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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
- Individual reproductive potential is high and population sperm limitation is unlikely
- Size-specific fecundity in 2022 was not different from that in 1986

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 quantity 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 similar to a fecundity estimate from 1986 (2.6 million eggs/female), but lower than an estimate from 1987 (4.0 million eggs/female). The 1987 estimate was likely biased high due to methodological differences. In 2022, size-specific fecundity did not differ from that in 1986. Size-specific fecundity was lower by 0.28 million eggs in multiparous females (i.e., those that produced at least one previous egg mass) compared with primiparous females (i.e., those producing their first egg mass). Size-specific fecundity was also greater in July and August than in June, however, females in June had a greater capacity for future reproductive potential because their average stored sperm quantity was three times greater than that of females in July and August. Most females in June were primiparous and would become multiparous females in July and August with higher size-specific fecundity. Our study is the first to pair individual fecundity, stored sperm quantity, and spawning history for blue crabs, which allows for a robust assessment of reproductive potential. Generally, the reproductive potential of individual female blue crabs was high at the individual level, such that 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 × exp(0.015 × Carapace Width)) and incorporating month or spawner history in models of stock production.

Previous

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Keywords

Decapoda; Fisheries; 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 varies and affects the rate at which a population may recover from disturbance or overexploitation (Morgan, 2008, Morgan, 2018). 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 the molt cycle (Lipcius, 1985, Lipcius and Herrnkind, 1987), 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 a decapod's lifetime (Sainte-Marie, 1993, Stevens and Swiney, 2007, Darnell et al., 2009), and selective fishing can truncate the age structure of fished populations (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).

Female and male blue crabs (*Callinectes sapidus*) in Chesapeake Bay are commercially fished with diverse fishing gear, although Bay-wide regulations aim to protect spawners from high levels of exploitation during spawning periods (Chesapeake Bay Stock Assessment Committee, 2023). Laws and regulations that pertain to crabbing in Chesapeake Bay differ by jurisdiction (see Chesapeake Bay Stock Assessment Committee, 2023 for fishery details). Management actions that specifically conserve female spawners were implemented, across Chesapeake Bay jurisdictions, 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); and the harvest of females with dark egg clutches, which hatch within days, was prohibited. In Virginia, females with eggs in early development stages are legal to harvest. In Maryland, access to the female fishery was restricted and female daily catch limits were lowered (Chesapeake Bay Stock Assessment Committee, 2023). Female blue crab fecundity has not been evaluated since these management actions took effect, despite concerns that increased fishing pressure on males due to female-centric management could lead to sperm limitation and declines in female reproductive success (Ogburn et al., 2014, Ogburn et al., 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.

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). Female blue crabs store sperm in specialized organs, spermathecae, and use the sperm reserve to produce multiple broods within a spawning season and over their lifetime (Hines et al., 2003, Darnell et al., 2009). In Chesapeake Bay, females spawn from mid-May to mid-September and can produce one to three broods per season (Van Engel, 1958, Schneider et al., 2024). 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 spawning grounds in the lower Bay, where they remain (Lambert et al., 2006b, Gelpi et al., 2013). These movements are known to crabbers, 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 reproduce, threatening reproductive output of the population.

Current projections of reproductive potential, defined here as the potential number of broods a female can produce in her lifetime, in Chesapeake Bay rely on average fecundity and average stored-sperm quantity 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 spawning history, which refers to the number of times a female has produced eggs. 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, Schneider et al., 2023b). These classifications can be used to improve our understanding of spawning stock demography, as well as lifetime reproductive potential.

In this study, we sought 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).

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 (VIMS) Trawl Survey, herein trawl survey (Tuckey and Fabrizio, 2023). This survey uses a randomly stratified design to conduct 5-min trawl tows monthly 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 transported back to the laboratory on ice and refrigerated until processed. Laboratory processing occurred within 72 h of collection.

