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An Age-structured Population Model for Horseshoe Crabs in the Delaware Bay Area to Assess Harvest and Egg Availability for Shorebirds

JOHN A. SWEKA[1,*], DAVID R. SMITH[2], and MICHAEL J. MILLARD[1]

[1] *U.S. Fish and Wildlife Service, Northeast Fishery Center, P.O. Box 75, Lamar, Pennsylvania 16848*
[2] *U.S. Geological Survey, Leetown Science Center, 11649 Leetown Road, Kearneysville, West Virginia 25403*

ABSTRACT: The objective of this simulation study was to create an age-structured population model for horseshoe crabs (*Limulus polyphemus*) in the Delaware Bay region using best available estimates of age-specific mortality and recent harvest levels. Density dependence was incorporated using a spatial model relating egg mortality with abundance of spawning females. Combinations of annual female harvest (0, 50, 100, and 200 thousand), timing of female harvest (before or after spawning), and three levels of density-dependent egg mortality were simulated. The probability of the population increasing was high (> 80%) with low and medium egg mortality and harvest less than 200 thousand females per year. Under the high egg mortality case, the probability of the population increasing was < 50% regardless of harvest. Harvest occurring after spawning increased the probability of population growth. The number of eggs available to shorebirds was highest when egg mortality was lowest and female abundance was at its highest levels. Although harvest and egg mortality influenced population growth and food availability to shorebirds, sensitivity and elasticity analyses showed that early-life stage mortality, age 0 mortality in particular, was the most important parameter for population growth. Our modeling results indicate areas where further research is needed and suggest effective management will involve a combination of harvest management and actions to increase early juvenile survival.

Introduction

The end of the 20th century marked a period of intense controversy over the harvest of horseshoe crabs (*Limulus polyphemus*) due to the fact that horseshoe crab eggs are a critical component of the diet of migrating shorebirds (Botton et al. 1994; Tsipoura and Burger 1999; Odell et al. 2005) and the observation that some migratory shorebird populations are in decline (USFWS 2003; Baker et al. 2004). In response, the Atlantic States Marine Fisheries Commission (ASMFC) developed and has begun to implement an interstate fishery management plan for horseshoe crabs (ASMFC 1998). A component of the ASMFC plan development process was the compilation and analysis of available data on horseshoe crab abundance and life history, followed by an assessment of the overall status of their population (ASMFC 1999). This process indicated there were insufficient data available to perform a formal, quantitative stock assessment for horseshoe crabs, and steps were identified to make such an analysis possible. Since then, fishery managers, driven by the precautionary principle, have reduced landings of horseshoe crabs in Delaware Bay states by ≥ 70% from reference landings, and then a 2-yr moratorium on harvest of females with restricted harvest of males was implemented (ASMFC 2006).

The unique life history of horseshoe crabs provides a challenge to assessing their population status and estimating critical population parameters (Berkson and Shuster 1999). This is particularly true since traditional finfish sampling protocols do not produce adequate or appropriate data for evaluating horseshoe crab status and trends (ASMFC 1999). Mortality during the egg stage is undoubtedly significant; indeed the large-scale predation on dislocated horseshoe crab eggs is believed to be the critical component in satisfying the energetic demands of shorebird migration (Castro and Meyers 1993; Tsipoura and Burger 1999; Robinson et al. 2003). Red knots (*Calidris canutus rufa*) have been estimated to require 1.54×10^{10} eggs, equal to the total egg output of approximately 170,000 spawning females (USFWS 2003). Age 0 larvae undergo several instar stages punctuated by molting events, and survival from the egg stage through this first year has been estimated to be as low as 0.001% (Carmichael et al. 2003). These early life stages reside in intertidal and nearshore habitats (Rudloe 1981; Botton and Loveland 2003; Carmichael et al. 2003) and as such are difficult to sample effectively. Horseshoe crabs require 9 or 10 yr to

* Corresponding author; tele: 570/726-4995 ext. 3; fax: 570/726-3255; e-mail: John_Sweka@fws.gov

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reach maturity (Shuster 1950), and most adults inhabit subtidal or continental shelf waters, except during spawning (Shuster 1982; Botton and Ropes 1987). Smith et al. (2006) raise the possibility that some portion of the adults do not migrate to the ocean after spawning and remain in Delaware Bay between spawning periods. Our understanding of adult movements and abundances in the Delaware Bay region has advanced, but recruitment and mortality rates remain unknown (ASMFC 1999; Hata and Berkson 2003; Brousseau et al. 2004; Smith et al. 2006).

