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Evaluation of fishery-induced sperm limitation in Chesapeake Bay blue crab using an individual-based model

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ABSTRACT: Sperm limitation, where the reproductive output of a population is restricted by its sperm production, is a concern for several crustacean species around the world. We used a simulation study to evaluate the effects of different fishing pressures and regulations on the male to female sex ratio and the average number of sperm received per female for the blue crab *Callinectes sapidus* population in Chesapeake Bay. We created an individual-based model that tracked a cohort of immature females on a daily step over a 2 yr period as the cohort grew, matured, and mated with mature males. The model included sex-specific growth, maturity, and mating of a closed population. We ran the model under multiple scenarios of mate choice behavior to quantify the patterns in sperm counts and sex ratios across a broad range of simulated fishing pressures and regulations. Average sperm counts in mated females and male to female sex ratios of the modeled population varied among scenarios, but were not related to each other. Fishing pressure had a significant negative effect on average sperm per female only in scenarios with unfished females and the exploitation rate for males at 5 times that currently estimated in Chesapeake Bay. Our results suggested that sperm per female is not linearly related to mature male to female sex ratios and that sperm limitation does not appear to be a concern for the blue crab population of Chesapeake Bay under current regulations.

KEY WORDS: *Callinectes sapidus* · Sperm limitation · Crustacea · Fisheries management · Demographic model · Blue crab

INTRODUCTION

In the management of many fisheries, reproductive output is often assumed to be directly proportional to, and constrained by, female abundance (i.e. egg limitation; Quinn & Deriso 1999). Less attention is usually given to male abundance because sperm limitation is thought unlikely, particularly in internally fertilizing species (Levitan & Petersen 1995). However, in populations where large males are the primary targets of exploitation, such as in many decapod crustaceans and protogynous fishes, male abundance may become low enough that sperm are limiting, thereby restricting reproductive output and population growth (Wenner 1989, Alonzo & Mangel 2005, Brooks et al. 2008). For example, sperm limitation due to fishing pressure (i.e. fishing-induced sperm limitation) has been observed in field manipulation studies of Japanese stone crabs *Hapalogaster dentata* (Sato & Goshima 2006) and in laboratory studies of snow crabs *Chionoectes opilio* (Rondeau & Sainte-Marie 2001).

Two conditions make sperm limitation more likely: a female-biased operational sex ratio, such that encounter rates between the reproductively capable males and females is low, and low levels of sperm transfer. In some species, the 2 conditions may be correlated (Kendall et al. 2001). Studies on sexual

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competition usually refer to the operational sex ratio of a population, or the number of mature males that can potentially mate to the number of reproductively available females (Kendall et al. 2001, Rondeau & Sainte-Marie 2001). Many female crustaceans are only receptive during short windows of time, such that finding a mate within this period is crucial for successful fertilization (Rondeau & Sainte-Marie 2001). If male abundance is low relative to females, sperm limitation could occur because either some females will not be able to find mates, or available males will have insufficient sperm for all receptive females as a result of repeated matings (Kendall et al. 2002). However, in many crustacean species, females mature asynchronously, causing the pool of receptive males to be larger than receptive females and making the operational sex ratio almost always skewed toward males (Rondeau & Sainte-Marie 2001). The operational sex ratio of a population has been suggested as an indicator of fishing-induced sperm limitation, particularly if the fishery selects for males (Kendall et al. 2001, Sato & Goshima 2006, Rankin & Kokko 2007, Ogburn et al. 2014).

Concern has been expressed over the existence of fishing-induced sperm limitation in blue crabs *Callinectes sapidus* in Chesapeake Bay, USA (Kendall et al. 2001, Hines et al. 2003, Ogburn et al. 2014). Female blue crabs are thought to mate only once when they undergo their maturation molt (Jivoff et al. 2007), although recent evidence has indicated that multiple paternity occurs (Hill et al. 2017, Wells et al. 2017). The female stores sperm in organs termed spermathecae. The amount of sperm a female receives will dictate how many eggs she will be able to fertilize in her lifetime (Hines et al. 2003, Jivoff 2003). Males, in contrast, can mate an indefinite number of times. However, males deplete a portion of their sperm during each mating and need approximately 20 d to fully recuperate (Kendall et al. 2001). In a population with an operational sex ratio skewed toward females, males may mate more frequently than this 20 d period and, accordingly, could pass fewer sperm to each mate, which could cause sperm limitation (Kendall et al. 2001). Furthermore, the operational sex ratio and number of sperm received per female may fluctuate during the year (Ogburn et al. 2014). Recent management of blue crabs in the Chesapeake Bay has focused on increasing female abundance, which has caused substantial changes in sex-specific exploitation rates (Miller et al. 2011).

Sperm limitation, as it may affect the population growth rate, is a population-level process. Population-level sperm limitation would be realized by individual females not receiving enough sperm to fertilize their eggs and, thus, reducing the number of progeny produced. Previous studies of sperm limitation in blue crabs have focused on using sperm limitation at the individual level by measuring the amount of sperm per female and comparing that value across regions (Hines et al. 2003, Rains et al. 2016), to values from lab experiments (Kendall et al. 2002), or over time (Ogburn et al. 2014) to infer its occurrence or intensity at the population level. Here, our focus is on whether fishing would be expected to cause a reduction in sperm per female and result in population-level sperm limitation, as has been suggested in several studies (Kendall et al. 2002, Hines et al. 2003, Ogburn et al. 2014).

We used a simulation model to evaluate the potential effects of sex-specific fishing mortality on average sperm received per female blue crab given a set of reasonable assumptions on molting, mating, and mortality. Our modeling approach allowed us to evaluate assumptions regarding the effects of mating behavior and fishing pressure on reproductive success. We modified an existing individual-based model (IBM) for Chesapeake Bay blue crabs (Bunnell & Miller 2005, Bunnell et al. 2010, Huang et al. 2015) to simulate the effect of harvest regulations, using Maryland regulations as a basis, and mating strategies on the average amount of sperm received by females. The IBM included a range of sex-specific fishing scenarios as well as several mate preference strategies to determine their effect on sperm per female. We compared sperm quantities received by females under different fishing scenarios to those of unfished conditions to estimate the potential for fishery-induced sperm limitation. If the average amount of sperm received per female is lower under fished conditions than unfished conditions, then fishing-induced sperm limitation may occur. However, if fishing does not affect the average amount of sperm received per female, then fishing-induced sperm limitation is unlikely to affect the population growth rate.

METHODS

The IBM tracked the fates and mating histories of 4500 blue crabs using a daily time step over the course of 2 yr (Fig. 1). Almost all female blue crabs in Chesapeake Bay are mature by the end of their second year (Hines 2007), so we assumed 2 yr were sufficient for the entire cohort of females to mature and mate. The model simulated crabs distributed in a 6 ha