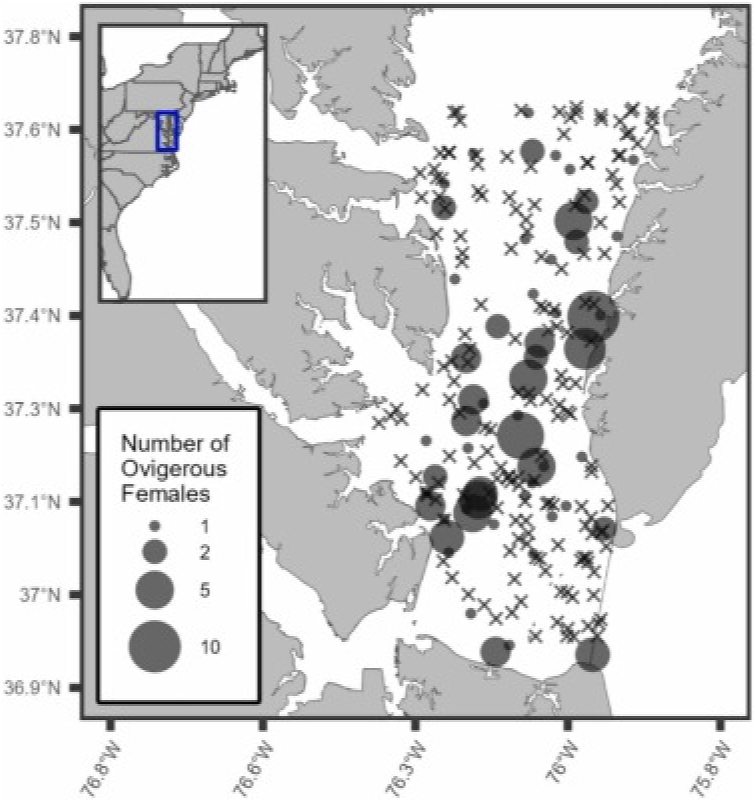

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Fig. 1. Locations of the VIMS Trawl Survey sampling sites from May to September 2022. Dark circles represent locations where ovigerous blue crabs were captured, with the size of the circle representing the number of ovigerous crabs captured. x = locations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

Females were measured for carapace width (CW), from epibranchial lateral spine to lateral spine, to 0.1 mm with Vernier calipers. 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 for the total wet weight of the brood. A sample, representing about 2.5 % of the brood on average, of the eggs 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 dry weight by 1 plus the proportion preserved (wet weight of preserved eggs / total wet weight of the brood). 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. On average, 0.02 g of eggs or about 800 eggs were counted. 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, as in Ogburn et al., 2014, Ogburn et al., 2019.

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. 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). Log-normal bias correction and 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 et al., 2022, Pinheiro and Bates, 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 (mean ± SE: 136.4 ± 1.6 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 ± 0.7 million eggs, the mean number of eggs per mm of CW was 15,643 ± 445, and the mean quantity of stored sperm was $1.4 \times 10^8 \pm 1.3 \times 10^7$.

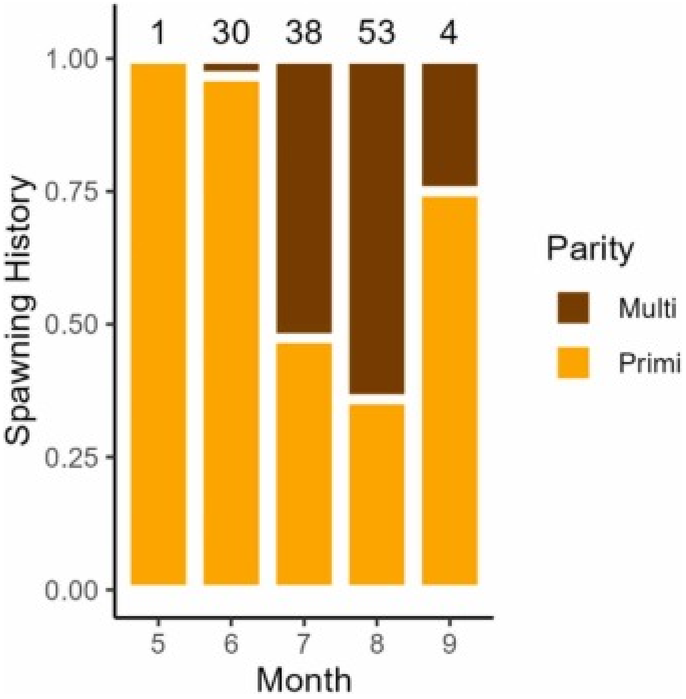

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Fig. 2. The proportion of multiparous (brown) and primiparous (light orange) female blue crabs across months during the 2022 spawning season in Chesapeake Bay. Month 5 corresponds to May, 6 to June, and so forth. Numbers at the top of the bars represent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