The catch-survey method (Collie and Sissenwine 1983; Helser and Kahn 1999) was proposed as the framework to quantitatively assess horseshoe crab populations along the Atlantic coast (ASMFC 2000). Between 5 and 10 yr of fishery independent and fishery dependent data are needed to implement this technique. While much of this data collection is underway, a formal analysis is years off and fishery managers would benefit from well-reasoned and quantitative analyses of horseshoe crab populations dynamics in the meantime. Simulation modeling that stochastically integrates available data and reasonable assumptions can provide some general insight into the parameters that drive the dynamics of horseshoe crab populations (Starfield 1997). This information can be useful in guiding the decisions facing fishery managers. Postulating at least some quantitative structure to available data and making this available to decision makers is generally preferable to ad hoc management policies (Hilborn and Walters 1992).

Davis et al. (2006) recently used an age-aggregated production model with juvenile (ages 0 to 9 or 10) and adult (ages 10+) indices (ASMFC 2004) to assess the Delaware Bay horseshoe crab population. Their results showed a depleted population that had the potential to recover to maximum sustainable yield (MSY) biomass in as few as 2 yr, which seems implausible given the horseshoe crab's long time to maturity (9–10 yr). We feel an age-structured model that explicitly accounts for horseshoe crab's life history would provide an appropriate alternative for making population projections and would allow comparisons to previous and ongoing modeling efforts.

The objective of our simulation study was to develop an age-structured population model for horseshoe crabs in the Delaware Bay region to evaluate effects of natural mortality and harvest on population growth, population age structure, and food availability to shorebirds. While accurate estimation of the vital population parameters will not result from this exercise, sensitivity and elasticity analyses assessing the relative influence of various parameters, within various life stages, may provide useful information for fishery managers. We believe this represents an improvement over the recent methodology that relied on past trends and did not incorporate cues from stock processes and rates.

TABLE 1. Life history parameters used in the age structured horseshoe crab population model.

Age	S	M	Reference
Age 0 – 1	0.00003	10.4143	Botton et al. 2003
Ages 1 – 8	0.9738	0.0265	Carmichael et al. 2003 (Table 13)
Age 9 – 10	0.7994	0.2239	Mean of 1–8 and 11–17 - assumption
Age 10 – 11	0.7994	0.2239	Mean of 1–8 and 11–17 - assumption
Ages 11 – 17	0.6250	0.4700	Carmichael et al. 2003 (Table 10, mean of instars 20–23)
Ages 18 – 19	0.08	2.5257	Carmichael et al. 2003 (Table 10, instar 24)
Age 20	0		All dead – assumption

Materials and Methods

The entire life cycle of the horseshoe crab was modeled, from egg through age 20. We assumed that age 20 was the maximum age of a horseshoe crab and that all age 20 individuals died following spawning. The model was developed in a Microsoft Excel spreadsheet with the add-in @Risk, which allows modeling of uncertainty and conducts sensitivity analyses.

Values for age-specific mortality rates (M_i) were taken from existing literature (Botton et al. 2003; Carmichael et al. 2003; see Table 1). The survival of each age i in year t was

$$S_{i,t} = e^{-M_{i,t}} \tag{1}$$

where $M_{i,t}$ = the instantaneous rate of natural mortality at age i in year t.

Harvest was modeled as a quota, i.e., a constant number of female crabs taken each year. Four harvest quotas were modeled: 0, 50, 100, and 200 thousand female crabs per year. These levels covered recent harvests of females in Delaware and New Jersey (Table 2). We assumed that only sexually mature animals were harvested and simulated two scenarios for time of harvest: before spawning and after spawning. In the model, harvest was proportional to abundance of a given age class that had recruited to the spawning stock. The number of females in the subsequent year was

$$N_{i,t+1} = (N_{i,t} - H_{i,t})S_{i,t} \tag{2}$$

where $N_{i,t}$ = then number of females at age i in year t, and $H_{i,t}$ = the number of females at age i harvested in year t. The age-specific harvest was

TABLE 2. Harvest of female horseshoe crabs in Delaware and New Jersey from 1998 to 2004 (ASMFC 2004). Data for 2004 are from Michels (personal communication).

