# 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.

KEY WORDS: *Callinectes sapidus* · 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 global commercial fisheries landings, but assessments of reproductive potential over the lifespan of an individual 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.

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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. spermathecae, 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 the gill cavities of their host or on the carapace as juveniles; *C. 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 the eggs, mature, and reproduce (Humes 1942). Upon maturation, the worms become a distinct pink or red color (Humes 1942). After the host 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 USA, where its populations have fluctuated dramatically during the past 30 yr, contributing to significant fishery instability (NOAA Fisheries 2022). Across the USA, 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 (CBSAC 2022). Blue crab population abundance in Chesapeake Bay declined 81% after 1992 (Lipcius & Stockhausen 2002), rebounded after 2008, and has 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 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, i.e. crabs that have spawned once, and multiparous females, i.e. crabs that have spawned at least 2 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 2 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 1 to 3 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 mated 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 1 brood. These 2 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 in-vestigated 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, so 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, i.e. 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 of the blue crab defined by the volume of the ovary due to 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 longevity of a female 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 carapace represents the minimum possible age of the carapace of a mature female (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 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 fur-

ther 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 the spawning history of a female. 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. MATERIALS AND 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
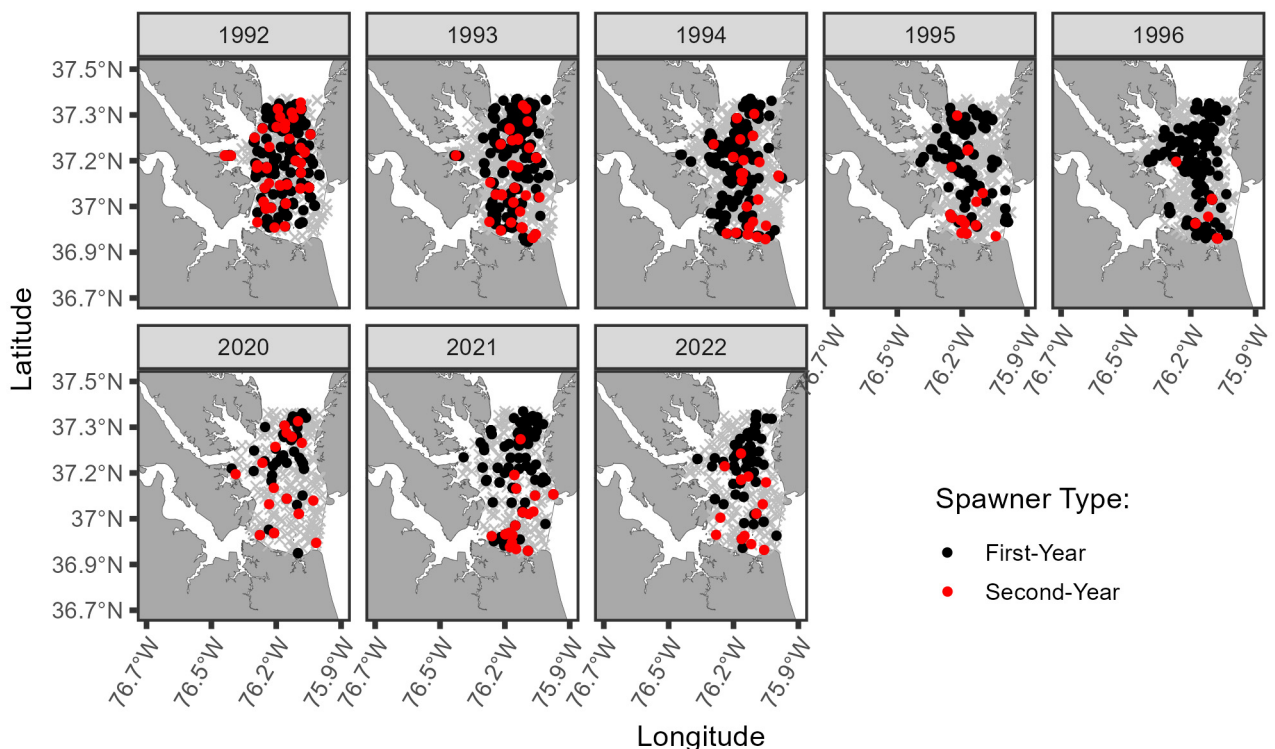