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 overparameterized. 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:

$$\text{Fecundity} = 268{,}337 \times \exp(0.015 \times \text{CW})$$

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

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 squares 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).

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, $\text{Egg Stage}_{\text{early}}$, $\text{Parity}_{\text{Multiparous}}$ 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
$\text{Egg Stage}_{\text{mid}}$	-0.057	0.06	-0.96	0.34
$\text{Egg Stage}_{\text{late}}$	0.080	0.06	1.26	0.21

Variable	Estimate	SE	t	p
Month$_{July}$	0.32	0.07	4.54	< 0.0001
Month$_{August}$	0.41	0.07	5.94	< 0.0001

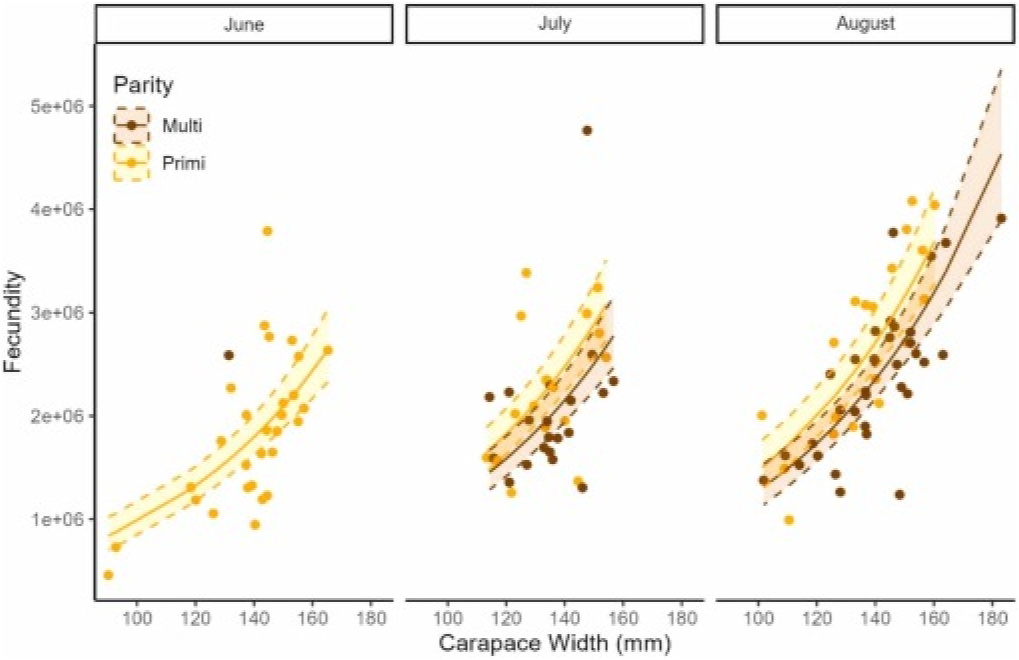

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Fig. 3. Relationship between fecundity (number of eggs) and carapace width (mm) by female parity and month for blue crabs from Chesapeake Bay in 2022. The solid lines represent the predicted values from the global model (Table 2), with egg stage held 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.

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, Table 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. 4 A). Mean CW also varied substantially across years (Table 4): 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.

