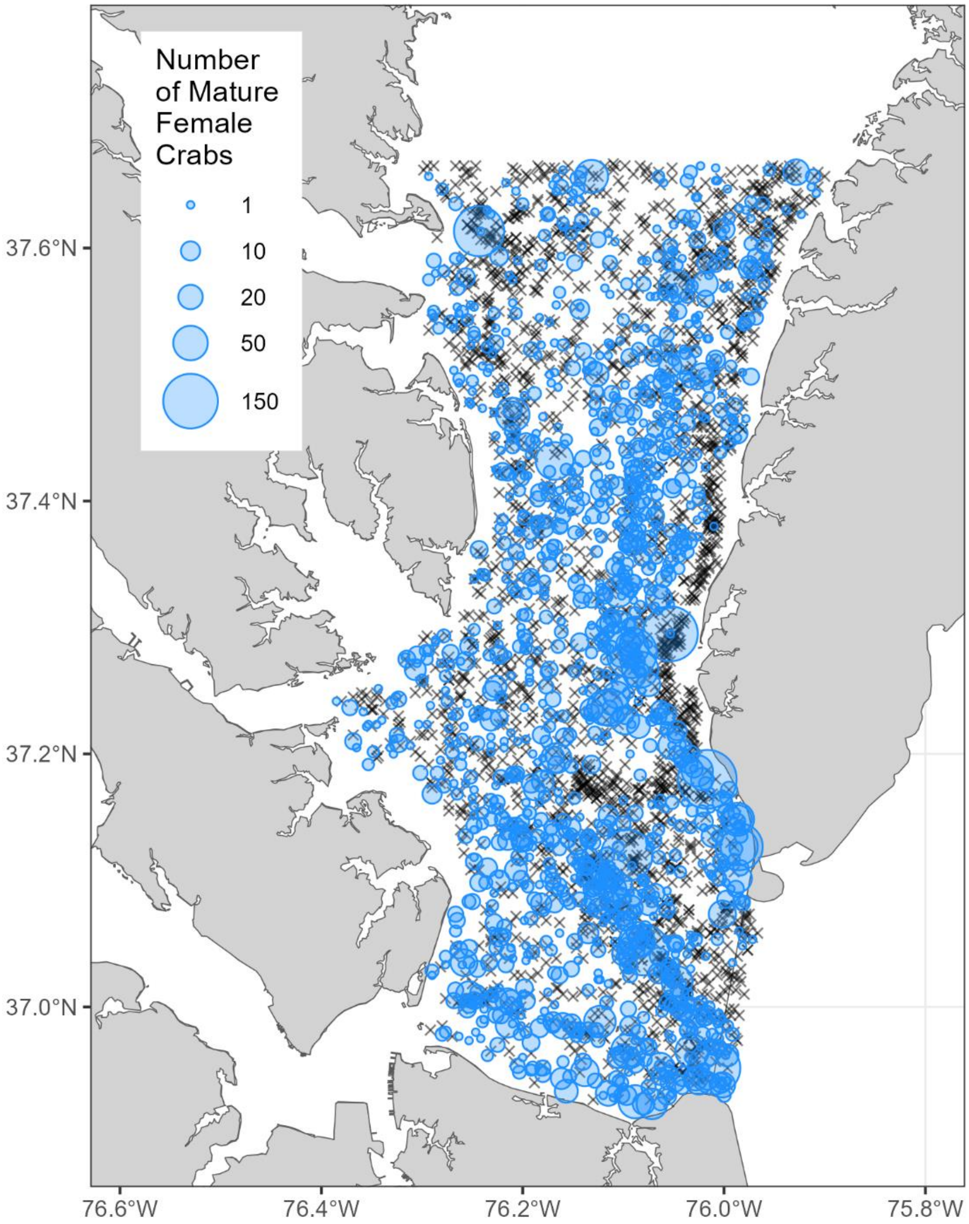

Figure 1. Location of tows for the Virginia Institute of Marine Science Trawl Survey from 1988 to 2023 in June, July and August. The x symbols represent locations where a tow occurred but no mature female blue crabs were captured, while the partially transparent blue circles represent locations of a tow that encountered mature female blue crabs. The size of the blue circle reflects the number of mature females captured.

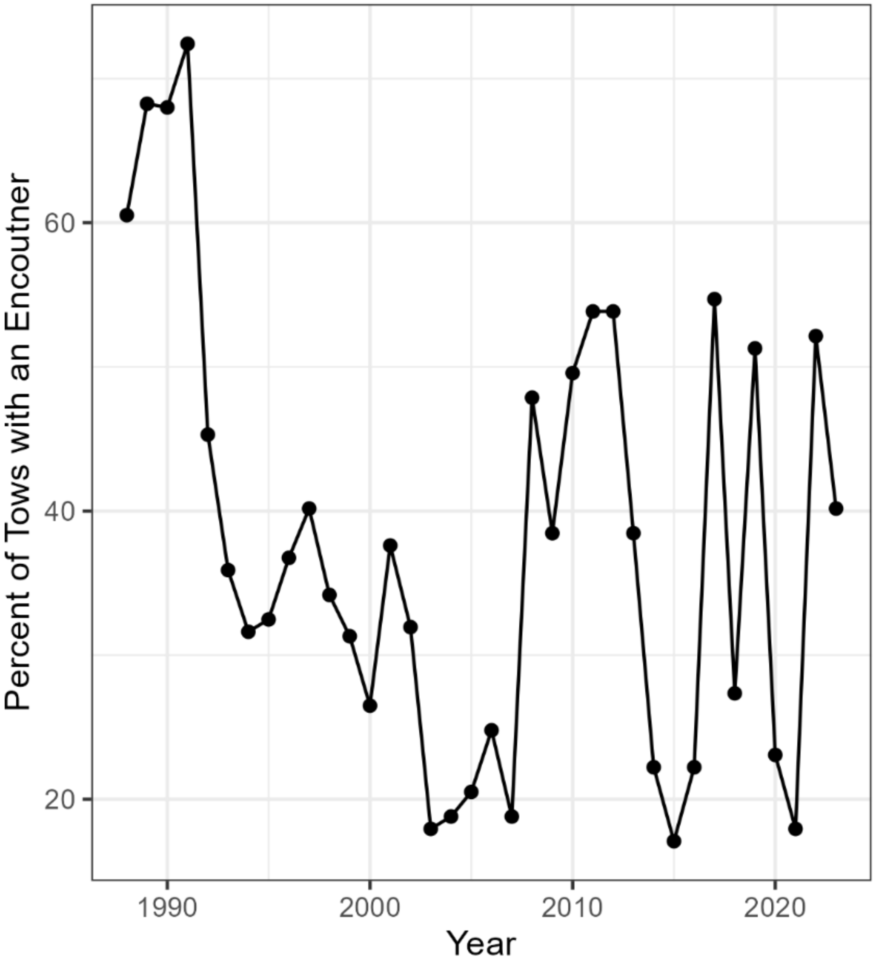

Figure 2. The annual percent of trawl tows by the Virginia Institute of Marine Science Trawl Survey that encountered mature female blue crabs from 1988 to 2023. Only tows conducted in the Bay mainstem (Figure 1) in June, July and August were considered.

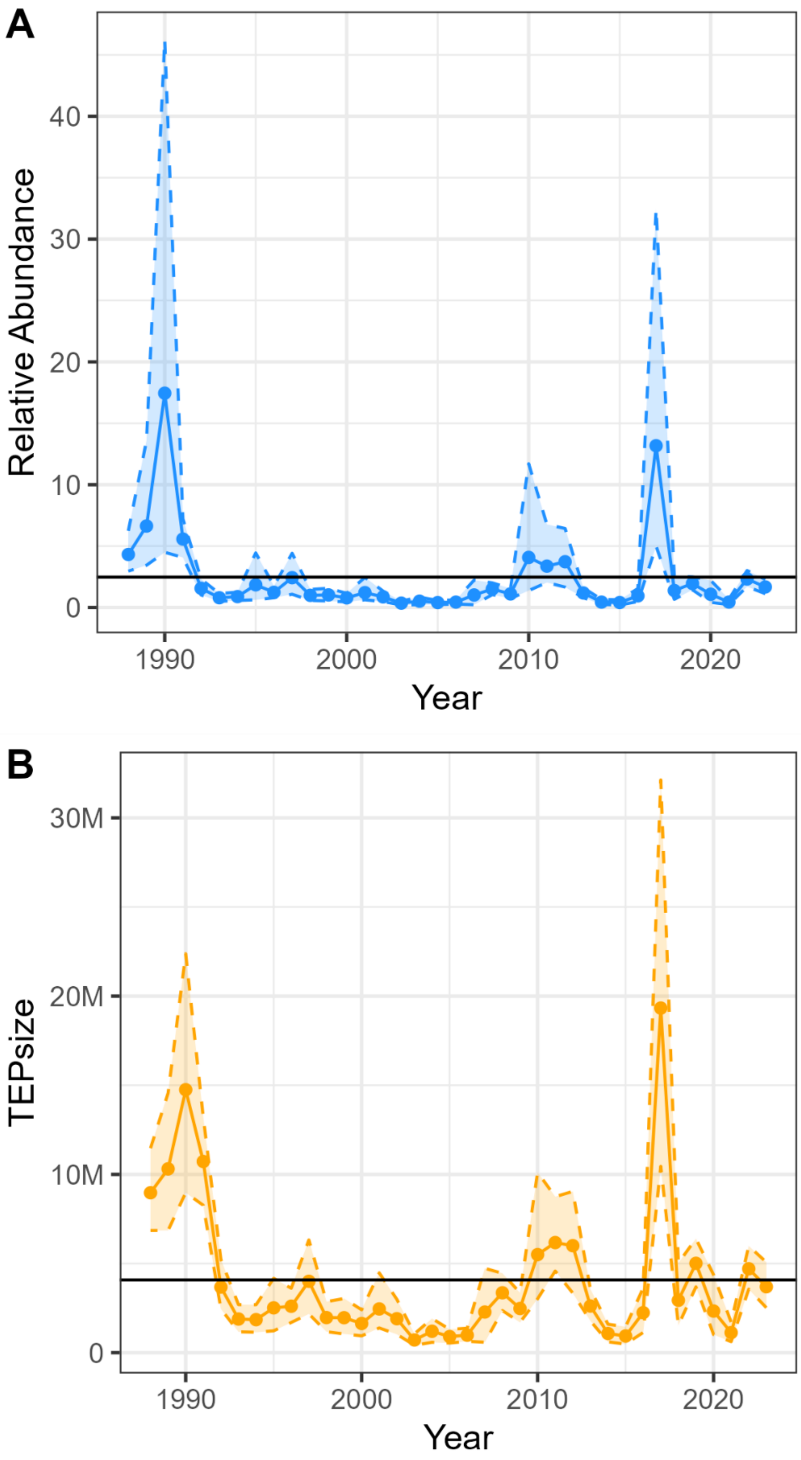

Figure 3. Random stratified index (RSI_{delta}) of the abundance of mature female blue crabs (A) and the total egg production (TEP_{size}) of mature female blue crabs in millions (B), captured by the Virginia Institute of Marine Science Trawl Survey from 1988 to 2023 in June, July, and August. Colored bands represent 95% confidence intervals and the black horizontal line represents the long-term mean.

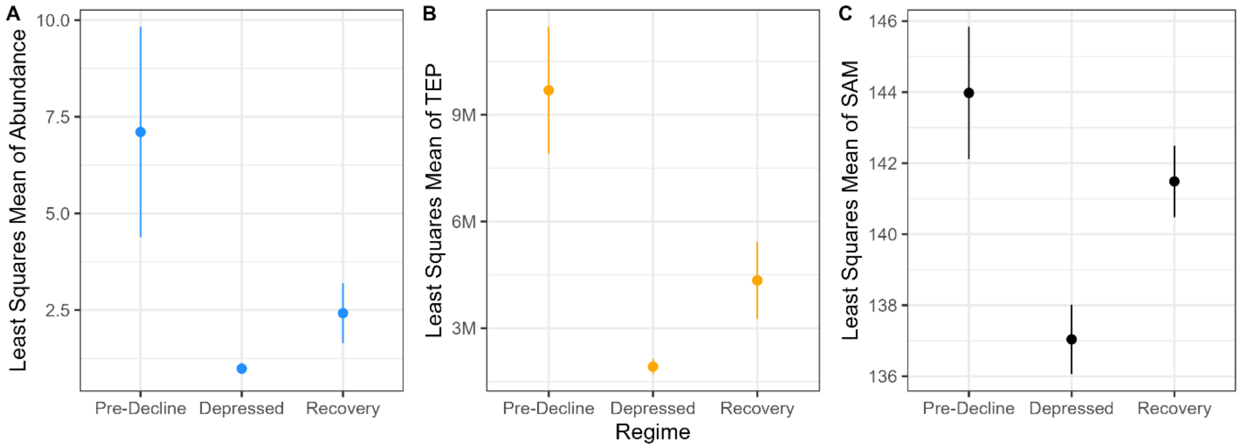

Figure 4. Least squares means and standard errors of spawning stock indicators across three blue crab regimes: the pre-decline (1988 to 1992), depressed (1993 to 2007), and recovery regime (2008 to 2023). Least squares mean estimates were derived from models of relative abundance (A), Total Egg Production (TEP, B), and annual size at maturity (SAM, C).