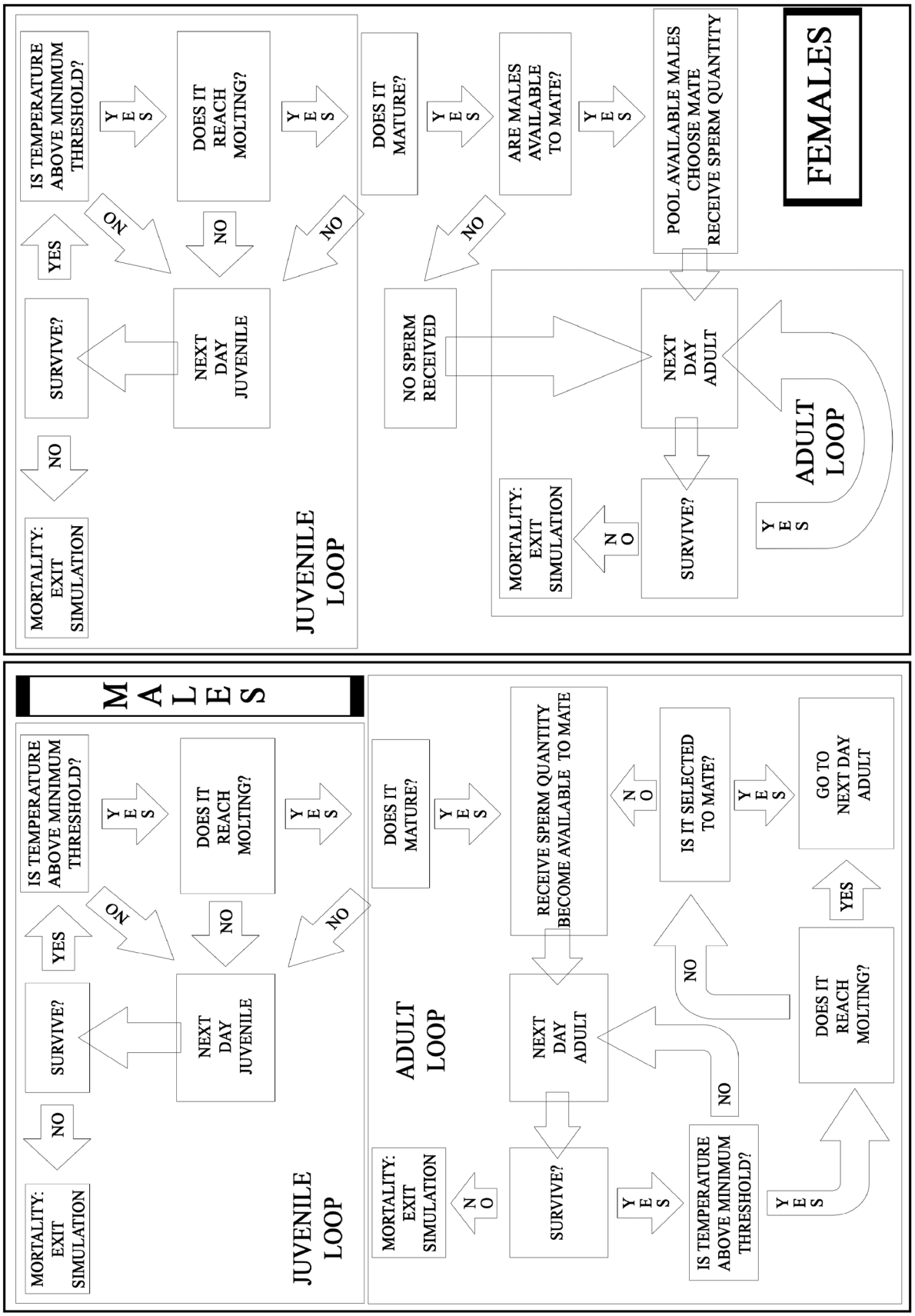

Fig. 1. Individual-based blue crab model simulation process separated by gender

area. The population was considered closed to movement into or out of the area. The resultant crab density (72 crabs 1000 m^{-2}) was similar to the average density observed in the 2010 Chesapeake Bay blue crab winter dredge survey (CBWDS). Blue crabs move on average about 5–15 m h^{-1} (Hines 2007), so the modeled area approximates a 3 d ambit of an individual crab. Within the model, crabs grew, matured, mated, and died according to stochastic functions based on previously published relationships (Bunnell & Miller 2005). The model does not track the position of each individual relative to the other individuals, and mating is the only interaction allowed between crabs in the model. The model rules determine which crabs can potentially mate based on their status relative to maturity, whether they are already mating with another individual, have a soft or hard shell, the recent number of mates, and the mating preference scenario. Each scenario was run once for the analysis, similar to Bunnell & Miller (2005) and Bunnell et al. (2010), but scenarios were run multiple times to ensure that results were replicated. The model was developed in the R programming language.

The IBM was parameterized for 39 different scenarios that included combinations of overall fishing mortality, sex-specific regulations, and mate preference strategies. Scenarios were given identifiers based on fishing mortality and size limits on each sex of blue crab (Table 1). We compared the amount of sperm per female under scenarios of fishing mortality and size limits to both a no-fishing scenario for 3 different assumed mating strategies and to data collected by the field and laboratory studies of Hines et al. (2003), Carver et al. (2005), Wolcott et al. (2005), Ogburn et al. (2014), and Rains et al. (2016).

Table 1. Fishing scenario IDs explaining fishing patterns by regulation description and fishing mortality of each sex. 'Current' indicates regulations that were in place in Maryland in 2011, which differed for males and females. Regulations are described in more detail in 'Methods; Scenarios'

Scenario ID	Fishing pattern	Fishing mortality	
		Male	Female
NO0	No fishing	0	0
MF1	Current	1.05	1.05
MF2	Current	2.1	2.1
MF5	Current	5.25	5.25
MO1	Current on males only	1.05	0
MO2	Current on males only	2.1	0
MO5	Current on males only	5.25	0
FO1	Current on females only	0	1.05
FO2	Current on females only	0	2.1
FO5	Current on females only	0	5.25
YR1	Current on females/current on males but open all year	1.05	1.05
AM1	Current on females/all mature males	1.05	1.05
AM5	No female fishing/all mature males	5.25	0

Initial conditions

The model introduced 2000 females as age-0 juveniles on 1 January in Year 1 that represented a cohort that had settled the previous summer. We assumed that all mature females from the previous year would have migrated out of the system to spawn the previous fall (Aguilar et al. 2005). In addition, 2500 males were apportioned between age-0 and age-1+ (an aggregate age class including individuals age-1 and older) based on estimates from CBWDS data from 2008–2010, with 69% of the males as age-0 juveniles and 31% as age 1+. These starting abundances were calculated from the CBWDS data for 2008–2010, but they yield a sex ratio that is slightly more female (54%) than is used in the most recent stock assessment (52%; Miller et al. 2011). Multiple cohorts of males were present because they do not migrate to the mouth of Chesapeake Bay to spawn as do females (Hines 2007). The model then followed the growth, survival, and mating history of these individuals. No new age-0 individuals were added at the start of the second year.

The initial size distribution of each sex was based on carapace widths (CWs) collected from the CBWDS in 2008–2010. Female sizes at the beginning of the year were drawn from a lognormal distribution with a back-transformed mean = 23.2 mm and a log-scale standard deviation (SD) = 0.4. CWs for the age-0 males were drawn from a lognormal distribution with a back-transformed mean = 13.6 mm and a log-scale SD = 1.0. CWs for age-1+ males were drawn from a normal distribution with a mean = 124.2 mm and SD = 25.4.

Mortality

Mortality was a stochastic process and depended on crab size, sex, shell status (hard/active or soft/recently molted inactive), and fishing mortality scenario. Instantaneous fishing (F) and natural (M) mortality rates were

modeled as simultaneous and additive processes, with a daily survival rate, S, given by:

$$S = e^{-(M+F)} \quad (1)$$

Natural mortality was set at 0.9 yr^{-1} following Hewitt et al. (2007), Bunnell et al. (2010), and Miller et al. (2011). The annual rate was converted to a daily rate by dividing it by the number of days in a calendar year, so that M was 0.0025 d^{-1}. During soft-shell status, crabs were assigned a natural mortality of twice the hard-shell daily rate, as in Bunnell & Miller (2005). Fishing mortality depended on the size and sex of the crab as well as the fishing scenario. The annual F was converted to a daily rate by dividing it by the number of days in the Maryland blue crab season for that sex (205 for females, 258 for males). During days outside of the fishing season, F was set to 0. For each crab on each day, a number was drawn from a uniform (0,1) distribution; if that number was greater than S, then the model assigned the crab to be dead.

Growth

Growth was represented using a temperature-dependent molt process model (Bunnell & Miller 2005, Brylawski & Miller 2006). The model tracked each crab's maturity, shell status (hard or soft), number of growing degree-days accumulated, time until next molt, sperm number, and number of mates (for males only).