Year	Female harvest (thousands)
1998	327
1999	290
2000	187
2001	203
2002	196
2003	152
2004	56*

calculated as

$$H_{i,t} = Qp_{i,t} \tag{3}$$

where Q = the harvest quota of females, and $p_{i,t}$ = the proportion of sexually mature females of age i in year t. The partial recruitment schedule (i.e., $p_{i,t}$) was calculated as

$$p_{i,t} = N^*_{i,t} \Big/ \sum_{i=1} N^*_{i,t} \tag{4}$$

where $N^*_{i,t}$ = the number of sexually mature females of age i in year t. Not all females of a given age were sexually mature ($N^*_{i,t} \leq N_{i,t}$)

$$N^*_{i,t} = N_{i,t} R_i \tag{5}$$

where R_i = partial recruitment to the spawning stock of age i. For ages ≤ 8, R_i was set to 0; for ages 9 and 10, R_i equaled 0.5; and for ages ≥ 11, R_i was equal to 1.0.

In simulations where harvest occurred after spawning, the number of females in a given year available for spawning was

$$N^*_{.,t} = \left(\sum_{i=1} N^*_{i,t} \right) \tag{6}$$

For simulations in which harvest occurred prior to spawning, the harvest quota of females, Q, was subtracted from $N^*_{.,t}$. Total egg production was equal to the number of sexually mature females multiplied by fecundity. Shuster and Botton (1985) found the average number of eggs laid per cluster (± 1 standard deviation) was 3,650 ± 232 and that a female may lay about 22 clusters per spawning season. We assumed that total fecundity equaled 80,300 ± 5,115 eggs.

Density-dependent egg mortality curves (Fig. 1) were developed using a model that simulated horseshoe crab spawning (Smith 2007). In the model, egg mortality was derived from two density-dependent sources: nest disturbance from bioturbation (i.e., nest disturbed by other spawning females) and poor egg development due to low oxygen conditions when females nest in water-saturated zones of the lower foreshore (Penn and Brockmann 1994). Spawning was simulated on 10 m of shoreline near the high tide line with density rising and falling with the four spring tides in May and June. Spawning zones moved up and down the beach foreshore as the high tide line shifted diurnally and daily over spring tide cycles. Nests were disturbed when spawning occupied the same location as previously laid nests. As density of spawning females increased, nest disturbance increased and spawning moved lower on the beach as spawning zone widened. Eggs laid in the lower 15% of the beach width did not develop in that low oxygen zone. Among the eggs in the upper 85% of the beach, a proportion of eggs in disturbed nests died. Use of three assumed rates of mortality given disturbance (50%, 65%, and 80%) combined with eggs laid in the lower 15% of the beach resulted in the three density-dependent mortality curves (Fig. 1). Density of spawning females was converted to abundance by assuming a total of 141 km of sandy beach in Delaware Bay based on interpretation of aerial photographs (Young unpublished data). Survival from egg to hatch was expressed as

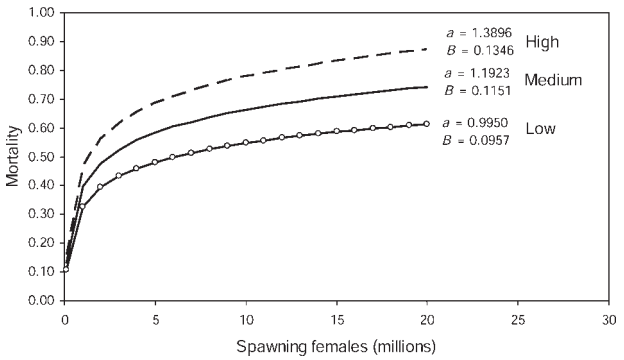

Fig. 1. Egg mortality as a function of spawning female abundance and nest disturbance in the Delaware Bay region. The curves were based on a simulation model of horseshoe crab spawning (Smith 2007).

$$S_{e,t} = 1 - \left[B \ln\left(N^*_{.,t}\right) - a \right] \tag{7}$$

where a and B are regression parameters for the mortality curves in Fig. 1. Hereafter, we will refer to the three curves of density-dependent egg mortality as low, medium, and high. These curves represent total egg mortality over the entire spawning season. Because we only modeled females, the resulting number of eggs that survived to hatch was divided by 2 to yield the number of age 0 females in year t ($N_{0,t}$), assuming an equal hatching ratio.