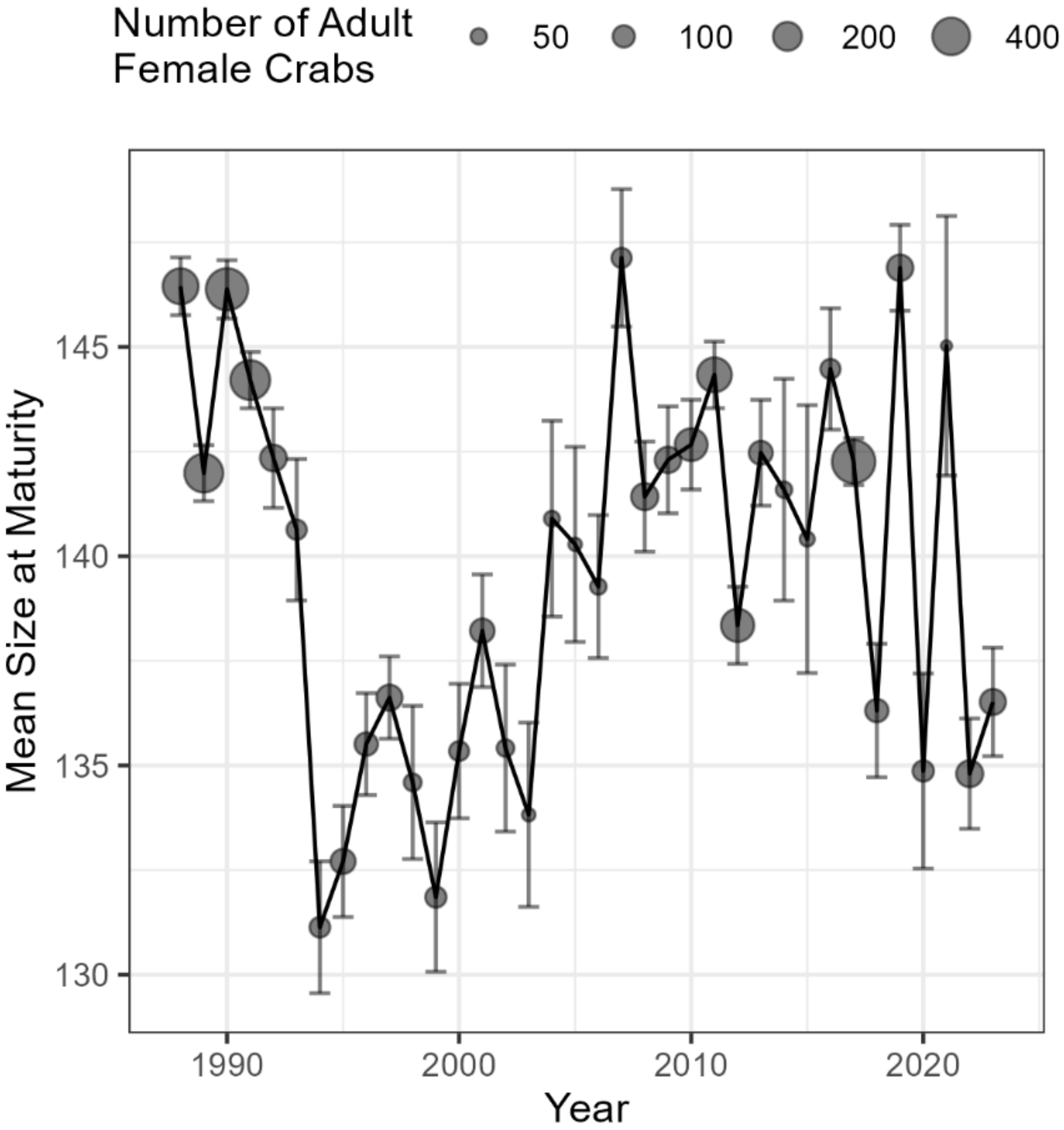

Figure 5. Mean size at maturity in mm carapace width for mature female blue crabs from 1988 to 2023. Error bars represent standard errors and the size of the point represents the sample size.

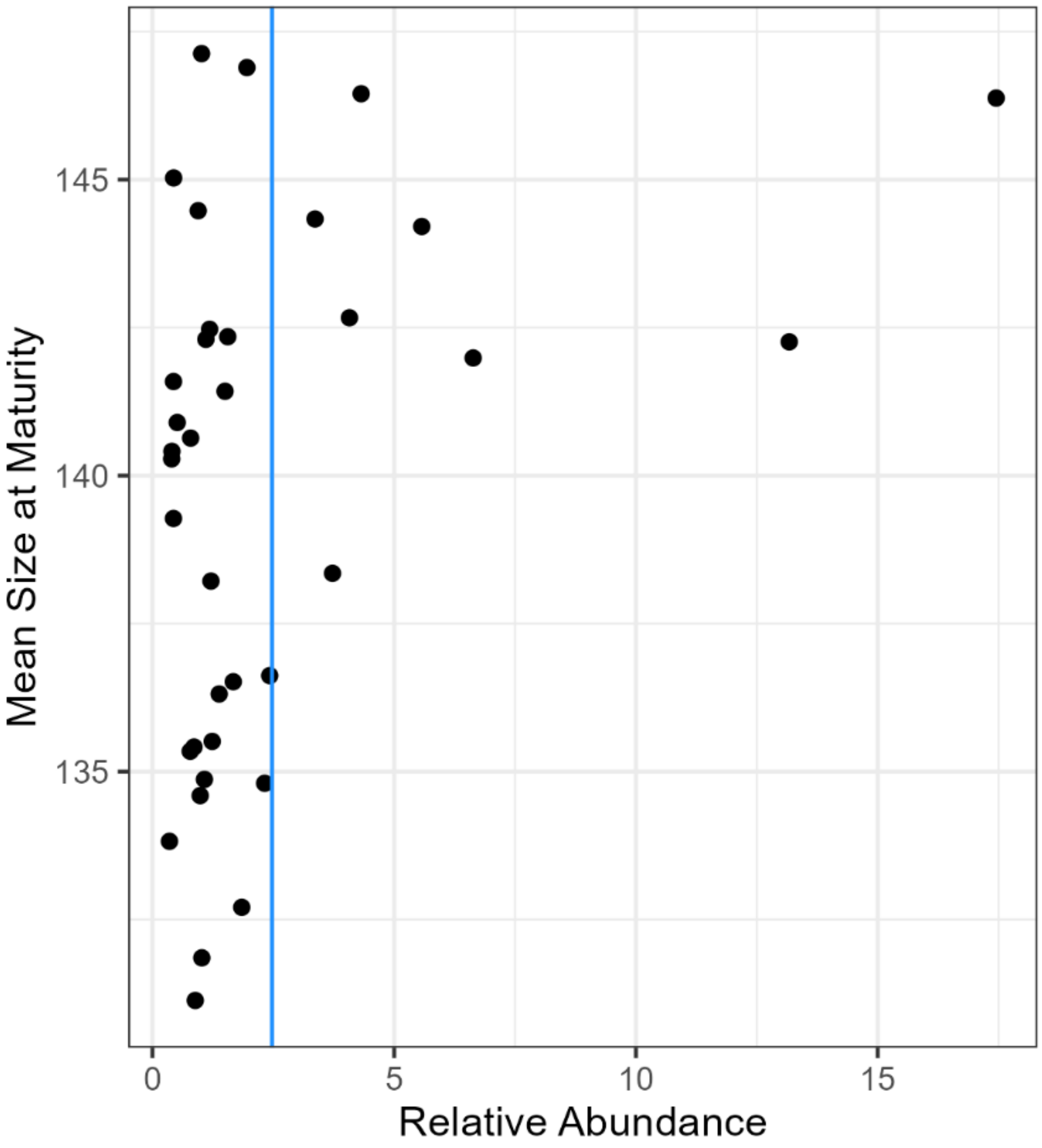

Figure 6. Mean size at maturity in mm carapace width and the relative abundance of mature female blue crab abundance from 1988 to 2023. The horizontal blue line, at 2.47 female crabs, represents the long term mean of relative abundance.

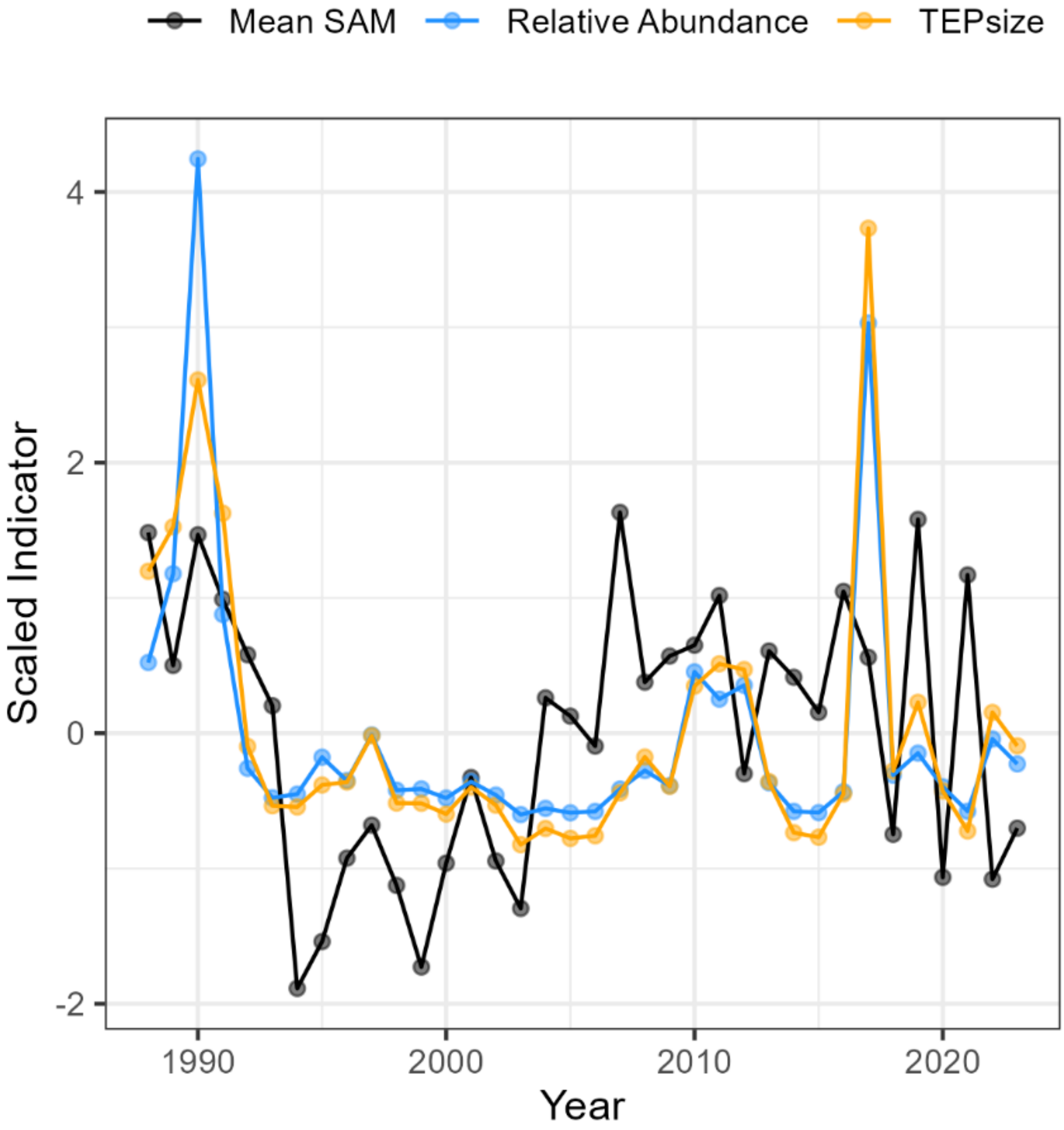

Figure 7. Scaled indicators of spawning stock health from 1988 to 2023, including mean size at maturity (SAM), relative abundance, and size-specific total egg production (TEP_{size}).