The molt process model recognized growth per molt (GPM) and intermolt periods (IP; Bunnell & Miller 2005). GPM was stochastic and was modeled using normal distributions with sex-specific mean GPMs and SDs. Results from blue crab growth studies by Newcombe et al. (1949) and Tagatz (1968) were averaged by sex to calculate the mean GPM. On average, male CW increased 24% $molt^{-1}$ with an SD of 7%, and the mean GPM for females was 25% with an SD of 6%, except for the maturation molt. The mean GPM for the maturation molt for females was 32% with an SD of 6% (Tagatz 1968). These GPM values are similar to those used by Bunnell & Miller (2005) and Smith & Chang (2007). Blue crabs were considered to be soft shell for 2 d following molting (Ryer et al. 1997, Bunnell & Miller 2005).

We adopted the approach of Bunnell & Miller (2005) to model the IP as a stochastic function of accumulated growing degree-days, with parameters derived from Tagatz (1968). On Day 1 and after each molting event, the value for the next IP for the i^{th} crab was drawn from a shifted exponential distribution:

$$f(\mathrm{IP}) = \left(\frac{1}{\beta_i}\right) e^{-\frac{\mathrm{IP}-\gamma_i}{\beta_i}}, \ \mathrm{IP} \geq \gamma_i \quad (2)$$

where γ is a power function of CW for the i^{th} crab (CW_i) and represents the minimum amount of growing degree days necessary for molting:

$$\gamma_i = 69.70 \times (1.0149)^{CW_i} \quad (3)$$

The β parameter describes the variability of the IP distribution and is also a function of CW:

$$\beta_i = (166.39 \times (1.0115)^{CW_i}) - \gamma \quad (4)$$

For each day above 8.9°C, the physiological minimum temperature for blue crab growth (Smith & Chang 2007), degree-days were accumulated by subtracting 8.9 from the day's temperature value. Once the number of accumulated degree-days exceeded the IP value of a given crab, that crab molted, grew based on its assigned GPM, became a soft-shell crab for 2 d, and a new IP and GPM were drawn for the next molt. Average daily temperature estimates from the Patuxent River during 1985–2011 were used.

Maturity and mating

Maturation occurred only during molting of immature crabs, and was parameterized differently for males and females. For simplicity, we assumed a knife-edge maturity function for males. In the model, all males matured at 107 mm, the median CW for male maturation (Van Engel 1990, Jivoff et al. 2007). Using a knife-edge function for male maturation simplifies the process because males mature over a range of sizes (82–227 mm; Van Engel 1990). However, using 1 maturation size should not cause bias in the operational sex ratio because males that mature at CWs smaller than 107 mm should approximately balance out those that mature at larger CWs. After maturation, each male was assigned a maximum number of sperm, drawn at random from a lognormal distribution with a back-transformed mean of 2.1×10^9 and an SD of 1.49×10^9 based on vas deferens counts from Kendall et al. (2001) and Carver et al. (2005). Multiple studies have shown that there is no relationship between sperm per male and male CW, so males retained their maximum number of sperm for the remainder of the simulation (Kendall et al. 2001, Carver et al. 2005). Once a male matured and its carapace hardened, it became eligible to mate. Males continued to grow after maturation.

The maturation probability for the i^{th} female followed a logistic function of CW_i, similar to the approach of Bunnell & Miller (2005):

$$p(\text{Maturity})_i = \frac{1}{1+\left(\frac{CW_i}{111}\right)^{-28.51}} \quad (5)$$

where the mean CW for the maturation molt was 111 mm. The mean CW for the maturation molt was estimated by back calculation of the average CW of mature females collected in Chesapeake Bay during 2011 (Rains et al. 2016), assuming that female CWs grew 32% with their maturation molt (Tagatz 1968). The determination of whether an individual female crab matured relied on comparing a uniform (0,1) random number to the p(Maturity) for each female crab for each molt. Once a female matured, she underwent her terminal molt and the model no longer allowed growth (Jivoff et al. 2007).

Potential matings occurred immediately following a female's maturation molt. All males in the population that were alive, mature, not already mating with another individual, hard-shelled, and above a minimum sperm threshold were considered as potential mates. Mating assignments for a given female were based on a multinomial distribution given their relative probability of mating (P):

$$P(\text{Mate}_i) = \frac{P_i}{\sum_j P_j} \quad (6)$$

The relative probability for each mature male varied according to 3 mate choice scenarios examined: random, size assortative mating (Jivoff 1997), or previous mating history (Kendall & Wolcott 1999), which are described subsequently.

Once a mating pair was determined, the female received half of her mate's sperm stores (i.e. the male's sperm was reduced by half). The amount of sperm transferred was based on studies that counted the average sperm decrease between recuperated males and males having mated twice consecutively, causing an approximate 75% reduction overall in sperm stores of males (i.e. a 50% reduction during each pairing; Kendall et al. 2001, Wolcott et al. 2005). The sperm a female received was further reduced by approximately 50% to account for degradation between mating and a female's first brood of eggs (Wolcott et al. 2005, Rains et al. 2016). Although, in reality, this reduction is a gradual process, we included it in the model as occurring at the time of mating to simplify computations.

The model also tracked sperm stores of males. All hard-shell, non-mating males that were not at their maximum sperm limit accumulated sperm daily at approximately 6% d^{-1} (Kendall et al. 2001):

$$\text{Sperm}_{i,t} = \text{Sperm}_{i,t-1} \times e^{0.057} \quad (7)$$

where $\text{Sperm}_{i,t}$ is the sperm the ith male had on Day t. Once the crab reached its maximum amount of sperm, sperm production stopped. Males cease mating after 3 consecutive mating events (Kendall et al. 2001, 2002, Hines et al. 2003, Wolcott et al. 2005), and a minimum sperm threshold was implemented to replicate this pattern. The minimum sperm threshold was an amount of sperm below which males would stop mating in order to begin the replenishment process. The minimum sperm threshold was calculated as the average amount of sperm a male would have after 3 consecutive matings, or about 3.0×10^8. When a male reached a sperm quantity below this threshold, the model would not include the male in the pool of potential mates until its sperm stores had been replenished to a level above the threshold.

Scenarios

The model was parameterized to evaluate the effects of 13 fishing mortality and regulation scenarios (Table 1) crossed with 3 mate preference scenarios for a total of 39 scenarios. Four fishing mortality scenarios included no fishing ($F = 0$ yr^{-1}, 41% annual survival), the current fishing level for the population ($F = 1.05$ yr^{-1}, 14% annual survival; Miller et al. 2011), twice the present fishing level ($F = 2.1$ yr^{-1}, 5% annual survival, a level estimated to reflect fishing mortality during 1970–1980; Miller et al. 2011), and 5 times the present fishing level ($F = 5.25$ yr^{-1}, 0.02% annual survival). Regulations similar to those in the Maryland portion of Chesapeake Bay were used to simulate the pattern of harvest. The 2013 Maryland blue crab regulations for males included a minimum legal size of 127 mm for hard shell and 89 mm for soft shell. Male harvests in the model occurred for 258 d from 1 April to 15 December. For females, harvest of all hard-shell mature females and soft-shell females above 89 mm was allowed for 205 d from 1 April to 23 October.

Five alternative fishery regulation scenarios were developed to test different effects of male and female fishing on average sperm per female. The alternative regulation scenarios included current regulations on one sex with a moratorium on fishing for the other sex, year-round fishing on males with current regulations on females, and a minimum size of 107 mm (size of maturity) on males with either current regulations or a moratorium on females.

We included 3 mate choice scenarios: random, size assortative mating, and previous mating history. The random mate choice scenario assigned all potential reproductively active males in the population with the same probability of being selected as a mate.

The size assortative mating scenario modeled an increase in probability of mating for similarly sized males and females and was developed from field observations of a linear relationship between CWs of coupled blue crabs in the Rhode River, Maryland (Jivoff 1997). To simulate this scenario, males had a higher probability of being selected the more similar they were to the maturing female's size. The relative probability was given by:

$$P_i = e^{\frac{(CW_F - mp)^2}{2*var}} \quad (8)$$

where CW_F is the CW of the molting female, *mp* is the mean preferred size from the linear relationship between a pre-copulatory female and its mate's CW (CW_i; $mp = 73.33 + [0.255 \times CW_i]$; Jivoff 1997), and *var* is the residual variance of the linear relationship from Jivoff (1997; approximately 72.2 mm^2).