Fig. 1. Location of Virginia Institute of Marine Science Winter Dredge Survey tows where adult female blue crabs were collected and assessed for spawning history from 1992 to 1996 and 2020 to 2022. Gray X: dredge tows in which no female crabs were caught

al. 2003). All live, mature females, classified by abdomen shape (Van Engel 1958), and collected by the WDS during 2 time periods (1992–1996 and 2020–2022), were measured on board for CW to the nearest 0.1 mm. Females were classified as first- or second-year spawners using the presence of the nemertean worm *Carcinonemertes carcinophila* in the gills, an approach that has been previously 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 and sampled at random, and these residuals were added to the modeled weight estimates (see Section S1, Fig. S1, and Table S1 in the Supplement at www.int-res.com/articles/suppl/m716 p077_supp.pdf).

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 the abdomen coloration of a female.

## 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; Table S2) 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 (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 from 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 2 eras

Generalized linear models (GLMs) were used to model the relationship between eras, i.e. pre- (1994–1996) and post-management (2020–2022) 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 CW 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 1994–1996.

## 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 (Supplement Section S3, Fig. S2).

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 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 the carapace, the barnacle diameter was recorded as 0.

Table 1. Variables used in generalized linear models of the probability of a mature, female blue crab being a second-year spawner for both the 2-year and 4-year model sets. The 2-year model set includes observations from 2020 and 2021, whereas the 4-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

| Predictor | 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 | ✓ | ✓ |
| 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 | ✓ | |

## 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 2 standard deviations (Gelman 2008, Schielzeth 2010). Two sets of candidate models were evaluated based on covariate data availability (Table 1): 2-year models including 2020 and 2021, and 4-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 2-year model set because their spermathecae weights were not recorded.

All crabs were treated as independent observations (Section S3). Models were checked for overdispersion by dividing the Pearson $\chi^2$ 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 $\alpha$ 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 2-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 nonsignificant (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 among 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 be-cause 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 2-year and 4-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).
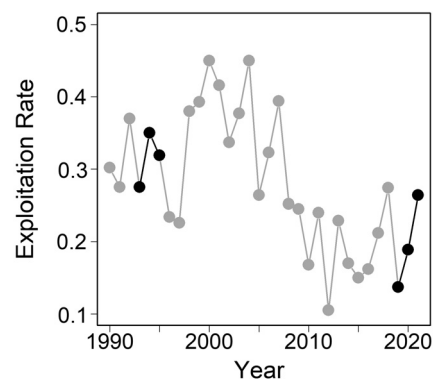


Fig. 2. Exploitation rates of female blue crabs in Chesapeake Bay from 1990 to 2021 (G. Davis pers. comm.). Black circles indicate years when spawning status was assessed. Stricter management actions were implemented in 2008 to protect the spawning stock

### 3.2. Proportion of second-year spawners and exploitation rates

We classified 2855 mature female crabs from 1992–1996 and 2020–2022 as first- or second-year spawners (Table S2) based on the presence and color of *Carcinonemertes carcinophila* in the gills. For 1994–1996 and 2020–2022, 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, although 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, $r^2 = 0.44$, $F = 3.097$, 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 second-year spawners, 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 4-year
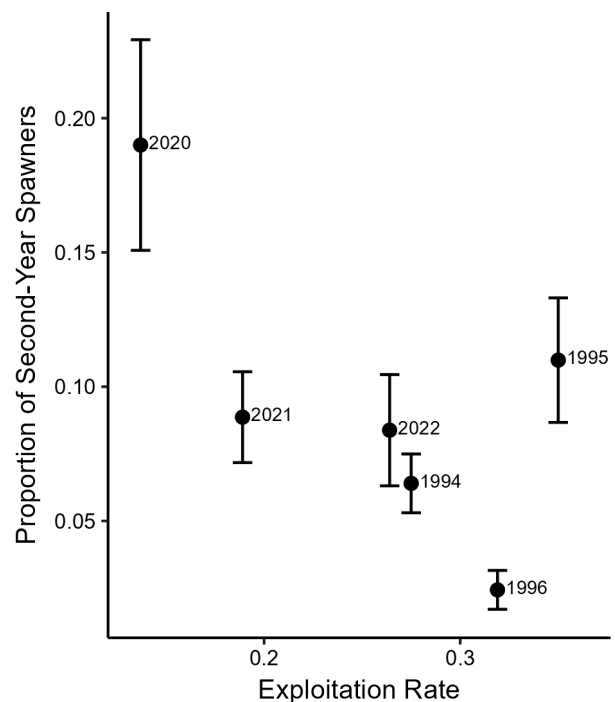