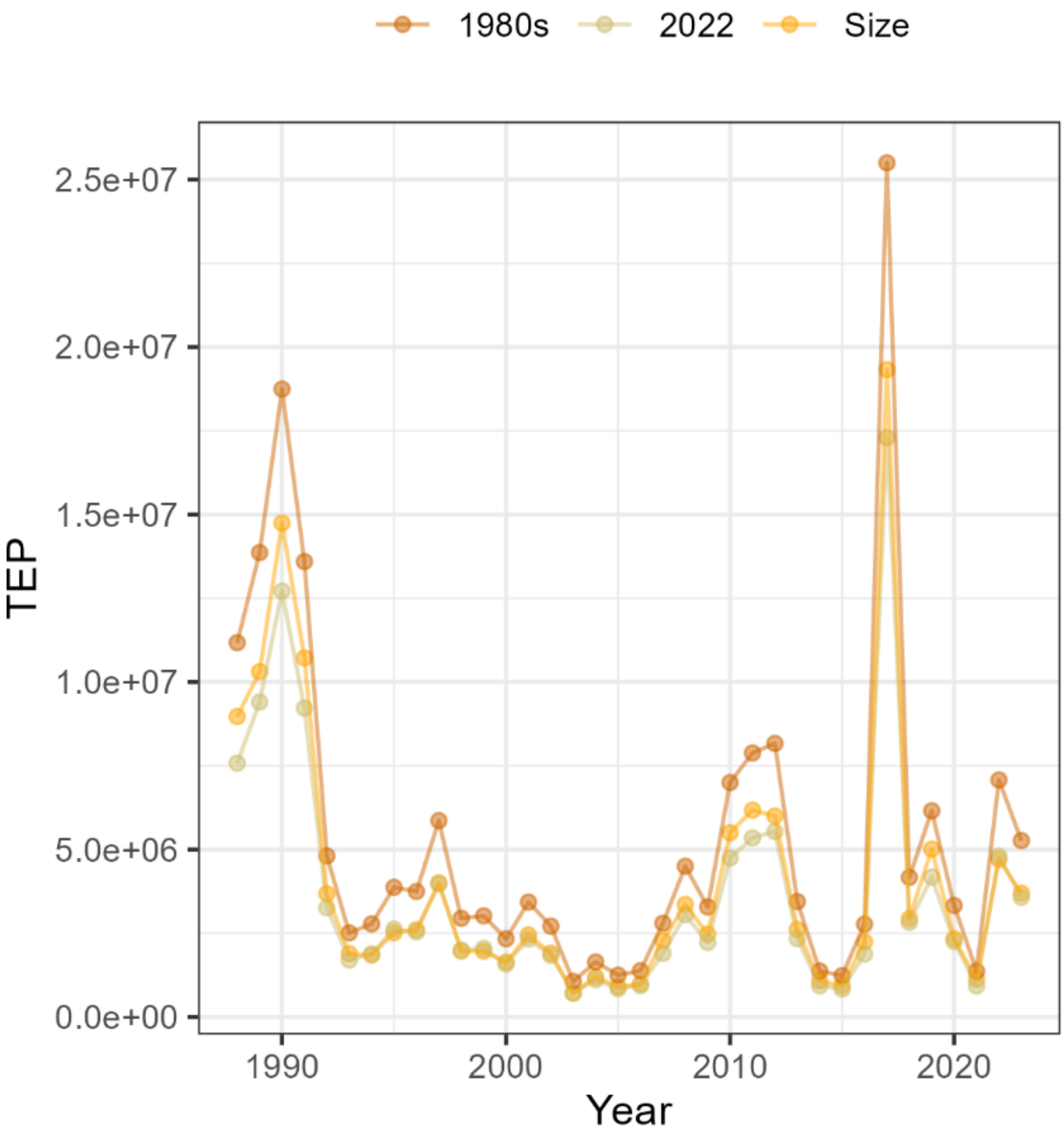

Figure 8. Scaled indicators of total egg production (TEP) using three methods of estimation: size-specific fecundity (size), mean fecundity derived in 2022 (2022), and mean fecundity derived in 1986 and 1987 (1980s).

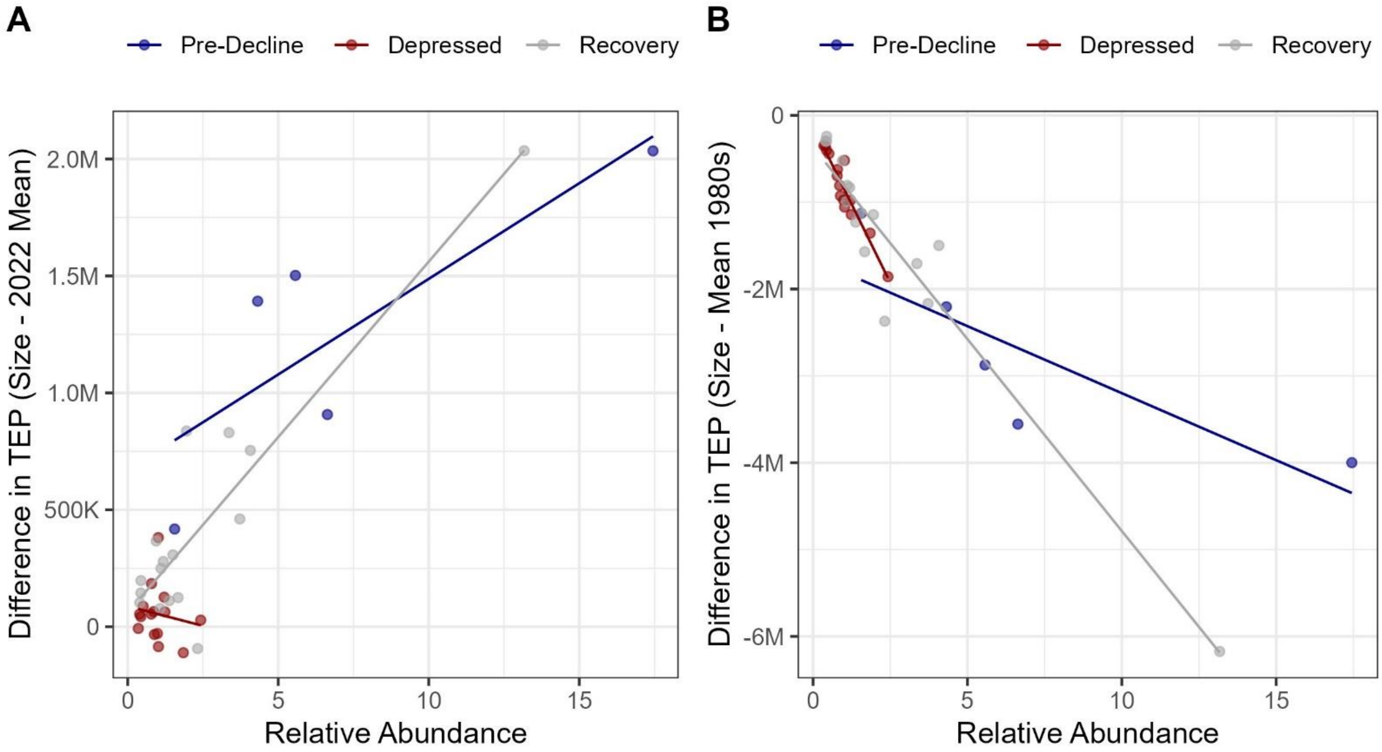

Figure 9. Difference in total egg production (TEP) when using size-specific fecundity and A) mean fecundity derived in 2022 and B) mean fecundity derived in the 1980s as a function of the relative abundance of mature female blue crabs. The colors denote blue crab regime: the pre-decline (1988 to 1992), depressed (1993 to 2007), and recovery regime (2008 to 2023). Lines are the predicted values for the generalized least squares model of the difference in TEP as function of RSI of abundance, regime, and an interaction between the two (Table 4, 5).

Appendix Chapter 1: Reproductive potential of the blue crab spawning stock in Chesapeake Bay across eras and exploitation rates using nemertean worms as biomarkers

Section S1. Data gaps

In 1992 and 1993, 29.6% of females caught were not weighed. An analysis of covariance with the 70.4% of females with weight data was performed *a priori* to determine if the relationship between CW and crab weight was statistically different in 1992 and 1993. Both variables were $\log_e$-transformed for linearity and CW was used as the covariate. There was no notable difference between the slopes of each year ($F = 0.2253$, $p = 0.64$) nor the intercept ($F = 3.67$, $p = 0.056$). Moreover, the model using both years had a very similar fit (Fig. S1) to those using an individual year, parameter estimates between models were also similar (Table S1). Therefore, one nonlinear least squares model was used to estimate the body weights of 408 crabs (145 in 1992 and 236 in 1993, Fig. 2). To make the modeled weights more realistic of the natural variation of blue crab weight at size, a normal distribution parametrized with the standard deviation of the model residuals was created, sampled at random, and added to the modeled weight estimates. The residuals of the model were assessed visually and met the model assumptions. Models were run in R Studio with the stats package (R Core Team 2022).

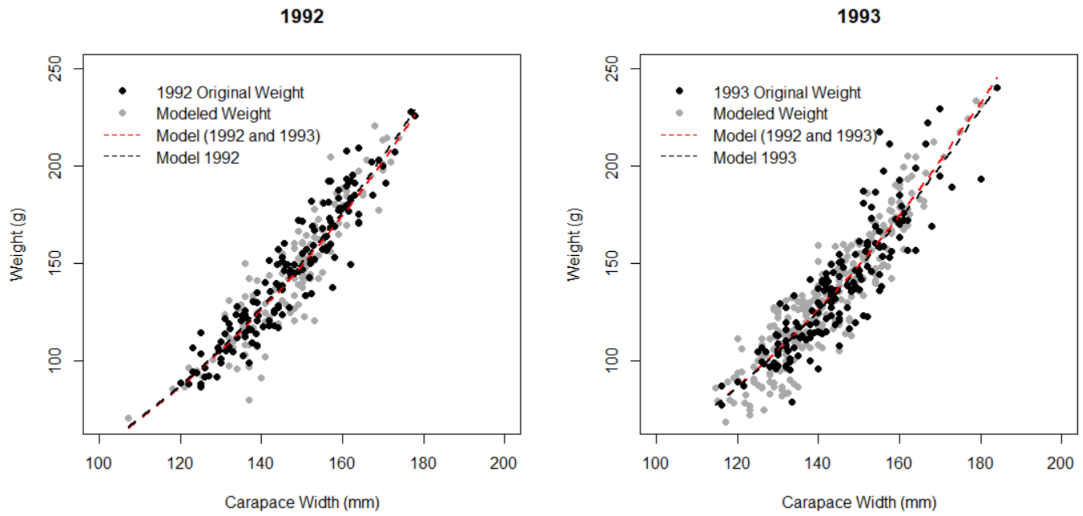

Fig. S1. Relationship between female carapace width and whole-body weight for females in 1992 and 1993, parameter estimates for all models (1992 and 1993, 1992 only, and 1993 only can be found in Table S1).

Table S1. Parameter estimates and standard deviation for modeled weight and carapace width (CW) relationship: $Weight = a * CW^b$

Parameter	Model:		
	Joint	1992 Only	1993 Only
a (± sd)	0.00078 ± 0.00025	0.00074 ± 0.00029	0.00090 ± 0.00045
b (± sd)	2.43 ± 0.063	2.44 ± 0.076	2.40 ± 0.099

Section S2. Proportion of second year spawners and exploitation, all years.