The previous mating history scenario is based on a laboratory study by Kendall & Wolcott (1999), who reported that recently mated males had a higher probability of mating again. In summary, males that had mated 2 times consecutively were 3 times as likely to successfully pair with a female as males that had not mated at all in mating experiments (Kendall & Wolcott 1999). They suggested this was mainly due to experienced males being more able to control females. Because Kendall & Wolcott (1999) allowed males 20 d to recuperate sperm levels before the beginning of their study, we assumed that only matings within the most recent 20 d window would affect the relative probability of mating. Therefore, the total number of mating events each male experienced over the previous 20 d was summed to calculate each male's relative mating probability, with the *P* equal to the number of mates in the last 20 d plus 1. This meant that a male with 0 mates had $P = 1$, a male with 1 mate had $P = 2$, and a male with 2 mates had $P = 3$. Males with 3 or more mates in the 20 d span had a 0 probability of being chosen because experiments indicated that males would not mate after 3 consecutive pairings (Kendall et al. 2001, 2002, Hines et al. 2003, Wolcott et al. 2005).

Analysis

For each of the 39 scenarios, a variety of performance metrics were calculated. Sex ratio for each scenario was calculated as the surviving males divided by the surviving females on 31 October (i.e. the end of the mating season) during the second year of the simulation to mimic a one-time study of sex ratio at the end of the season. Additionally, we calculated the true operational sex ratio for each scenario as the ratio of mature available (alive, non-molting, above sperm threshold) males divided by the maturing females on each day during the mating season and summarized the daily values as the average over the 2 yr. The means and standard deviations for number of mates per mature male and sperm per female over the simulation period were calculated for each scenario. The 95% confidence intervals for all metrics were calculated assuming a normal distribution. Using separate linear regressions, we tested for relationships between the average number of sperm per female (response variable) against male:female sex ratio, operational sex ratio, and fraction of mature males that mated. Saturation curves were fitted to the relationships of both the average number of sperm per female and average number of sperm per male to male:female sex ratio using maximum likelihood estimation, such that the average number of sperm per female, *S*, was given by:

$$S = \frac{S_{max} \times R}{B + R} \quad (9)$$

where S_{max} is the maximum number of sperm, *R* is the male to female sex ratio, and *B* is the half saturation constant, i.e. the male:female sex ratio where sperm is at half of S_{max}.

To determine if there were differences in average sperm per female among scenarios, we conducted an ANOVA with fishing pressure scenario (the combination of *F* and regulations placed on the population) as the independent variable and average sperm per female as the dependent variable, while accounting for each mate choice scenario as a random block design. Tukey's honestly significant difference (HSD) multiple means comparison test was performed when a significant p-value was found for an ANOVA. If the scenarios with fishing did not result in lower sperm per female than the unfished scenario, then fishery-induced sperm limitation would not be expected.

Sensitivity analysis

An analysis was performed to assess the sensitivity of model results to chosen population size (4500 blue crabs). We ran the model with a reduced population size, 1125 crabs (625 males and 500 females), which

corresponds to the same density as the base run with an area of 1.5 ha. We also considered a population size of 18 000 crabs (10 000 males and 8000 females), which corresponds to the same density of crabs as the base run in a 25 ha area. The average sperm per female, fraction of mature males that mated, and the operational sex ratio were then calculated in the same way as explained above to compare these results with our original ones.

RESULTS

The average number of sperm per female was significantly different among fishing pressure scenarios and mate preference scenarios ($F_{14,24}$ = 17.9, p < 0.0001; Fig. 2). However, only the scenario with 5 times fishing pressure on all mature males (AM5) had significantly lower average number of sperm per female than all other scenarios. Except for the 3 scenarios that had 5 times fishing pressure on all mature males only (AM5), all mature females found mates. In the high exploitation rate (AM5) scenarios, substantial numbers (15–25%) of females did not find mates and received no sperm.

Females received an average of 4.8×10^8 sperm ($\pm 1.67 \times 10^7$, mean ± SE) across scenarios. However, average sperm per female varied according to fishing pressure and mate selection scenario (Table 2, Fig. 2). The minimum average sperm per female occurred in the scenario for size assortative mate choice and 5 times current fishing pressure on all mature males only scenario (AM5), and the maximum was found in the random mate choice and no fishing pressure scenario (NO0). Among the 3 mate choice scenarios, the random mate choice simulations exhibited the greatest differences in average sperm per female among the fishing pressure scenarios and no fishing scenarios. However, the only fishing pressure scenarios that differed more than approximately 10% from the no fishing scenario were the 5 times fishing on all mature males only scenarios (AM5). Interestingly, within size assortative mating scenarios, the twice (MF2) and 5 times (MF5) fishing pressures on both males and females scenarios and the twice fishing pressure on females only scenario (FO2) actually had higher average sperm per female than the no fishing scenario.

Average sperm produced by males was fairly consistent across scenarios. Males stored an average of 2.08×10^9 ($\pm 9.04 \times 10^6$) sperm (Table 1). The minimum average sperm per male was found in the history mate choice and 5 times fishing pressure on males only scenario (MO5). The maximum occurred

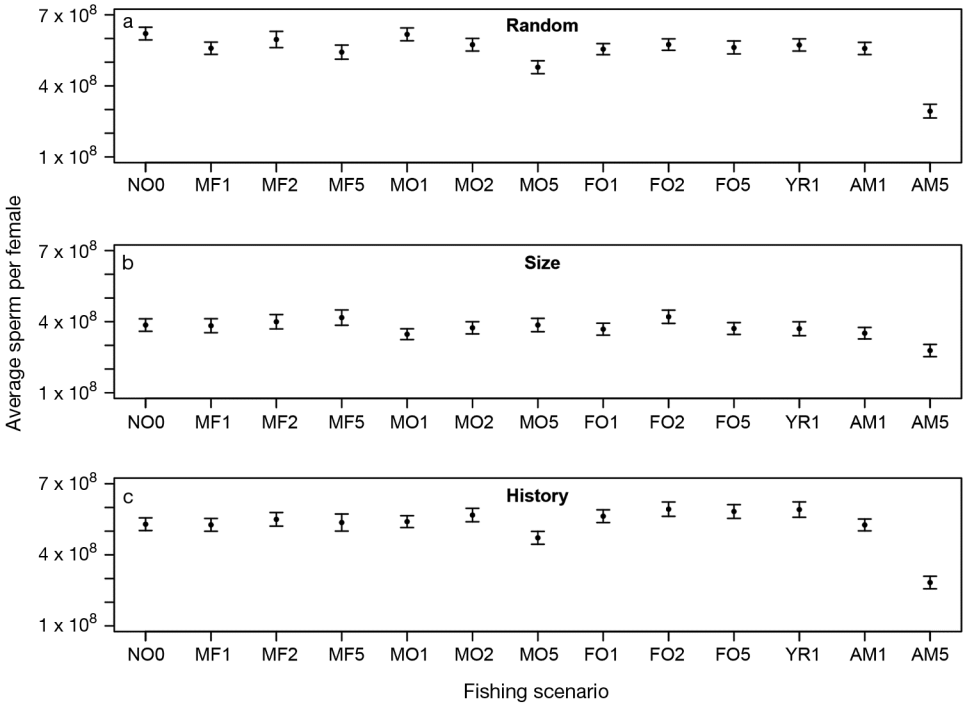

Fig. 2. Average number of sperm per blue crab female for each fishing scenario, separated by mate choice scenario: (a) random, (b) size assortative mating, or (c) previous mating history. Definitions of the fishing scenarios are given in Table 1. Dots are the mean value in each scenario, and whiskers are the 95% confidence intervals

Table 2. Results from all 39 simulations, grouped by mating strategy scenario (random, size assortative mating, or previous mating history) showing fishing scenario IDs of fishing patterns (see Table 1) and the associated statistics calculated for each. Sex ratio: seasonal male:female sex ratio at the end of the simulation, Operational sex ratio: average operational sex ratio over the simulation, Mean sperm - male: average amount of sperm a mature male had per day, Mean mates male^{-1}: average number of mates a mature male had per scenario, Mean (SD) sperm - female: average (SD) number of sperm transferred to a female upon mating, Mature females: number of females that matured over the simulation time period, Unfertilized mature females: number of females that matured but did not mate