Fig. 3. Relationship between exploitation rates of female blue crabs and the proportion of second-year spawners. Due to the dredge survey occurring from December through March, the exploitation rates represent exploitation during the previous year's crabbing season (March–November). The sample sizes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

model set, model $C_1$ 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 2-year set was model $T_4$, which had the lowest AICc and a weighted probability of 0.70. Model $T_4$ 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 $T_3$ had a weighted probability of 0.25 and considered the same predictors as model $T_4$, but also included salinity as a predictor. Due to the low ΔAICc between model $T_3$ and $T_4$ (Δ = 2) and the support for including salinity in the 4-year model set (model $C_1$, Table 2), model $T_3$ was chosen for interpretation; the interpretations from models $T_3$ and $T_4$ 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,

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 4-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; $\Delta_i$: 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 $C_1$ (in **bold**), the global model, was selected for interpretation, and includes observations from 1992, 1993, 2020, and 2021

| Model | Model structure | $k$ | AICc | $\Delta_i$ | $w_i$ |
|---|---|---|---|---|---|
| **$C_1$** | **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 2-year model set, represented by $T_i$, and corrected Akaike's information criterion (AICc). Details on model predictors are presented in Table 1; other abbreviations as in Table 2. Model $T_3$ (in **bold**) was chosen for interpretation and includes observations from 2020 and 2021

| Model | Model structure | $k$ | AICc | $\Delta_i$ | $w_i$ |
|---|---|---|---|---|---|
| $T_1$ | 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 |

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 × 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 4-year model set (29%) than for the 2-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 $C_1$ and $T_3$, 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

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 4-year ($C_1$, Table 2) and 2-year ($T_3$, Table 3) model sets. Details on model predictors are presented in Table 1. 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

| Parameter | Four-year model: $C_1$ | | | | Two-year model: $T_3$ | | | |
|---|---|---|---|---|---|---|---|---|
| | 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 |
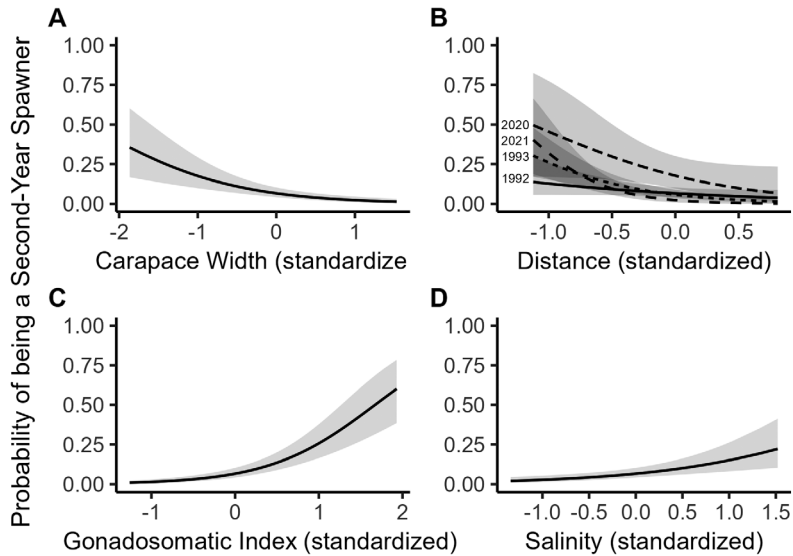
Fig. 4. Effect of (A) carapace width, (B) distance and year, (C) gonadosomatic index, and (D) salinity on the probability of a female blue crab being a second-year spawner based on the model chosen for inference from the 4-year model set (see Table 2, Model $C_1$). Note that the independent variables have been standardized for comparison. Gray bands show 95% confidence intervals