Table S2. Proportion of second-year spawners by year for females caught below 37.4°N and the prior year's exploitation rate

Year	Proportion ± SE (%)	Count	Exploitation Rate (%)
1992	8.9 ± 1.1	661	28
1993	11.6 ± 1.4	502	37
1994	6.4 ± 1.1	500	28
1995	11.0 ± 2.3	182	35
1996	2.4 ± 0.7	452	32
2020	19.0 ± 3.9	100	14
2021	8.9 ± 1.7	282	19
2022	8.4 ± 2.1	179	26

Section S3. Relationship with size and ovary weight

Data included in the generalized linear models were subsetted to include females with mature ovaries. In years where ovary stage was not documented (i.e. 1992 and 1993), crabs were considered mature if their ovary wet weight was greater than 2.5 g, regardless of CW. This delineation was chosen because the relationship between ovary weight and crab size shows a separation in data around 2.5 g (Fig. S2). Moreover, in 2020 and 2021, the majority (99.3%) of females with mature ovaries had an ovary weight greater than 2.5 g.

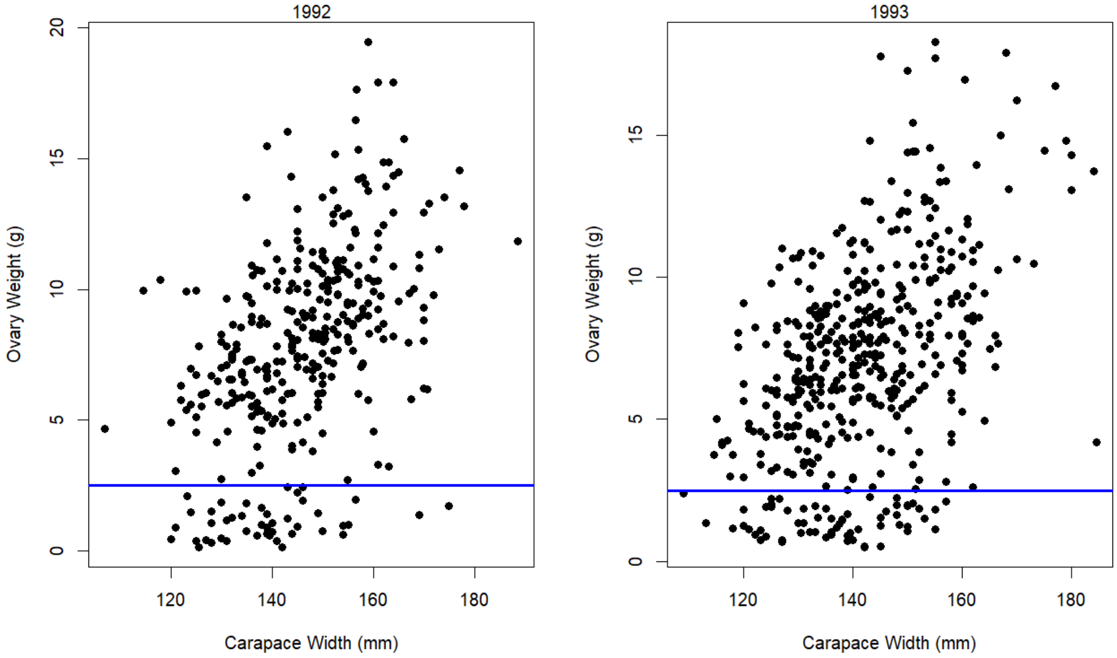

Fig. S2. Relationship between ovary weight (g) and female carapace width (mm) for mature females in 1992 (left) and 1993 (right). The blue horizontal line is set at 2.5 g.

Section S4. Exploring dependence within dredge tows

Concerns about correlation between crabs within the same dredge tow were not explored on the entirety of the model data because a large proportion of dredge tows only caught one crab. The potential correlation within tows was explored by removing tows with 5 or less crabs, running the models sets with a random effect of dredge tow, and calculating the intraclass correlation of the model using the performance package in R (Lüdecke et al. 2021). The conditional interclass correlation was 0.016 for the contemporary models and 0.062 for the GSI models, indicating a low correlation between crab spawning history within dredge tows. Temporal correlation between years was negligible due to low (6–10%) annual survival rates of adult females in the Bay (Lambert et al. 2006). Year was also included as a fixed effect within the model. Within years, females were assumed to be temporally independent of one another because they were in winter dormancy and inactive during the time of sampling (Lambert et al. 2006). Potential spatial autocorrelation was assessed visually with annual spline correlograms of the binary data and modeled residuals using the ncf package in R (Bjørnstad 2020); spline correlograms indicate negligible spatial correlation if the covariance is not significantly different than 0 (Bjørnstad & Falck 2001). Spatial autocorrelation for all years and model sets was considered negligible as 95% confidence interval generally overlapped with 0 for all distances of the residual correlograms.

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Lambert DM, Hoenig JM, Lipcius RN (2006) Tag return estimation of annual and semiannual survival rates of adult female blue crabs. Trans Am Fish Soc 135:1592–1603

Lüdecke D, Ben-Sachar MS, Patil I, Waggoner P, Makowsk D (2021) Performance: An R Package for Assessment, Comparison and Testing of Statistical Models. Jounal Open Source Softw 6:3139

R Core Team (2022) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna

Appendix, Chapter 2: Reproductive phenology of the Chesapeake Bay blue crab population in a changing climate

1. Missing data

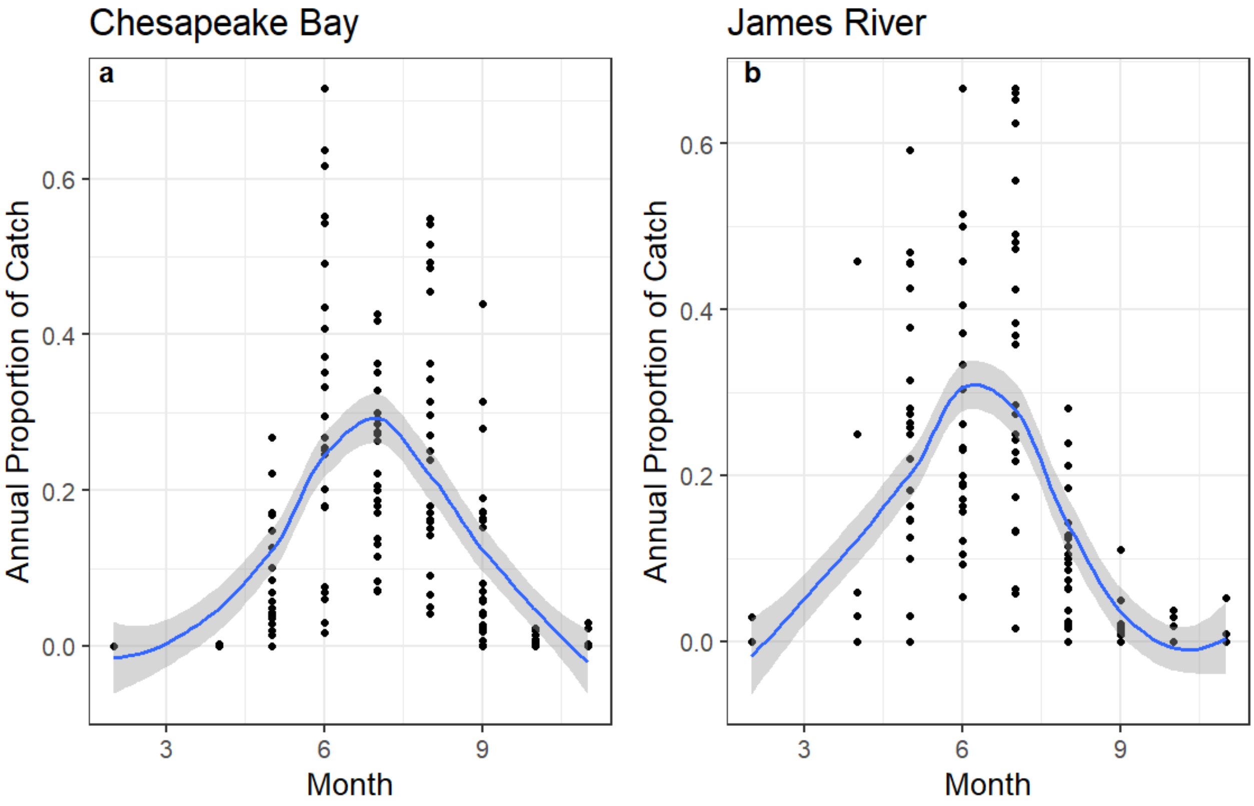
The 25-year fishery independent dataset had multiple instances of missing data. The majority of these missing values were due to vessel mechanical failures, funding disruptions, and inclement weather preventing sampling. Missing data were imputed as follows.

In Chesapeake Bay the month of February was not sampled in 2001 or 2018. Zero ovigerous females were imputed into the model for missing February data, as no ovigerous females were previously caught by the trawl survey in February in Chesapeake Bay (1995 – 2019). April 2001 was also not sampled in Chesapeake Bay. In Chesapeake Bay, 0.13% of mature females (1 out of 733) caught by the trawl from 1995 – 2019 were egg bearing, therefore, a zero was also imputed for April 2001. In 1998, sampling was disrupted in August and 1 out of 45 stations was sampled. The catch for August 1998 was estimated via the relationship between catches of ovigerous females from July to September. August catch was regressed as a function of July catch and August catch was regressed as a function of September catch using years 1996 – 1997 and 1999 – 2007. Years 2008 – 2019 were omitted due to changes in management in 2008. The resulting regressions were then used to estimate August catch in 1998 based on the 1998 September and July catch values, which resulted in an estimated August catch of 20.07 and 20.88, respectively. The rounded average of these values (20) was imputed for August 1998.

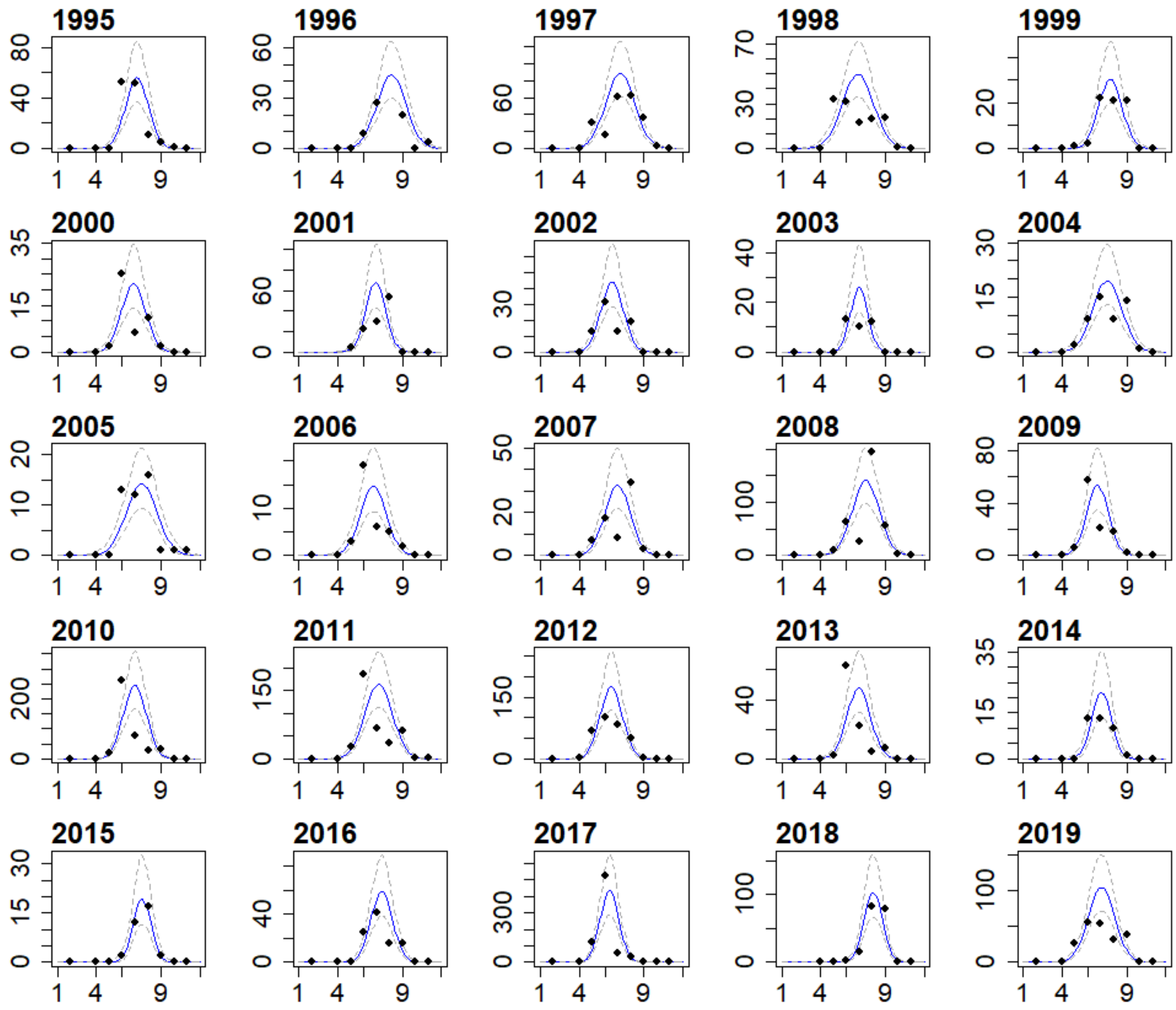
In the James River sampling did not occur in January 2018, February 2018 or November 2006. The trawl survey has never previously caught (1995 – 2019) an ovigerous female in the James River in January or February, and thus these values were imputed at zeros. A zero-catch value was also used for November 2006 as 0.2% of mature females (2 out of 997) caught in the James River in November were ovigerous.