Mating scenario	Scenario ID	Sex ratio	Operational sex ratio	Mean sperm - male ($\times 10^9$)	Mean mates male^{-1}	Males that mated (n)	Mean sperm - female ($\times 10^8$)	SD sperm - female ($\times 10^8$)	Mature females (n)	Unfertilized mature females
Random	NO0	1.12	235.72	2.11	0.23	363	6.21	3.32	585	0
	MF1	1.07	146.29	2.13	0.22	301	5.59	3.10	550	0
	MF2	0.80	81.73	2.08	0.21	276	5.96	4.01	525	0
	MF5	0.99	35.04	2.08	0.19	219	5.42	3.32	476	0
	MO1	0.65	147.95	2.12	0.25	336	6.17	3.43	620	0
	MO2	0.43	91.27	2.09	0.25	326	5.74	3.38	614	0
	MO5	0.34	37.90	1.98	0.23	249	4.79	3.34	579	0
	FO1	2.08	234.63	2.10	0.23	372	5.55	2.88	586	0
	FO2	2.95	257.45	2.09	0.20	350	5.74	2.77	508	0
	FO5	5.53	315.46	2.09	0.20	355	5.62	3.13	499	0
	YR1	1.04	117.09	2.09	0.23	327	5.73	3.12	565	0
	AM1	0.84	124.77	2.10	0.21	299	5.58	3.03	529	0
	AM5	0.09	10.70	1.97	0.18	131	2.93	3.61	600	150
Size	NO0	1.17	291.91	2.12	0.24	145	3.86	3.31	607	0
	MF1	0.85	148.17	2.09	0.20	141	3.83	3.33	489	0
	MF2	0.82	102.36	2.11	0.20	157	3.99	3.43	489	0
	MF5	1.68	54.88	2.02	0.19	158	4.17	3.58	472	0
	MO1	0.65	139.50	2.03	0.23	158	3.47	2.80	583	0
	MO2	0.46	76.11	2.06	0.21	178	3.74	3.03	534	0
	MO5	0.21	33.96	2.01	0.22	175	3.86	3.36	544	0
	FO1	1.90	253.52	2.10	0.22	141	3.68	2.98	538	0
	FO2	2.05	248.12	2.11	0.20	144	4.21	3.23	512	0
	FO5	5.47	270.58	2.13	0.21	136	3.71	2.93	525	0
	YR1	0.93	119.82	2.13	0.22	146	3.70	3.48	540	0
	AM1	0.93	141.49	2.13	0.22	154	3.51	2.90	549	0
	AM5	0.06	14.00	1.97	0.20	122	2.78	3.21	593	97
History	NO0	1.21	259.57	2.12	0.23	352	5.29	3.29	581	0
	MF1	1.09	158.97	2.10	0.22	293	5.27	3.21	539	0
	MF2	0.89	93.48	2.12	0.23	281	5.50	3.52	582	0
	MF5	1.13	52.14	2.10	0.19	209	5.36	3.96	464	0
	MO1	0.66	135.36	2.06	0.23	323	5.40	3.06	569	0
	MO2	0.46	83.68	2.04	0.24	275	5.68	3.58	605	0
	MO5	0.15	35.13	1.93	0.23	225	4.72	3.33	580	0
	FO1	2.04	275.27	2.11	0.23	377	5.63	3.30	580	0
	FO2	3.01	254.48	2.16	0.21	355	5.93	3.57	529	0
	FO5	5.32	286.42	2.10	0.21	335	5.83	3.40	528	0
	YM1	1.01	132.21	2.08	0.22	308	5.91	3.92	558	0
	AM1	0.92	100.78	2.10	0.22	250	5.26	2.98	551	0
	AM5	0.11	13.81	1.94	0.17	115	2.83	3.05	508	79

in the history mate choice and twice present fishing pressure on females only scenario (FO2). Across mate choice scenarios, average sperm per male only decreased noticeably when males were fished at 5 times current fishing pressure and there was a moratorium on female harvest (MO5, AM5), but even then, it was never less than 8% of the no fishing scenario for the same mate preference strategy.

The mean number of mates per male was variable and depended on the mate preference scenario, with fishing mortality and number of females present being the main causes of differences (Fig. 3). The mean number of mates per male was 0.22 (±0.003, Table 2), which indicates that most males never mated. In the random mate preference scenario, almost all scenarios differed by less than 5% from the unfished scenario, except when females were fished at 2 or 5 times current fishing or all mature males were fished, resulting in fewer mates per male. The number of mates per male under the size assortative

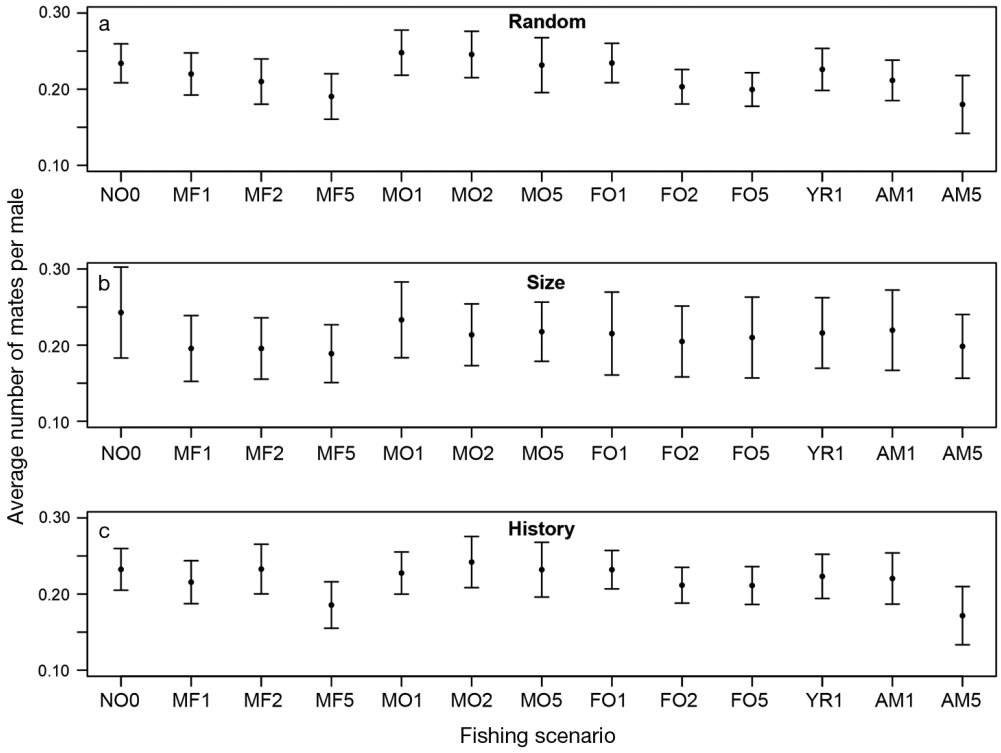

Fig. 3. Fraction of mature blue crab males that mated for each fishing scenario, separated by mate choice scenario: (a) random, (b) size assortative mating, or (c) previous mating history; details as in Fig. 2

mate preference scenarios were between 10 and 20% lower than the unfished scenario, except for the current fishing pressure on males only. However, the size assortative mate preference scenarios had very wide and overlapping standard errors across fishing scenarios. The history mate preference scenarios were all within 10% of the unfished scenario, except for the 5 times fishing pressure on all mature males only (AM5) and the 5 times current regulations on males only (MO5) scenarios.

The sex ratio of mature males:females at the end of the mating season in the second year and the operational sex ratio were variable, but were not affected by mate preference scenarios (Figs. 4 & 5). This was expected because the fishing scenario was the primary driver of the sex ratio across scenarios. The mean mature sex ratio (male:female) was 1.36 (±0.22, range 0.06–5.52). Operational sex ratios ranged considerably across the scenarios but also followed expected patterns with the fishing scenarios. The mean operational sex ratio (male:female) was substantially higher than the nominal sex ratio, 143.89 (±14.72, range 10.70–315.46), because a small fraction of the females matured on any given day. The operational sex ratio was, on average, always ≥10 males for each maturing female even in the scenario that achieved the most skewed operational sex ratio.