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

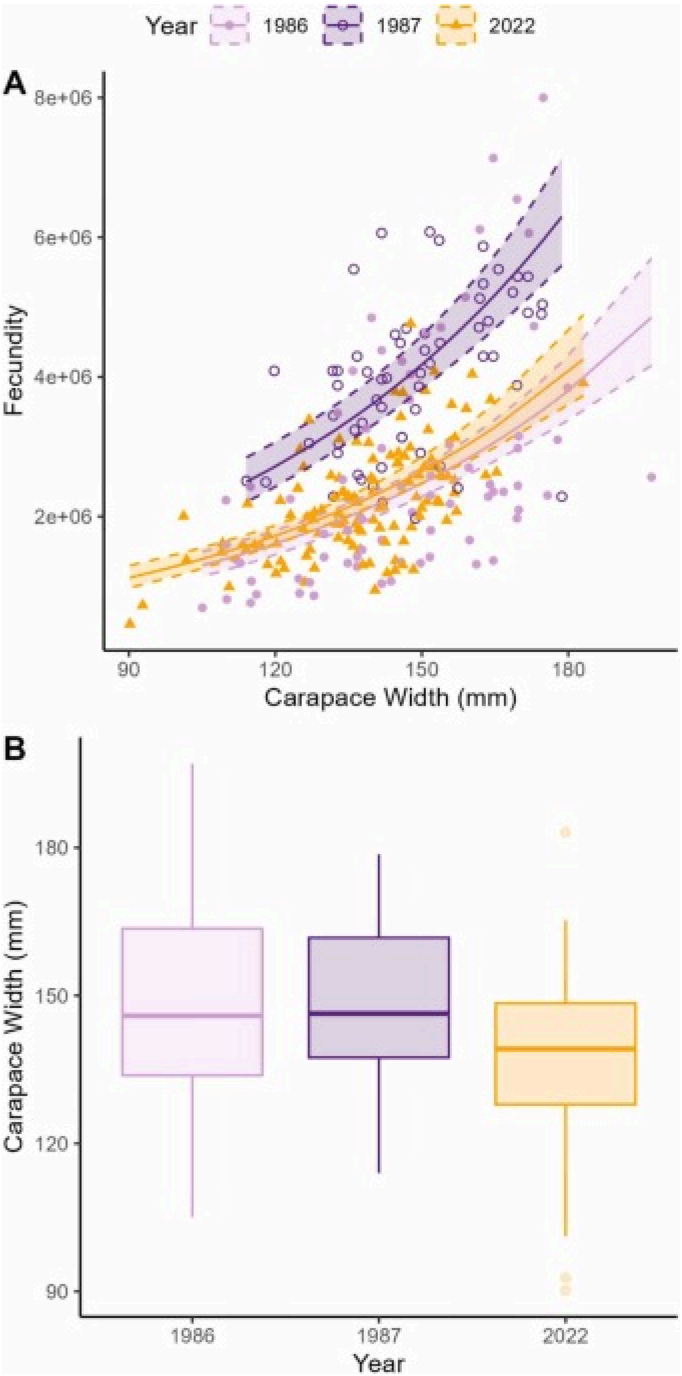

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Fig. 4. (A) The relationship between carapace width (mm) and year (1986, 1987 and 2022) on blue crab fecundity in Chesapeake Bay. Solid lines represent back-transformed linear regressions, and the shaded regions denote the 95 % confidence intervals 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.

Table 4. Analysis of variance (ANOVA) results for carapace width (CW) among years (1986, 1987, and 2022); df = degrees of freedom, SS = sum of squares, MS = mean sums of squares, F = F statistic; p = probability of observing an equal or more extreme value under the null hypothesis.

Source of Variation	df	SS	MS	F	p
Year	2	5517.0	2758.6	9.6	< 0.0001
Error	250	71,925	287.7		

Similar to the fecundity models, crabs from May (n =1) and September (n = 4) 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 5). Mean stored-sperm quantity increased with CW of female blue crabs, except for primiparous females in July whose mean stored-sperm quantity decreased with CW (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).