2. Unimodal spawning season assumption

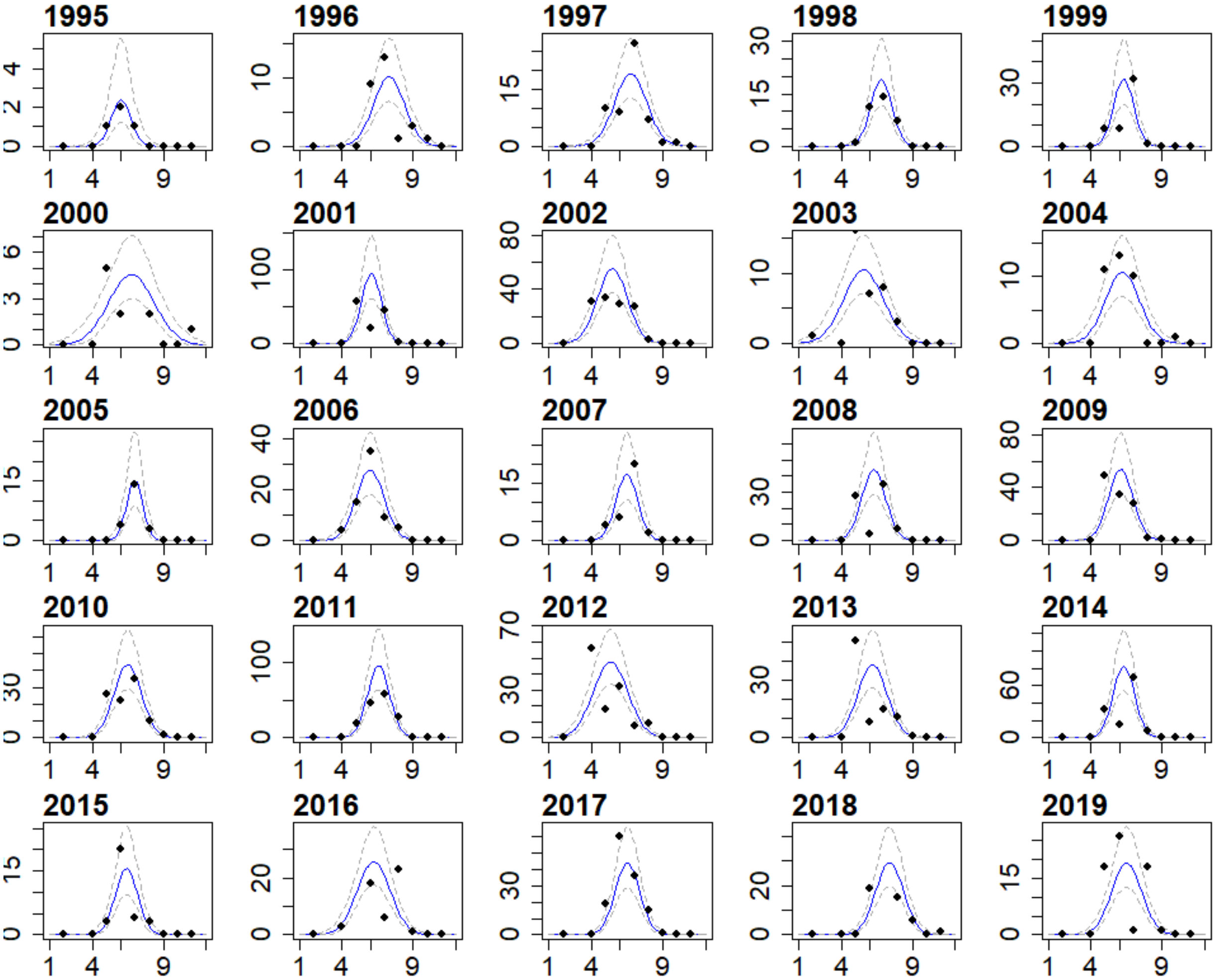
Estimation of phenological metrics (onset, duration, conclusion) used methods adapted from Edwards & Crone (2021), assuming a unimodal spawning season. To validate this assumption, we fit a Loess curve to the annual proportion of ovigerous crabs per month across years (1995 – 2019), for each region (Figure S1). Visual inspection of all the Loess curves indicated that a unimodal spawning season is a valid assumption for this dataset. Moreover, fits of Gaussian curves supported this assumption as well (Figure S2a, S2b).



Supplementary Figure 1: Annual proportion of catch of ovigerous crabs captured by the Virginia Institute of Marine Science Juvenile Fish Trawl Survey from 1995 – 2019 for the A) Chesapeake Bay and B) James River. Blue lines represent Loess curves with a span of 0.75. Gray bands represent 95% confidence intervals. Months are numbered with reference to January as month 1.



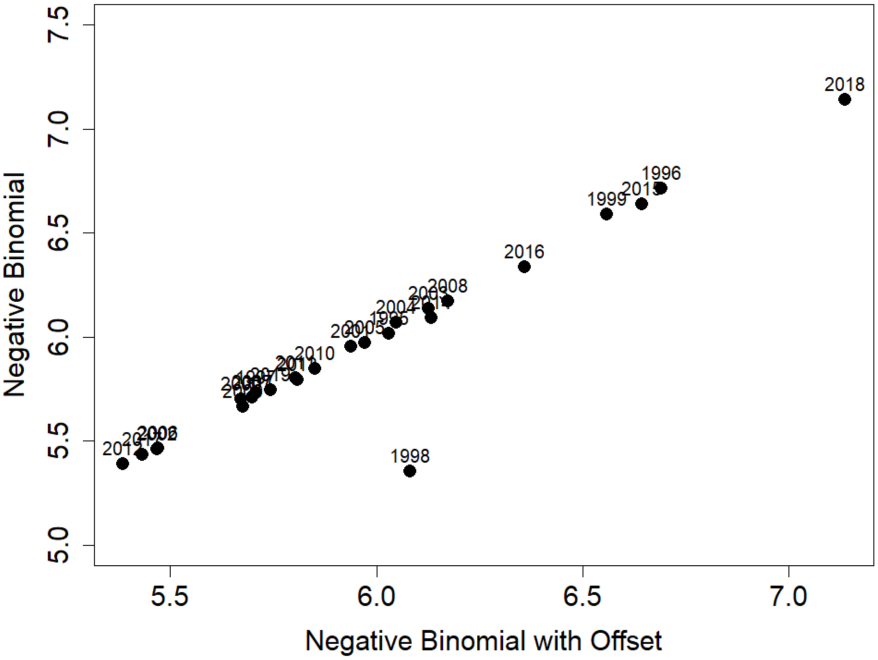
Supplementary Figure 2a: Negative binomial model fits for Chesapeake Bay from 1995 – 2019. Blue lines are the model fit, black circles show raw data of catches of ovigerous female crabs by month and dashed lines represent bootstrapped 95% confidence intervals. Note difference in Y-axis scale. Months are numbered with reference to January as month 1.



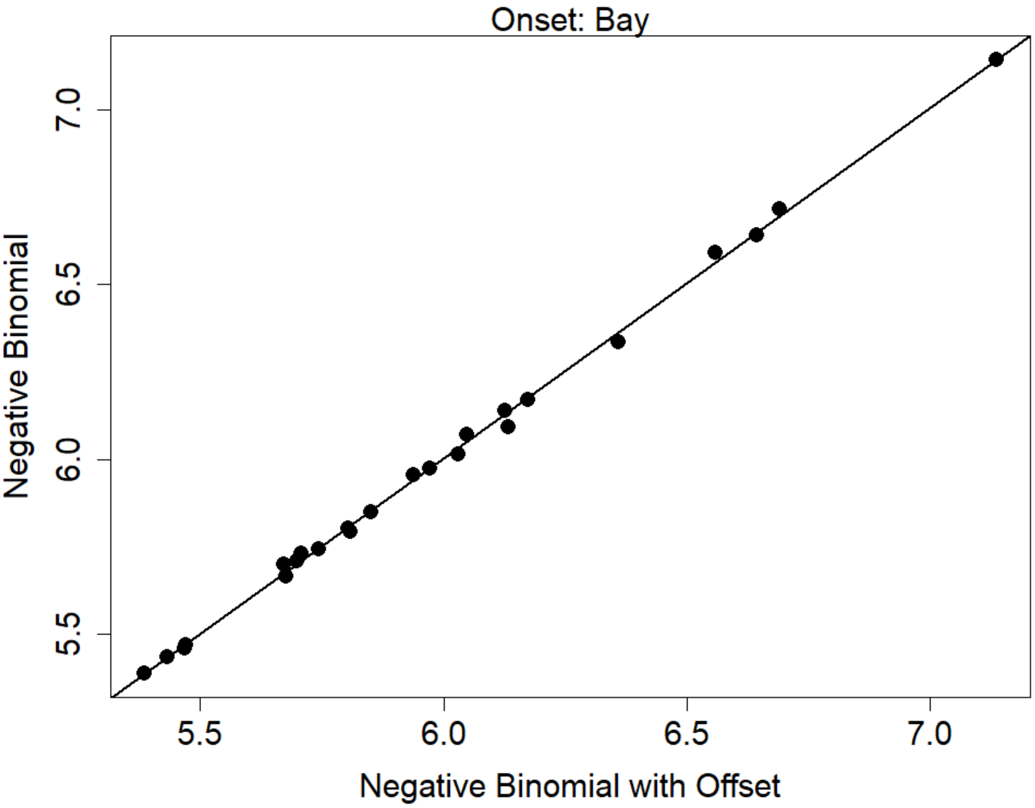
Supplementary Figure 2b: Negative binomial model fits for the James River from 1995 – 2019. Blue lines are the model fit, black circles show raw data of catches of ovigerous female crabs by month and dashed lines represent bootstrapped 95% confidence intervals. Note difference in Y-axis scale. Months are numbered with reference to January as month 1.