The average number of sperm per female and the average number of sperm per male were nonlinearly related to the male:female sex ratio at the end of the spawning season in the second year (Fig. 6). There was also a positive linear relationship between the average number of sperm per female and the fraction of mature males that mated in each scenario, but the relationship did not explain much of the variation and was driven primarily by the low values of both average sperm per female and fraction of mature males that mated in the 5 times fishing pressure on all mature males only scenarios for each mating preference (R^2 = 0.19; p = 0.006; Fig. 7). The average sperm per female was not related to the average operational sex ratio and only showed a significant decreasing pattern at the lowest operational sex ratios around 10:1 male:female in the 5 times fishing pressure on all mature males only scenarios for each mating preference (R^2 = 0.07; p = 0.06; Fig. 7).

Changing the population size, by doubling (25 ha, 18 000 crabs) or halving the population area (1.5 ha, 1125 crabs), resulted in nearly identical patterns as the original simulations. The operational sex ratio of all populations and scenarios did not drop below 1,

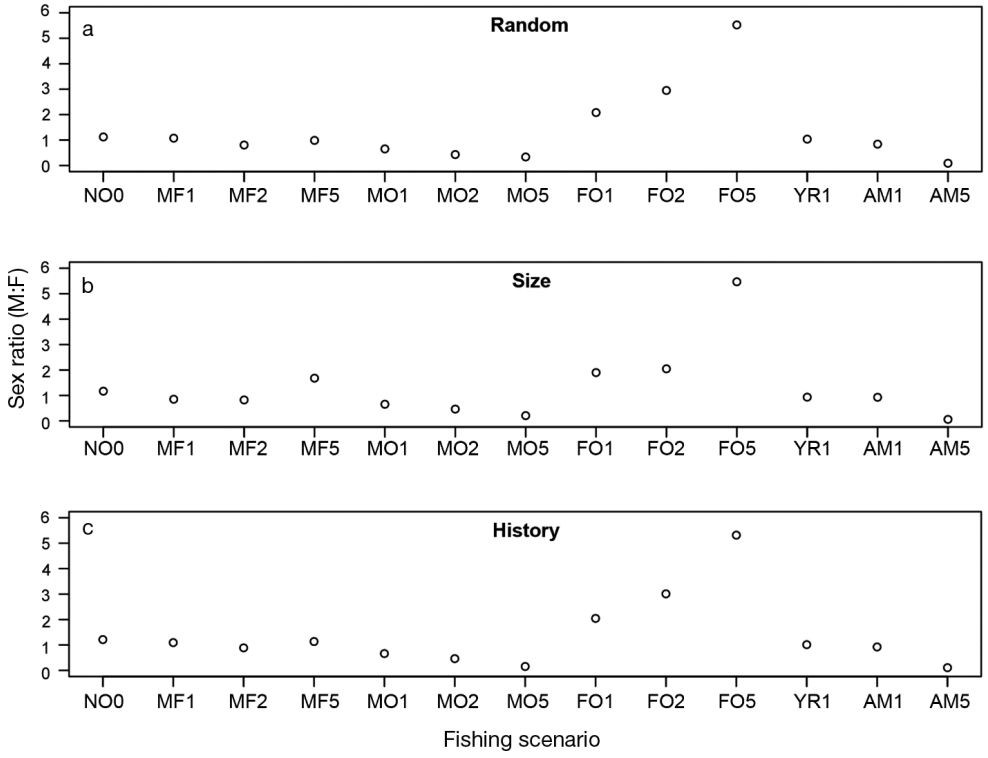

Fig. 4. Male:female sex ratio of blue crabs at the end of the second year mating season for each fishing scenario, separated by mate choice scenario: (a) random, (b) size assortative mating, or (c) previous mating history. Definitions of the fishing scenarios are given in Table 1

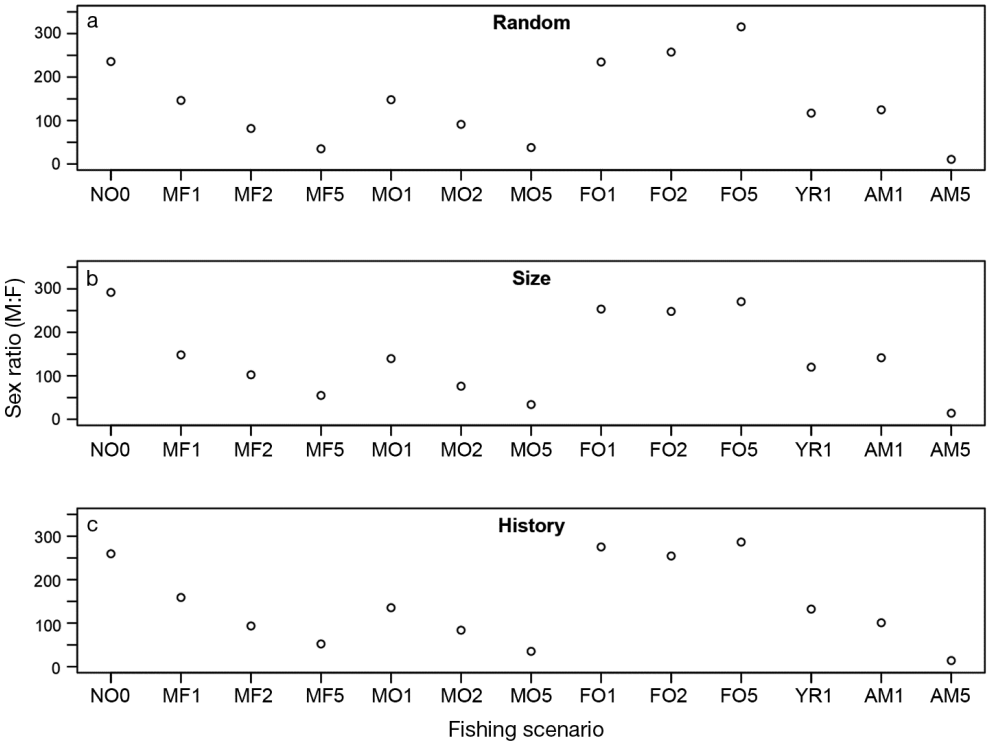

Fig. 5. Average operational male:female sex ratio of blue crabs for each fishing scenario, separated by mate choice scenario: (a) random, (b) size assortative mating, or (c) previous mating history. Definitions of the fishing scenarios are given in Table 1

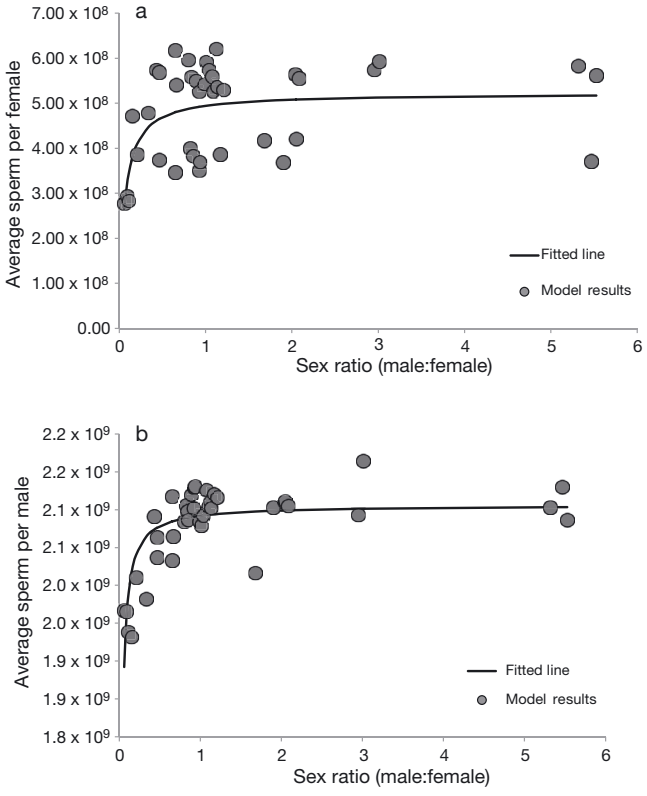

Fig. 6. Average number of sperm per blue crab (a) female and (b) male by male:female sex ratio with fitted non-linear regression line