Table 5. 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

Variable	Estimate	SE	t	p
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

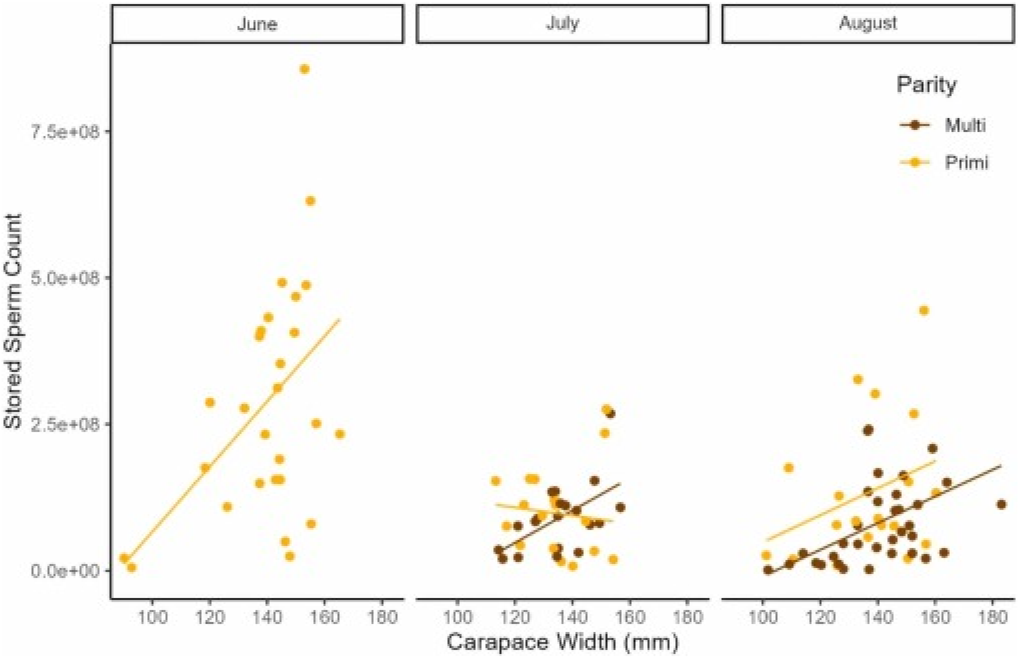

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Fig. 5. Stored sperm quantity in ovigerous blue crabs from Chesapeake Bay in 2022 as a function of carapace width, female parity, and month. Solid lines represent predictions from generalized least-squares regression (Table 5).

The degree to which sperm limitation impacts brood production depended on the sperm-to-egg ratio and month (Table 6, Table 7). 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 7).

Table 6. 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 7. 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

		Sperm-to-egg ratios			
Primiparous	**n**	**1:1**	**4:1**	**10:1**	**25:1**
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

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, our study indicates that 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 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) did not cover the entire extent of the spawning grounds (Jones et al., 1990, Lipcius et al., 2003). Although annual fecundity data are lacking from 1987 to 2022, fecundity at size was similar between 1986 and 2022, suggesting that size-specific fecundity has not changed over four decades.

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 ± 1.6 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). The method used in this study assumes that all egg-bearing females will become infested with nemerteans (Hopkins, 1947, 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 a trawl survey with short tow durations (5 min), which does not cause as much prolonged stress as being confined in a trap with conspecifics or trawl surveys with longer tow durations (e.g., 20 min, A.K. Schneider personal observation). 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 quantity (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, Ogburn et al., 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 quantity, 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 mid-June when crabbing is banned (Va. Admin. 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 in 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.

CRediT authorship contribution statement

Alexandra K. Schneider: Writing – original draft, Visualization, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation. **Jeffrey D. Shields:** Writing – review & editing, Supervision, Resources, Methodology, Investigation, Formal analysis, Conceptualization. **Mary C. Fabrizio:** Writing – review & editing, Supervision, Resources, Methodology, Investigation, Funding acquisition, Formal analysis, Conceptualization. **Romuald N. Lipcius:** Writing – review & editing, Supervision, Resources, Methodology, Investigation, Funding acquisition, Formal analysis, Conceptualization.

Declaration of Competing Interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Alexandra Schneider reports financial support was provided by Virginia Sea Grant. Mary C. Fabrizio reports financial support was provided by Virginia Marine Resources Commission. Mary C. Fabrizio reports financial support was provided by US Fish and Wildlife Service. If there are other authors, they declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary material

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Supplementary material

Special issue articles Recommended articles

Data availability

Data will be made available on request.

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