3. Including an offset for effort

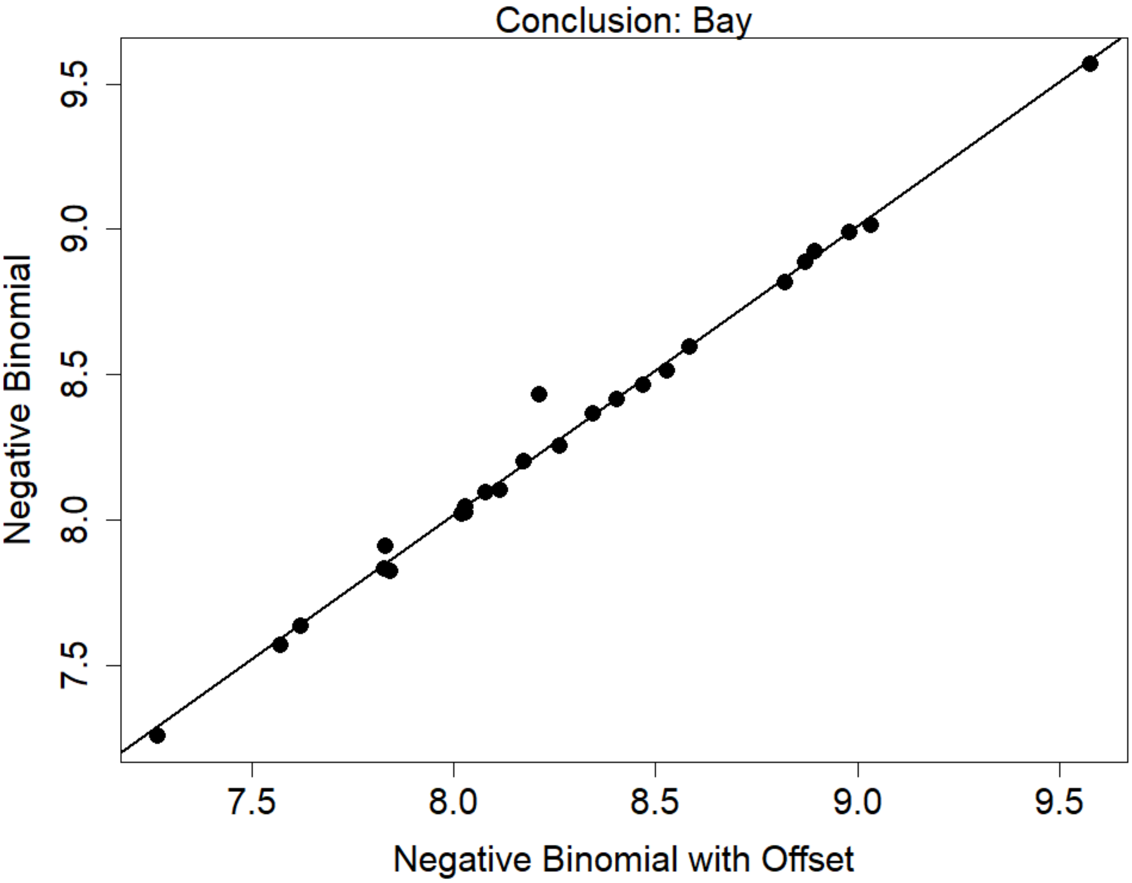
We tested the relative importance of including effort into our models by comparing estimates of spawning season onset and duration between models with and without an offset of effort. Effort was defined as the total area swept (1000 m2) by the trawl per month. Phenological estimates were compared using linear models and paired t-tests. Model estimates for onset in Chesapeake Bay were highly correlated, with the exception of 1998 (Figure S3). The discrepancy in 1998 is likely a result of the sampling disruption in August (SM section1), which produced an abnormally low effort. The catch of ovigerous females was augmented in August 1998 to account for this in both models, as explained in Appendix 1. Without 1998, onset estimates in Chesapeake Bay were aligned (Figure S4), and estimates were not significantly different (paired t-test: t = 0.68, p-value = 0.50). In Chesapeake Bay, the conclusion estimates were also well correlated (Figure S5), and the estimates were not significantly different (paired t-test: t = 1.59, p-value = 0.12). The estimates of onset produced by both James River models were also well correlated (Figure S6) and the estimates were not significantly different (paired t-test: t = -1.066, p-value = 0.297). The estimates of conclusion in the James River were aligned (Figure S7), and were not statistically different (paired t-test: t = -0.726, p-value = 0.4744).



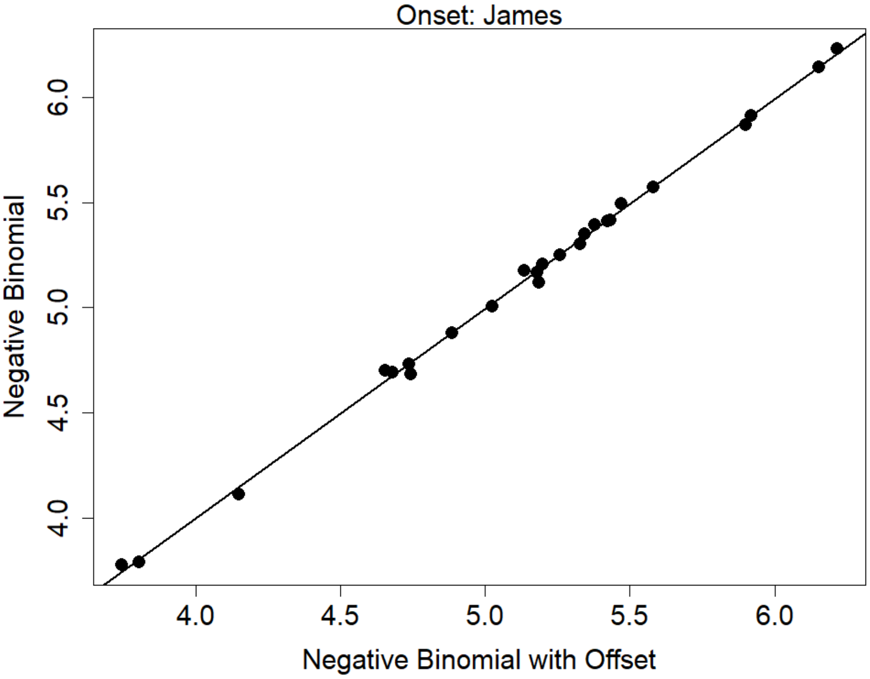
Supplementary Figure 3: Estimates of spawning season onset derived from negative binomial models with and without the offset of effort in Chesapeake Bay from 1995 – 2019 with the year listed above the relevant datapoint.



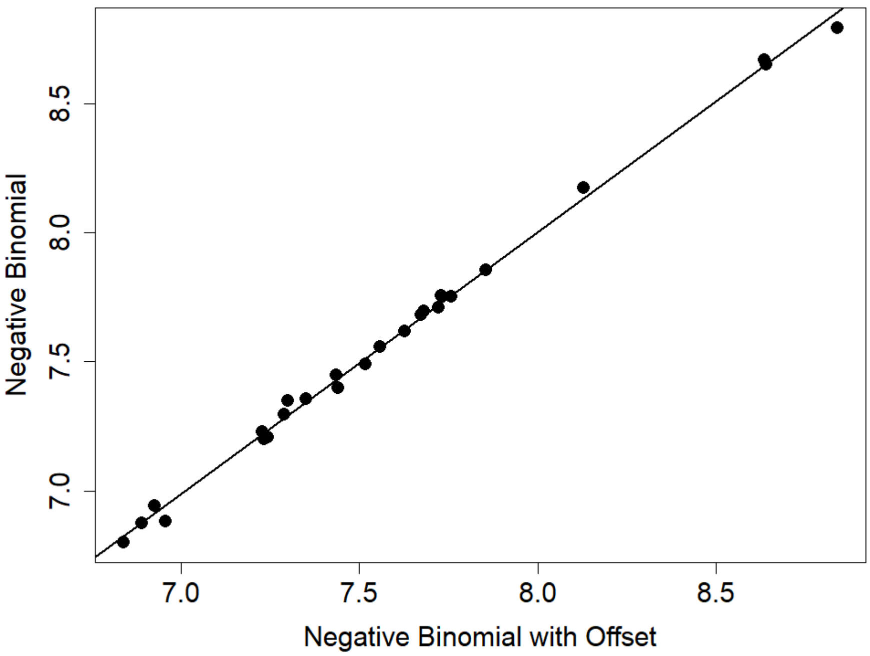
Supplementary Figure 4: Estimates of spawning season onset derived from negative binomial models with and without the offset of effort in Chesapeake Bay from 1995 – 2019. The line represents a linear regression relating the two estimates ($r^2 = 0.999$, $p < 0.001$): $y = -0.0182 + 1.003x$.



Supplementary Figure 5: Estimates of spawning season conclusion derived from negative binomial models with and without the offset of effort in Chesapeake Bay from 1995 – 2019. The line represents a linear regression relating the two estimates (r^2 = 0.992, *p* < 0.0001): y = 0.0834 + 0.992x.



Supplementary Figure 6: Estimates of spawning season onset derived from negative binomial models with and without the offset of effort in the James River from 1995 – 2019. The line represents a linear regression relating the two estimates ($r^2 = 0.998$, $p < 0.0001$): y = 0.0049 + 0.99x.



Supplementary Figure 7: Estimates of spawning season conclusion derived from negative binomial models with and without the offset of effort in the James River from 1995 – 2019. The line represents a linear regression relating the two estimates ($r^2 = 0.997$, $p < 0.0001$): $y = -0.12 + 1.016x$.

4. Data from National Estuarine Research Reserve Systems (NERRS)

National Estuarine Research Reserve System (NERRS) sites originally selected for the analysis: delblwq, deldswq, delllwq, delslwq, grbgbwq, grblrwq, grborwq, grbsqwq, gtmfmwq, gtmpcwq, gtmpiwq, gtmsswq, jacb6wq, jacb9wq, jacbawq, jacnewq, narncwq, narpcwq, nartbwq, nartswq, niwcbwq, niwdcwq, niwolwq, niwtawq, niwwswq, niwwbwq, nocecwq, noclcwq, noczbwq, welhtwq, welinwq, wellmwq.

Ultimately 32 stations were included in the analysis (Figure S8). The station “welsmwq” was excluded because of recent inactivity of the buoy. The station “nocrcwq” was also excluded due to multiple years of implausible temperature values. For the stations “narpcwq” and “niwdcwq”, 2015 was excluded because of implausible temperature values (e.g., 300 ◦C).

Supplementary Figure 8: Locations of National Estuarine Research Reserve System water quality monitoring buoys used in calculations of spawning and reproductive degree days.

5. Model parameters

Parameter estimates for models tested in Table 2 that were suboptimal models (per AIC) and therefore not included within the text of the article are presented in supplementary Tables 1 through 4.

Supplementary Table 1: Parameter estimates for weighted linear regression models of spawning season conclusion in Chesapeake Bay and the James River as a function of spring reproductive degree days (RDD) and spawning degree days (SDD), calculated from Jan. 1 – April 30.

		Chesapeake Bay Model				James River Model			
Parameter	Effect	Estimate	Standard Error	*t*	*p*	Estimate	Standard Error	*t*	*p*
β_0	Intercept	9.15	1.39	6.57	< 0.0001	4.80	1.098	4.37	< 0.001
β_1	RDD	-0.0014	0.0020	-0.69	0.50	0.0040	0.0017	2.38	= 0.026
β_0	Intercept	8.29	0.62	13.44	< 0.0001	6.19	0.34	18.01	< 0.0001
β_1	SDD	-0.00048	0.0029	-0.17	= 0.87	0.0056	0.0016	3.59	= 0.0015

Supplementary Table 2: Parameter estimates for weighted linear regression models of spawning season duration in the James River as a function of annual reproductive degree days (RDD) and spawning degree days (SDD), calculated from Jan. 1 – Dec. 31.

		James River Model			
Parameter	Effect	Estimate	Standard Error	*t*	*p*
β_0	Intercept	0.011	1.96	0.006	0.99
β_1	RDD	0.00087	0.00078	1.11	0.28
β_0	Intercept	1.32	1.028	1.28	0.21
β_1	SDD	0.00090	0.0011	0.86	0.40

Supplementary Table 3: Parameter estimates for weighted linear regression models of spawning season conclusion in Chesapeake Bay and the James River as a function of spring reproductive degree days (RDD) and spawning degree days (SDD), calculated from Jan. 1 – April 30.

		Chesapeake Bay Model				James River Model			
Parameter	Effect	Estimate	Standard Error	*t*	*p*	Estimate	Standard Error	*t*	*p*
β_0	Intercept	9.15	1.39	6.57	< 0.0001	4.80	1.098	4.37	< 0.001
β_1	RDD	-0.0014	0.0020	-0.69	0.50	0.0040	0.0017	2.38	= 0.026
β_0	Intercept	8.29	0.62	13.44	< 0.0001	6.19	0.34	18.01	< 0.0001
β_1	SDD	-0.00048	0.0029	-0.17	= 0.87	0.0056	0.0016	3.59	= 0.0015

Supplementary Table 4: Parameter estimates for weighted linear regression models of spawning season duration in the James River as a function of annual reproductive degree days (RDD) and spawning degree days (SDD), calculated from Jan. 1 – Dec. 31.

		James River Model			
Parameter	Effect	Estimate	Standard Error	*t*	*p*
β_0	Intercept	0.011	1.96	0.006	0.99
β_1	RDD	0.00087	0.00078	1.11	0.28
β_0	Intercept	1.32	1.028	1.28	0.21
β_1	SDD	0.00090	0.0011	0.86	0.40

6. Parameters for latitude models:

Supplementary Table 5: Parameter estimates for linear regression models of mean annual spawning degree days (SDD) and reproductive degree days (RDD) for blue crab as a function of latitude. Degree days were estimated from temperature data collected by monitoring buoys in coastal waters along the East Coast of the U.S. Means represent annual degree days averaged across 2015 – 2019. All temperature data were retrieved from the National Estuarine Research Reserve System (Appendix 4), except Chesapeake Bay and James River temperatures which were calculated as described in section 2.1 of the methods.