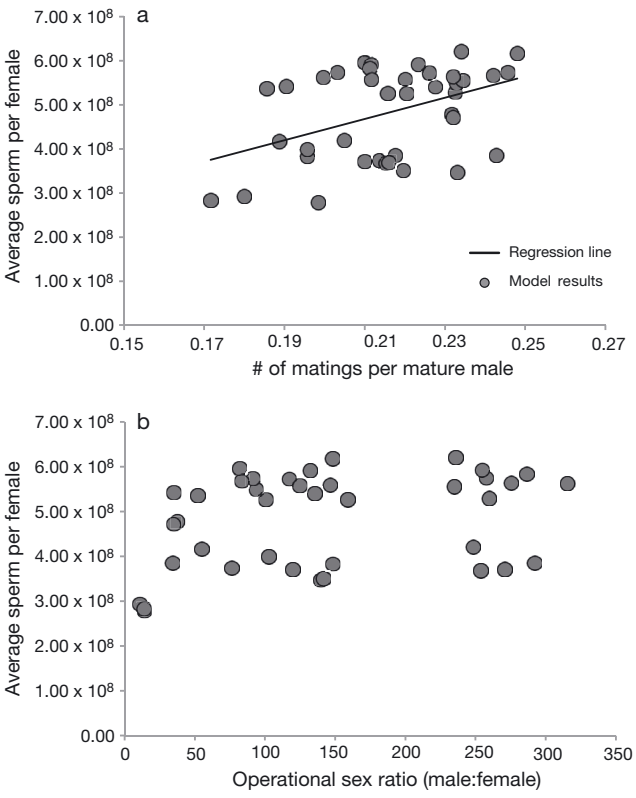

Fig. 7. Average number of sperm per blue crab female (a) by the fraction of mature males that mated ($F_{1,37}$ = 8.552; p = 0.006) and (b) by the operational male:female sex ratio

with the minimum being 3.2 in the halved population. The operational sex ratio did scale with population (doubled population range = 54–1727; halved population range = 3–106), but followed almost identical patterns among scenarios.

DISCUSSION

We draw 2 principal conclusions regarding the potential for fishery-induced sperm limitation in blue crab based on the results of our simulation modeling. First, our simulations indicated that extreme increases in fishing were necessary to substantially reduce the average number of sperm per female, a variable often used to indicate the presence of sperm limitation. Indeed, we observed reductions in the average sperm per female only for levels of exploitation considerably greater than those currently estimated in the blue crab fishery of Chesapeake Bay (i.e. when exploitation removed approximately 99% of all of the mature males and sperm limitation became induced through the inability of females to find mates, such as an Allee effect). We believe the reason for a lack of relationship between sex ratio and average sperm per female is that females mature throughout an extended portion of the year, rather than a scenario in which all females of a cohort mature over a few days or weeks. This extended period of maturation skews the operational sex ratio toward mature males, because males are able to mate multiple times per season whereas females only mate once per lifetime. This means that when a female is ready to mate, there is likely more than 1 male prepared to mate with her, regardless of what the population sex ratio is at that time. Other crustacean species have operational sex ratios skewed toward males (e.g. Rondeau & Sainte-Marie 2001) and according to our calculated operational sex ratios for each scenario, and recent field studies of Ogburn et al. (2014), blue crabs also follow this pattern.

Our finding that it was hard to generate fishery-induced sperm limitation in our blue crab population differs from conclusions of other studies (Kendall et al. 2001, Hines et al. 2003, Ogburn et al. 2014). There are 3 potential reasons for the difference from field studies: (1) we are using a different definition of sperm limitation than Ogburn et al. (2014)—they

defined sperm limitation as an individual-level process, whereas we defined it at the population level; (2) the results from the field studies may differ due to varying sperm loss in females based on time since mating (Ogburn et al. 2014, Rains et al. 2016), although Ogburn et al. (2014) attempted to correct for this by only using females they identified as having recently mated; and (3) the model's assumptions around molting, maturation, and mating may be incorrect despite our best efforts to represent hypotheses and patterns from the literature. Hines et al. (2003) compared sperm received per female among field-collected female blue crabs of the heavily fished Chesapeake Bay and the less fished Indian River Lagoon, Florida, USA. Hines et al. (2003) reported that females in Indian River Lagoon had a much higher average number of sperm per female than females in the Chesapeake Bay and concluded that females in Chesapeake Bay were likely sperm limited. However, the analyses by Hines et al. (2003) accounted for neither sperm loss nor differences in the mating seasons, which both vary between the 2 locations and may help explain the observed differences. Other studies compared numbers of sperm per female under laboratory conditions to those observed in wild crabs to assess sperm limitation. In laboratory studies, Kendall et al. (2002) found that males gave roughly 50% less sperm in subsequent matings when not given sufficient time to recover between them. Ogburn et al. (2014) compared the laboratory data of Kendall et al. (2002) on the number of sperm per female with observations from field-collected females of Rhode River, Maryland, USA. Ogburn et al. (2014) concluded that most females within the tributary were receiving amounts of sperm similar to those of laboratory females mated with depleted males (laboratory average: ca. 2.86×10^9; field average: ca. 2.02×10^9). However, the sperm numbers per female reported by Kendall et al. (2002) are substantially higher than other laboratory and field studies from the same region (Kendall et al. 2001, Carver et al. 2005, Wolcott et al. 2005) and suggest that females in the study by Ogburn et al. (2014) were, in fact, receiving comparable amounts of sperm to recovered males.

Our results also differed from those of the field study by Ogburn et al. (2014) in that we did not see a difference in the amount of sperm per female across months, with only the scenario with random mating preference and 5 times fishing pressure on males only (MO5) showing a significant difference in amount of sperm per female among months. This difference in results may be due to our model potentially missing an aspect of blue crab biology that may cause females to synchronously mature, such as the temperature data we used being abnormal and/or missing a cue seen in the peeler fishery in Chesapeake Bay, which targets maturing females, during periods of high activity (called the 'peeler run') during some springs. The temperature data we used were from the Patuxent River, which does not have a large peeler fishery. Indeed, there is a latitudinal pattern in peeler runs in the Chesapeake Bay, with stronger runs occurring at lower bay latitudes, suggesting that the results may have differed if we had based our model on temperature data from a lower tributary, such as the York River. However, Rains et al. (2016) did not find monthly differences in sperm per female in 6 tributaries of Chesapeake Bay, which spanned the latitudinal gradient of the bay. Alternatively, the monthly differences observed by Ogburn et al. (2014) may be due to factors other than the amount of sperm transferred by the male, such as a difference in average time since mating among months that would lead to more sperm loss in some months. Additionally, male blue crabs may have longer periods of inactivity during the molt cycle than we included in our model. We assumed that male blue crabs were able to mate any time they were not softshell (about 95% of the time). However, in other crustacean species, activity is decreased before and after molting, and all mating is done in molt stage C (Jivoff et al. 2007), which would be roughly 70% of their time. Therefore, our model may overestimate the number of males available for mating on any given day. However, as only the scenarios with extremely high fishing mortality showed any evidence of sperm limitation, we believe that a longer period in which males did not mate around molting would not substantially change our results. Furthermore, our model is somewhat conservative in our calculation of male maturation size, which may offset bias in the time males are available to mate.

Our modeled population did not have an incoming cohort of females for the second year, making it difficult to predict if the lack of relationship between sex ratio and average sperm per female is a property of the model. However, over 75% of females matured by the middle of the mating season in the second year, which is the time that an incoming cohort would have grown to sizes ready to mature. Because the incoming cohort of the second year only overlaps with a small portion of our maturing cohort, this should not have a substantial effect on fishery-induced sperm limitation because most of a cohort's females would have received sperm, making the

exclusion of the next cohort less important for fertilization purposes.