from the Chesapeake Bay population 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
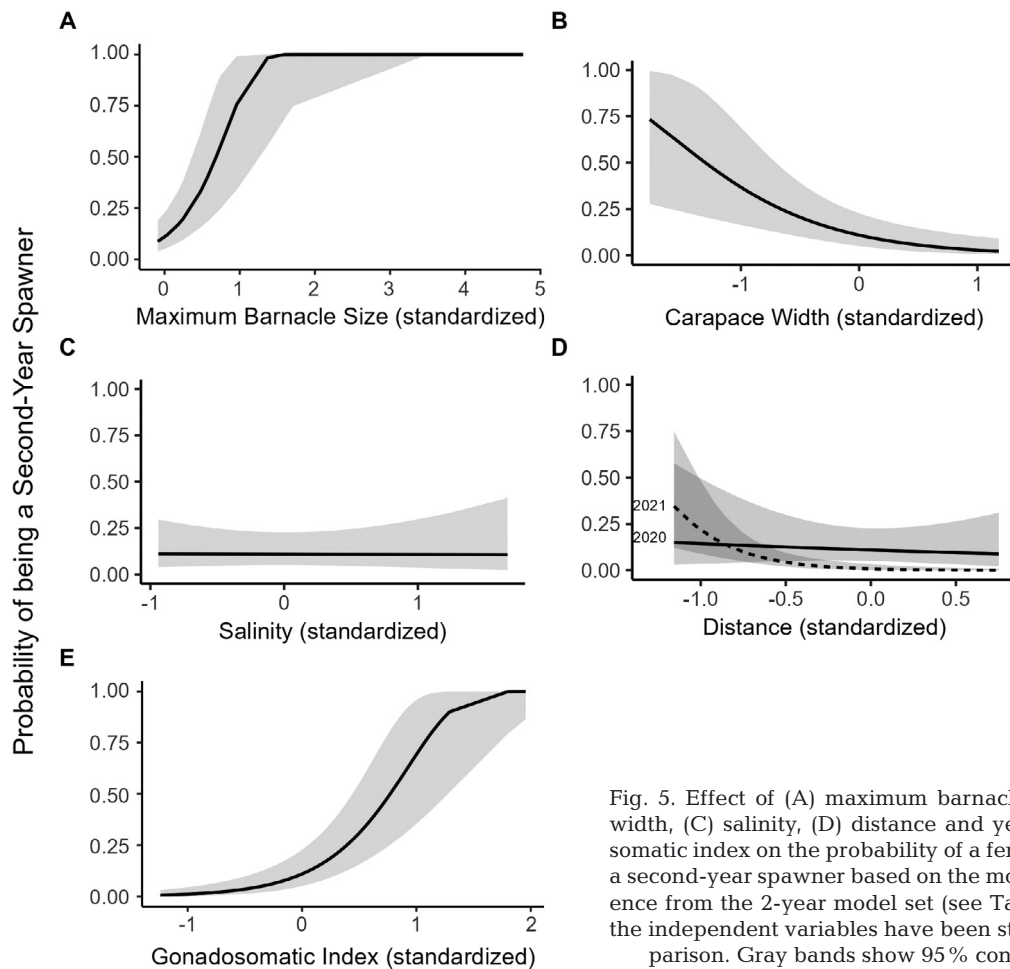


Fig. 5. Effect of (A) maximum barnacle size, (B) carapace width, (C) salinity, (D) distance and year, and (E) gonadosomatic index on the probability of a female blue crab being a second-year spawner based on the model chosen for inference from the 2-year model set (see Table 3, $T_3$). Note that the independent variables have been standardized for comparison. Gray bands show 95% confidence intervals

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 to 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 1992–1996 (0.08) and in 2020–2022 (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 unpubl. 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 4-year models, but not in 2-year models. The probability of being a second-year spawner declined with distance from the mouth of the Bay, although the rate of decline varied by year. In the 4-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 removal of mature females from overwintering hotspots by the winter dredge fishery 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 unpubl. 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 4-year models, salinity was positively correlated with the probability of being a second-year spawner, but not in 2-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 3 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 female CW (Prager et al. 1990), and the ovary enlarges as the female approaches spawning (Hard 1942). Given that (1) relatively larger first-year spawners produce bigger clutches than relatively smaller second-year spawners; (2) the first brood is the largest brood; and (3) 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 81–92% 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 17 March, 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 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 assessments. 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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