		SDD Model				RDD Model			
Parameter	Effect	Estimate	Standard Error	*t*	*p*	Estimate	Standard Error	*t*	*p*
β_0	Intercept	5674.28	227.58	24.93	< 0.0001	10743.53	352.88	30.45	< 0.0001
β_1	Latitude	-125.57	6.006	-20.19	< 0.0001	-223.68	9.31	-24.02	< 0.0001

Literature cited:

Edwards, C., and Crone, E. E. (2021). Estimating abundance and phenology from transect count data with GLMs. Oikos 130, 1335–1345.

NOAA National Estuarine Research Reserve System (NERRS). System-wide Monitoring Program. Data accessed from the NOAA NERRS Centralized Data Management Office website: http://www.nerrsdata.org/;

Appendix, Chapter 3: Spawning history, fecundity, and potential sperm limitation of female blue crabs in Chesapeake Bay

Section S1. Logical framework

The logical framework supporting the use of size, spawning history, egg development stage, and time of year in models of blue crab batch fecundity from females collected in 2022 from the Chesapeake Bay is:

Size: Size is represented in fecundity models as carapace width (CW), a continuous variable. We hypothesized that fecundity would have a positive, exponential relationship with female size. Size has a well-established positive relationship with fecundity for Brachyurans (Hines, 1982), and blue crabs specifically (Prager et al., 1990; Dickinson et al., 2006; Darnell et al., 2009; Graham et al., 2012).

Spawning History: Spawning history was included in the fecundity models as a categorical variable, with two levels: primiparous or multiparous. Females were classified as primiparous or multiparous based on the location and maturity of nemertean worms (Schneider et al. 2023b). Primiparous females have only produced their current egg mass, while multiparous females have produced at least one more egg mass than their current brood. We expected multiparous females to have a lower fecundity than primiparous females because they have already fertilized at least one egg mass, and brood size decreases with subsequent broods (Darnell et al., 2009).

Egg Development Stage: Egg stage is a categorical variable in the fecundity models with three levels: early development, mid-development, and late-development. Egg development stage was based on egg color with orange, brown, and black eggs representing early, mid, and late-development stages, respectively (Van Engel, 1958). We expected females with late-stage eggs to have a lower fecundity than females with early-stage eggs due to egg mortality, mechanical abrasion and stripping that occurs during embryogenesis (Kuris, 1991; Goldstein et al. 2022).

Time of Year: Time of year was included as a categorical variable in our models and expressed as month: June, July, and August. We expected fecundity to be highest in June and lowest in August because of higher fecundity in spring for a Gulf of Mexico population (Graham et al., 2012) and a hypothesized higher fecundity in Chesapeake Bay at the beginning of the spawning season (Schneider et al., 2023a).

The logical framework supporting the use of size and year in the ANCOVA of blue crab batch fecundity from this study and Prager et al. (1990) is:

Size: See rationale above.

Year: The years 1986, 1987, and 2022 were included as levels of a categorical variable. We expected fecundity would be lower in 2022 than that in 1986 and 1987 due to recent low spawning stock biomass and concerns about sperm limitation (Ogburn et al., 2019; Chesapeake Bay Stock Assessment Committee, 2023).

The logical framework supporting the use of size, spawning history, and time of year in models of blue crab stored-sperm quantity from females collected in 2022 from the Chesapeake Bay is:

Size: Size is represented in stored-sperm quantity models as carapace width (CW), a continuous variable. We included size in the model because of the expected interaction with spawning history.

Spawning History: Spawning history was included in the stored-sperm quantity models as a categorical variable with two levels: primiparous or multiparous. Females were classified as primiparous or multiparous based on the location and maturity of nemertean worms (Schneider et al. 2023b). We hypothesized that multiparous females would have less stored sperm than primiparous females because they have fertilized at least one additional brood (Webb et al., 2016).

Size × Spawning History: An interaction term between spawning history and size was included in the model because we expected that stored-sperm quantity would decrease with crab size for multiparous females and increase with crab size for primiparous females. The quantity of sperm passed to a female is independent of crab size (Kendall et al., 2002); therefore, large females should lose sperm at a faster rate than smaller females because they fertilize more eggs per brood, although this was not observed in Darnell et al (2009). Theoretically, multiparous females would have already fertilized at least one additional egg mass, and therefore should experience a greater rate of sperm loss by size than primiparous females.

Time of Year: Time of year was included as a categorical variable, and expressed as June, July, and August. We expected stored-sperm quantity to decline across months, independently of female spawning history. As the time progresses between mating and spawning, sperm stores decline even in the absence of fertilization (Wolcott et al., 2005), and females who mate later in the summer are more likely to be sperm limited from high fishing pressure on males reducing the operational sex ratio (Ogburn et al., 2014).

Section S2. Testing an interaction between month and spawning history

The global model included all hypothesized predictors of fecundity as fixed effects: carapace width (CW), spawning history (categorical: primiparous or multiparous), egg stage (categorical: early, mid and late-stage eggs) and month (categorical: June, July, August). A model including an additional term: an interaction between month and spawning history was also considered. We hypothesized a potential interaction between month and spawning history because multiparous females in August (near the end of the spawning season) are more likely to have produced more than 2 egg masses, and therefore the relationship between parity and fecundity may differ by month. The global model, including the interaction between month and parity, was tested and the interaction was meaningful (Table S1). However, this relationship was driven by only one crab captured in June that was multiparous. When this crab is excluded from the analysis, the interaction was no longer meaningful (Table S2). Because the interaction term is being driven by one observation, the model used for inference excludes the interaction, but retains the multiparous crab in June.

Table S1. Analysis of deviance for the global model (defined in Table 1) of loge fecundity with an interaction between month and parity; p = probability of observing an equal or more extreme value under the null hypothesis.

Variable	Sum of Squares	Degrees of freedom	F statistic	p
CW	6.67	1	103.38	< 0.0001
Parity	0.43	1	6.66	0.011
Egg Stage	0.26	2	2.04	0.14
Month	2.43	2	18.85	< 0.0001
Parity × Month	0.51	2	3.96	0.022

Table S2. Analysis of deviance for the global model (defined in Table 1) of $\log_e$ fecundity with an interaction between month and parity. The one multiparous female captured in June was excluded from the model dataset.

Variable	Sum of Squares	Degrees of freedom	F statistic	p
CW	6.67	1	103.38	< 0.0001
Parity	0.63	1	9.80	0.0022
Egg Stage	0.26	2	2.04	0.14
Month	2.85	2	22.09	< 0.0001
Parity × Month	0.014	1	0.22	0.64

Section S3. Model plots for all fecundity models (Table 1), in log space

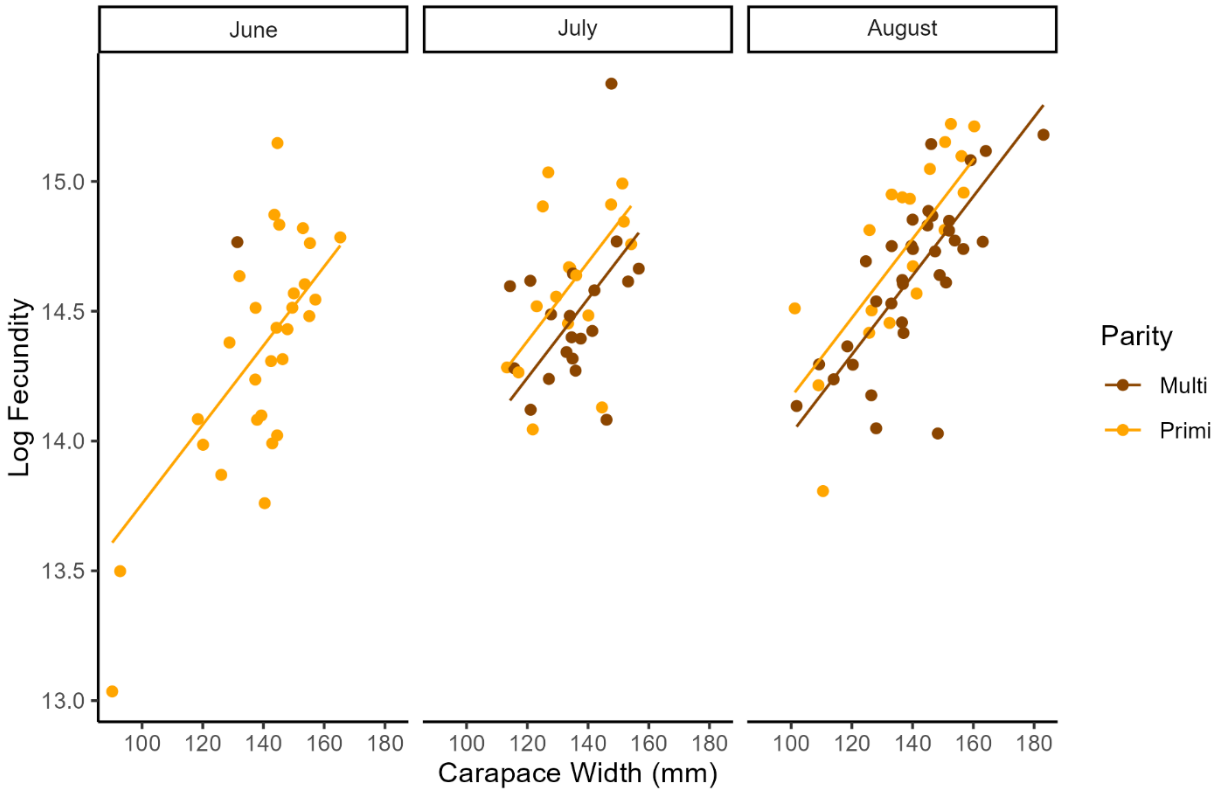


Figure S1. Relationship between carapace width (mm), female spawning history (parity), and month on the $\log_e$ fecundity of blue crabs from the Chesapeake Bay in 2022. The solid lines represent the predicted values from the global model (Table 2), with egg stage held at early development.

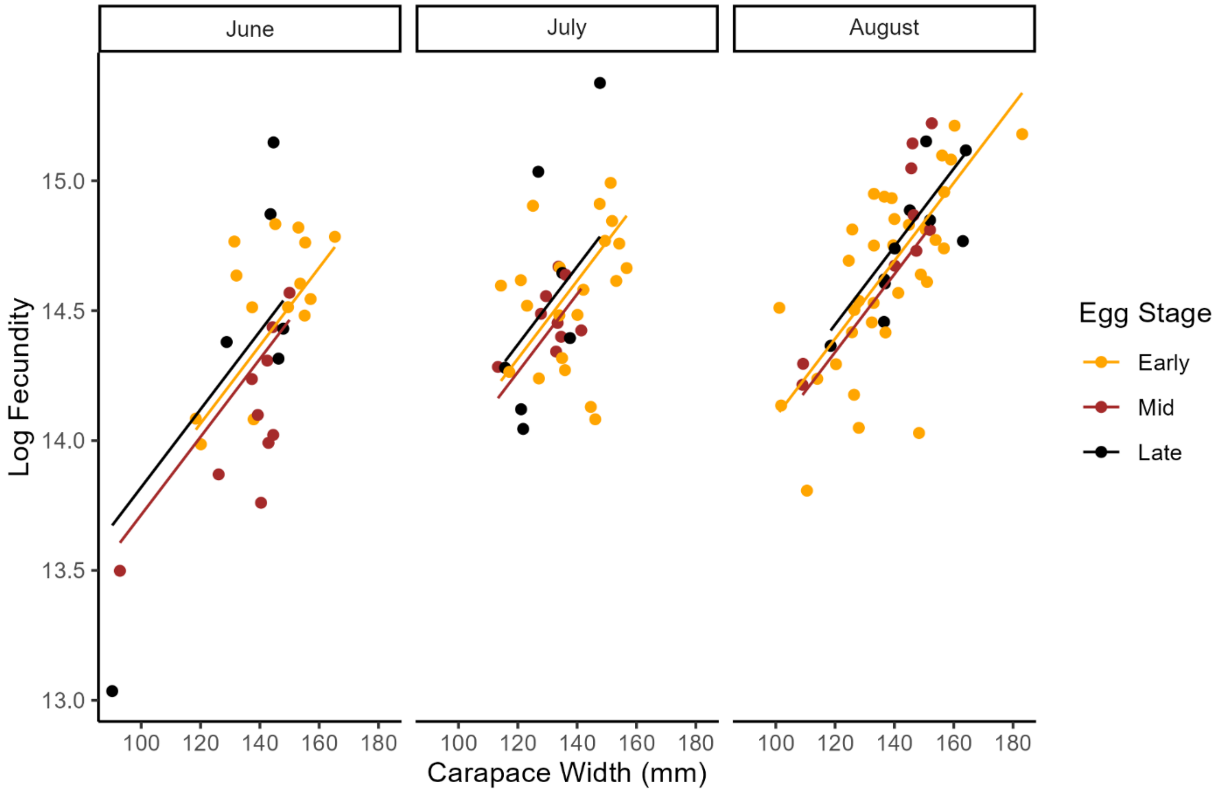


Figure S2. Relationship between carapace width (mm), egg stage, and month on the $\log_e$ fecundity of blue crabs from the Chesapeake Bay in 2022. The solid lines represent the predicted values from the management model (Table S9).