The goal of our analyses was to determine if fishing was likely to cause a reduction in sperm per female, which may indicate the potential for fishing-induced sperm limitation. Under unfished conditions, some female blue crabs may not receive enough sperm to fertilize their lifetime supply of eggs (Ogburn et al. 2014). However, if increased fishing pressure does not change the average number of sperm per female, then that type of sperm limitation is likely not important for fishery management. Thus, it is possible that some individuals' lifetime fitness is limited by the amount of sperm they receive. We think it is unlikely that blue crabs are naturally sperm limited in unfished conditions because they do not exhibit the physiological characteristics of a sperm-limited population. The sex with the limiting gamete will allocate more resources to its production than the sex with the non-limiting gamete (Levitan & Petersen 1995). In blue crab reproduction, females allocate disproportionately more of their internal cavity and energy resources to the storage of sperm and creation of eggs, which would theoretically have evolved because eggs are the limiting factor in reproduction (Jivoff et al. 2007).

Our model results corresponded well with field observations of blue crabs in Chesapeake Bay. The CW of simulated mature females followed a normal distribution similar to the mature females reported in the CBWDS, with our average crabs being slightly larger than ones from the CBWDS (model: 166 mm; CBWDS: 142 mm). We do not believe that this difference in female size would cause a bias in the sperm limitation results because the size of blue crabs is not correlated to the amount of sperm per male nor to the amount of sperm per female (Kendall et al. 2002, Rains et al. 2016). Crab survival also followed patterns expected by population dynamic equations based on the natural and fishing mortalities experienced in the scenario. In the current fishing mortality scenarios, all females found mates, which closely followed field observations where less than 2% of mature females are uninseminated at current fishing pressures (Kendall et al. 2002, Hines et al. 2003, Wolcott et al. 2005). Female blue crabs in the model matured between May and October, with a majority maturing in July and August. Maturation of females ceased in late November when modeled temperatures begin to drop, which agrees with the pattern observed in Chesapeake Bay (Jivoff et al. 2007). Average amount of sperm per male for all scenarios differed by less than 1% of the average counts from laboratory studies (Kendall et al. 2001, Carver et al. 2005). Average sperm per female in scenarios in which fishing exploitation rates were equivalent to current conditions in the Chesapeake Bay fishery (MF1), for both the random and history mate preference scenarios, were within 10% of observed average sperm per female from Hines et al. (2003; 5.0×10^8) and Wolcott et al. (2005; 5.9×10^8). Average sperm per female during the current fishing pressure scenarios (MF1) for the size assortative mate preference scenario was about 23 and 33% lower than the average sperm per female reported by Hines et al. (2003) and Wolcott et al. (2005), respectively. Male: female sex ratios were within the range of those observed in Chesapeake Bay during 2011 (Rains et al. 2016).

Our simulation model adequately represents the range of reproductive behaviors and dynamics observed in blue crabs. The different mating strategies used in our simulations were chosen to represent a range of potential mating systems that have been suggested for blue crabs. However, our mating strategies only considered female mate preference in our model and did not include male mate preference or a differential ability of males to secure mates throughout their lives. Our model also did not include the potential for multiple paternities that has been found in blue crabs (Wells et al. 2017). Our previous mating history scenario, however, represents the hypothesis that some males are better at securing mates over time windows of multiple weeks. The different mating systems impacted our results in our simulation study. Moreover, all fishing scenarios for which the average sperm per female was slightly above that found in unfished scenarios had regulations to limit harvest of males >127 mm CW. In contrast, scenarios that allowed harvest of all mature males (>107 mm), regardless of fishing pressure and mate preference scenario, exhibited a decrease in average sperm per female compared to the unfished scenario, albeit sometimes small. This seems to indicate that current regulations that include a 127 mm CW minimum size limit on hard-shell males are conservative because they provide males opportunities to mate before becoming susceptible to harvest. This provides maturing females a consistent supply of mates throughout the mating season and leads to females receiving sperm numbers larger than if they had mated with previously mated males. We also assumed that sperm limitation did not influence adult mortality and that females could not match their number of eggs with the amount of sperm they had stored. We think that both of these assumptions are

reasonable, but are unaware of specific studies that have tested these aspects of blue crab biology.

Furthermore, our model included a sperm threshold below which males ceased mating. Inspection of simulation results suggested that this is a biological control that stops sperm limitation from occurring in the population. We based our threshold on the level of sperm expected after 3 successive matings based on evidence from previous research (Kendall et al. 2001, 2002, Hines et al. 2003, Carver et al. 2005, Wolcott et al. 2005). This mechanism was a reason that our scenario with 5 times fishing pressure on males only (MO5), where over 99% of males above 127 mm died, only had decreases in average sperm per female of less than 25% of unfished conditions in all mating scenarios (random: 22%, size: <0.1%, history: 11%), whereas when the same scenario of 5 times fishing pressure on males only was applied to all mature males (AM5), average sperm per female was closer to 50% less than in unfished conditions (random: 52%; size: 28%; history: 46%).

We used a population size of 4500 crabs in our model, which was chosen based on average crab densities of the CBWDS in 2010. We assumed that crabs within a 6 ha area could reasonably interact with one another during a 1–3 d period. Although population size could affect our results if the area of interaction for blue crabs is substantially larger or smaller than what we included in the model, our sensitivity analysis of populations about 4 times or one-fourth the size of our baseline model shows that our results still apply if the area of interaction is larger or smaller. Indeed, if the area of interaction is larger than any of the ones we included, it is unlikely that we would see larger effects of sperm limitation because there would be more crabs as potential mates. Little is known about the physical and chemical cues associated with blue crab mating, and so the size of the area in which males will respond to pre-pubertal females is uncertain. However, female blue crabs are expected to release hormones for several days before their terminal molt, which we assumed would allow the entire population of males ample time to reach females before they molt (Shirley et al. 1990, Jivoff et al. 2007).

An increase in the frequency of mating by males has been the primary mechanism suggested for fishery-induced sperm limitation in blue crabs (Kendall et al. 2002, Hines et al. 2003, Ogburn et al. 2014). We did not see evidence of increased mating frequency of males with increased fishing mortality in our model. The average number of mates per male was usually <1, which was well below the model's threshold of 3 consecutive matings within a short period. Additionally, the model predicted a positive relationship between the average sperm per female and the average fraction of mature males that mated (Fig. 7), which is the opposite relationship of what other studies have suggested should happen if sperm limitation due to males mating more frequently were occurring (i.e. there would be a negative relationship between the fraction of mature males that mated and average sperm per female). The positive trend in sperm per female versus matings per mature male is because the lowest numbers of matings per mature male resulted from scenarios with very low male survival. Reductions in sperm per female in our study were due to a different type of sperm limitation, where females are not able to find mates, and was driven by almost complete removal of mature males from the population through fishing. The positive relationship between fraction of mature males that mated and average sperm per female provides evidence that sperm limitation should only happen when mates are unavailable. This was also true of our relationship between average sperm per female and mature male:female sex ratio, which showed that sex ratios must be below 0.06 (or 3 males for every 50 females) in order to reduce the sperm numbers females receive to half of the maximum sperm, or what Kendall et al. (2002) had predicted a male's second consecutive mate would receive (Fig. 6).

Our model suggests that it should be very difficult for fishery-induced sperm limitation to occur in blue crabs and that the sex ratio of the population, at any single point in time, is likely not a good indicator of fertilization success for the population. Our results suggest that female blue crabs in Chesapeake Bay are not currently receiving significantly less sperm than they would in an unfished scenario, which indicates that fishery-induced sperm limitation is likely not an issue at present. Additionally, regulations similar to Maryland, which protects males under 127 mm, likely have a beneficial effect of maintaining a portion of available small mature males for mating, although altering male size limits may affect female fishing mortality by causing changes in total effort. We conclude that current regulations of Chesapeake Bay appear to be effective at avoiding fishery-induced sperm limitation for this blue crab population.

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