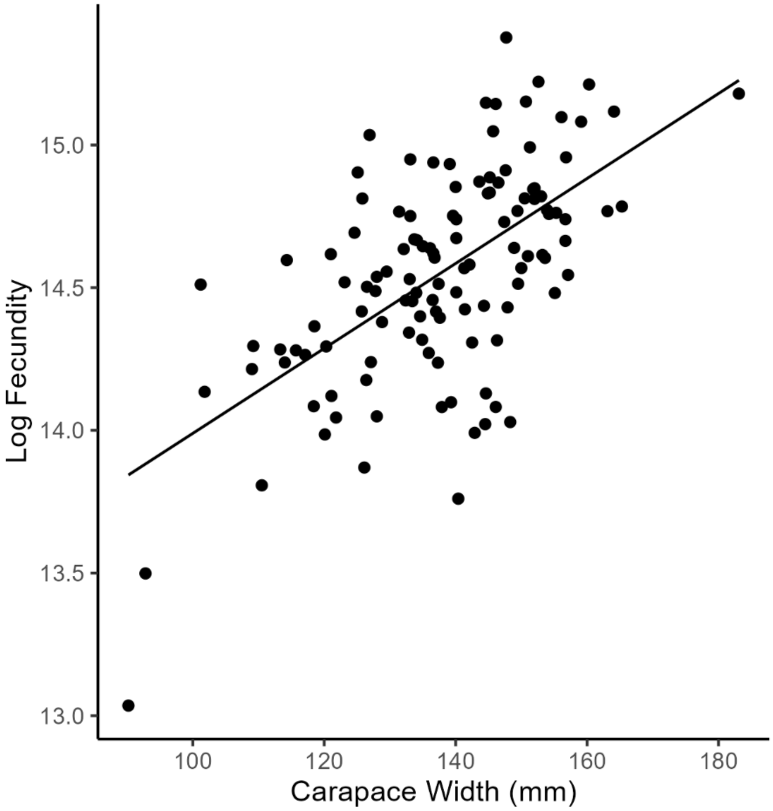


Figure S3. Relationship between carapace width (mm) and the $\log_e$ fecundity of blue crabs from the Chesapeake Bay in 2022. The solid lines represent the predicted values from the comparative model (Table S10).

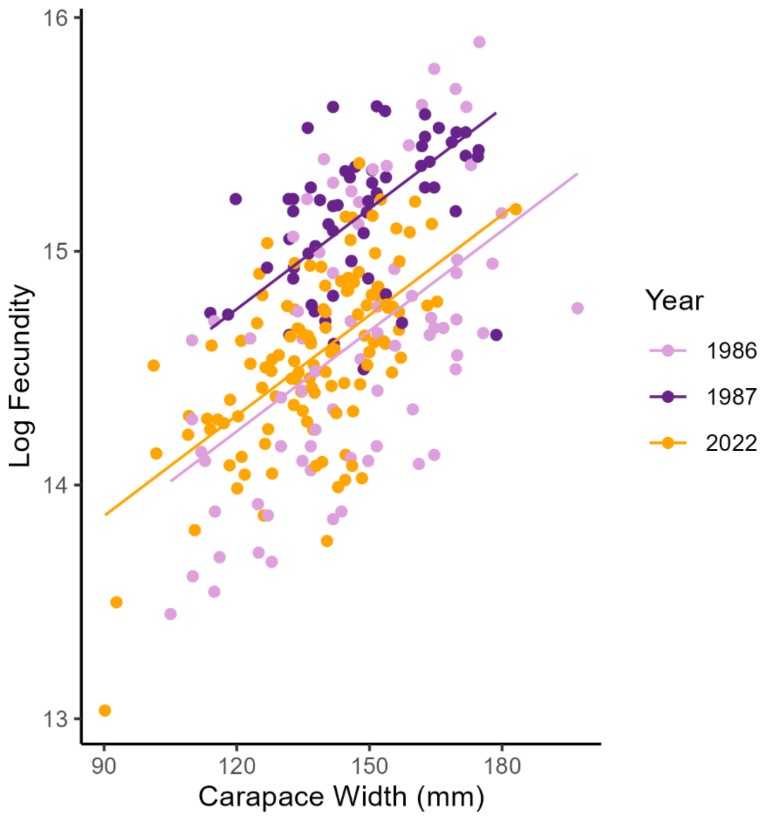


Figure S4. Relationship between carapace width (mm) and the log$_e$ fecundity of blue crabs from the Chesapeake Bay in 2022, 1986, and 1987. The solid lines represent the predicted values from the ANCOVA presented in Table 3.

Section S4. Interaction between carapace width and year

Within the loge fecundity model, comparing fecundities from 2022 and from 1986 and 1987 (Prager et al. 1990), the interaction between year and carapace width (CW) was examined (Table S6). The parameter estimates for the interaction between CW and 1987 was meaningful (Table S6). However, the interaction was ultimately excluded because the analysis of deviance indicated the interaction was not a meaningful factor in the model (Table S7) and the AIC was nearly identical for the ANCOVA with and without the interaction (Table S8).

Table S6: Parameter estimates in loge space for the ANCOVA model of loge fecundity as a function of carapace width (CW) and years (2022, 1986, and 1987) with an interaction between CW and year; SE = standard error; t = t statistic; p = probability of observing an equal or more extreme value under the null hypothesis. The intercept represents the base condition with Year_{1986}.

Variable	Estimate	SE	t	p
Intercept	12.24	0.30	40.78	< 0.0001
CW	0.016	0.002	7.96	< 0.0001
Year_{1987}	1.62	0.55	2.95	0.0035
Year_{2022}	0.26	0.42	0.63	0.53
CW × Year_{1987}	-0.0074	0.004	-2.012	0.045
CW × Year_{2022}	-0.0013	0.003	-0.44	0.66

Table S7: Analysis of deviance for the ANCOVA model of $\log_e$ fecundity as a function of carapace width (CW), year (2022, 1986, and 1987), and an interaction with CW and year; Df = degrees of freedom; p = probability of observing an equal or more extreme value under the null hypothesis.

Variable	Sum of Squares	Df	F statistic	p
CW	14.73	1	117.34	< 0.0001
Year	10.58	2	42.13	< 0.0001
CW × Year	0.52	2	2.086	0.13

Table S8. ANCOVA model of $\log_e$ fecundity as a function of carapace width (CW) and year (1986, 1987, and 2022) with and without the interaction between Year and CW and the small sample size corrected Akaike's Information Criteria (AICc). Fecundity was $\log_e$ transformed for both models. K = number of parameters in the model including the intercept and model variance; Δ_i = difference in AICc values between a given model and the model with the lowest AICc within model groupings; w_i = weighted probability of a model being the best in the set; CW = carapace width. The model with the lowest AICc and highest w_i is in bold.

Model	Predictors	k	AICc	Δ_i	w_i
ANCOVA	**CW + Year**	**5**	**201**	**0**	**0.503**
ANCOVA with interaction	CW + Year + (CW × Year)	7	201	0	0.497

Section S5. Parameter estimates for the management and comparative models

Table S9. Parameter estimates in $\log_e$ space for the management model (Table 1) of $\log_e$ fecundity; SE = standard error; t = t statistic; p = probability of observing an equal or more extreme value under the null hypothesis. The intercept represents the base condition with Egg $\text{Stage}_{\text{early}}$ and $\text{Month}_{\text{June}}$.

Variable	Estimate	SE	t	p
Intercept	12.26	0.23	52.9	< 0.0001
CW	0.015	0.0016	9.38	< 0.0001
Egg $\text{Stage}_{\text{mid}}$	-0.051	0.06	-0.85	0.40
Egg $\text{Stage}_{\text{late}}$	0.054	0.06	0.85	0.40
$\text{Month}_{\text{July}}$	0.25	0.07	3.77	< 0.001
$\text{Month}_{\text{August}}$	0.33	0.06	5.28	< 0.0001

Table S10. Parameter estimates in $\log_e$ space for the comparative model (Table 1) of $\log_e$ fecundity; SE = standard error; t = t statistic; p = probability of observing an equal or more extreme value under the null hypothesis.

Variable	Estimate	SE	t	p
Intercept	12.50	0.24	51.23	< 0.0001
CW	0.015	0.0018	8.45	< 0.0001

Section S6. Histogram of all ovigerous female crabs

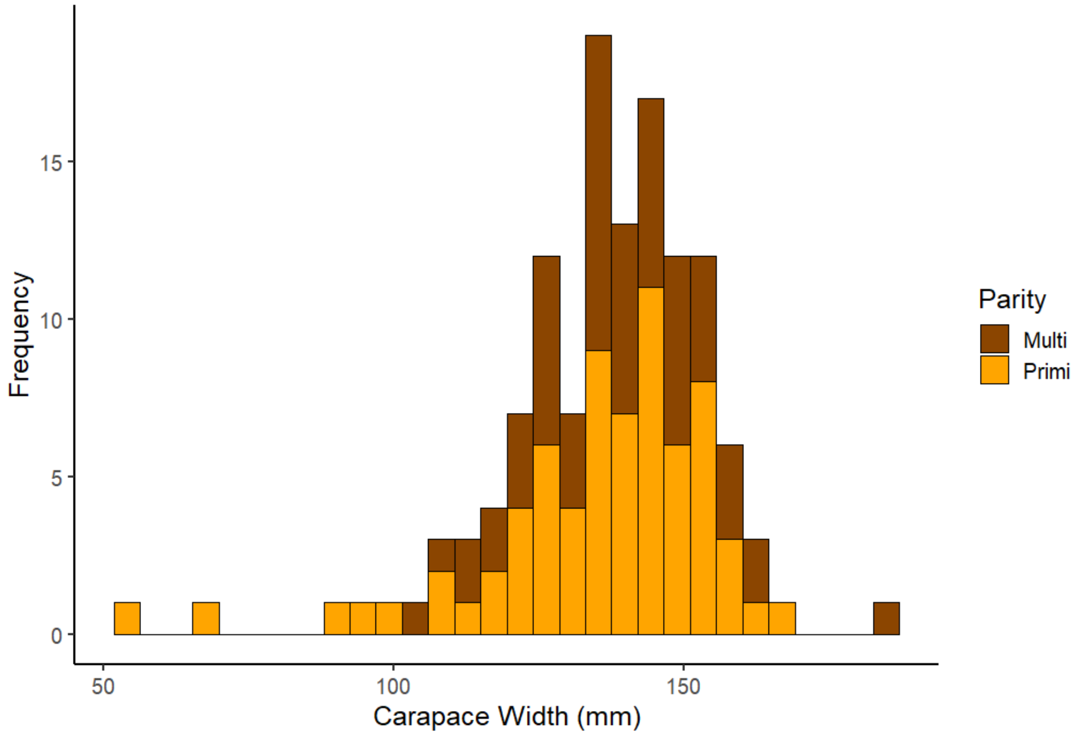


Figure S5. Histogram of carapace width (mm) for multiparous and primiparous ovigerous blue crabs captured by the VIM Trawl Survey from the Chesapeake Bay mainstem from May to September 2022.

Vita

Born in Manchester, CT on February 25th 1997. Graduated from Suffield High School in 2015 in Suffield, CT. Attended Villanova University in Villanova, PA and graduate *summa cum laude* in 2019 with a Bachelor's of Science in Environmental Science with minors in biology and political science. Entered the Doctorate of Philosophy program in Marine Science with a concentration n Fisheries Science at the Virginia Institute of Marine Science, William & Mary, in 2019, through the Master's Bypass Program.