Population dynamics were simulated beginning with a 20-yr period of constant harvest (300,000 females per year) followed by a 30-yr period of

reduced harvest. During the initial high harvest period (year -19 through year 0), all harvest occurred before spawning. Beginning in year 1, simulations were adjusted to reflect current management options including reduction in harvest and harvest occurring after spawning. Harvest strategies remained constant, and populations were projected from year 1 through year 30. Using age-specific survival parameters (Table 1), we estimated the abundance of all age classes in year 1. The initial population of mature females in year -19 was adjusted for each level of egg mortality so that the population of mature females in year 1 equaled 3 million, which was near the lower 90% confidence limit for the estimated female population in 2003 from Smith et al. (2006) and within the upper confidence interval for the estimate from Hata and Berkson (2003). Twenty-four cases of simulations were replicated with 10,000 iterations each. These cases were combinations of harvest quotas on spawning females (0, 50, 100, and 200 thousand per year), the three egg mortality curves as a function of spawning female abundance (Fig. 1), and harvest timing (before or after spawning). During each simulation, age-specific survival was allowed to vary randomly each year according to beta distributions with expected values equal to those in Table 1. We assumed that variability in age-specific survival decreased with increasing age, and we used coefficients of variation of 30% for age 0, 15% for ages 1–8, and 7% for ages 9–20. Also during each simulation, fecundity was allowed to vary according to a normal distribution with a mean of 80,300 and standard deviation of 5,115 eggs.

The total number of spawning females each year was the response variable monitored through time. We calculated the intrinsic rate of population increase for each year as:

$$r = \ln\left(N^*_{.,t}/N^*_{.,t-1}\right) \tag{8}$$

and estimated the probability of $r > 0$ (indicating an increasing population) for all cases.

We also conducted a population projection with a deterministic model (no variability in mortality parameters) to ensure that the inherent model structure and density dependence would not allow the population to grow to infinity. Harvest after year 0 was set to 0 and the population was projected to year 200 for each level of egg mortality.

Life history parameters were used to construct a population projection matrix (Caswell 2001). We used this matrix to estimate sensitivity and elasticity values of age-specific survival and fecundity using the Microsoft Excel add-in PopTools. Sensitivity values indicate the slope of λ (finite rate of population increase = $N^*_{.,t}/N^*_{.,t-1}$) as a function of a given life history parameter; the greater the sensitivity value, the greater effect an absolute change in the life history parameter will have on λ. Elasticity values for all life history parameters sum to 1.0 and they indicate the proportional contribution of each life history parameter to λ. Sensitivity and elasticity analyses were conducted for each level of egg mortality assuming a population size of 3 million spawning females.

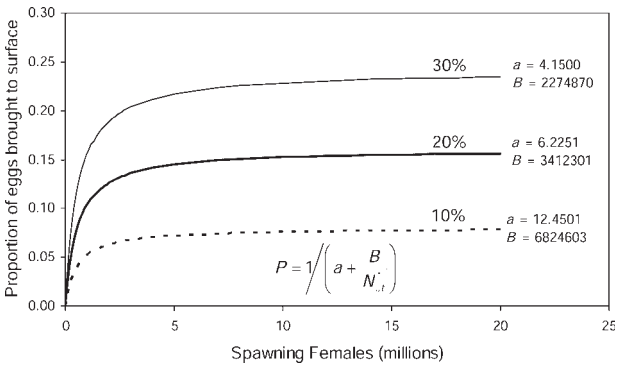

Fig. 2. Proportion of total eggs brought to the surface as a function of spawning female abundance. Percentages correspond to 10%, 20%, and 30% of eggs brought to the surface given disturbance by subsequent spawning females.

We also conducted additional simulations to estimate the number of eggs that may be available as food for shorebirds by employing the nest disturbance models described above (Smith 2007) to estimate the proportion of eggs brought to surface sediments. Smith (2007) suggested that the percentage of disturbed eggs that are brought to the surface is 10% or greater. We assumed that 10%, 20%, and 30% of disturbed eggs were brought to surface sediments and available to shorebirds. A Beverton-Holt type function (Beverton and Holt 1957) was fit to the simulated data to estimate the proportion of total eggs brought to the surface as a function of spawning female abundance (Fig. 2). Shorebirds are generally present on Delaware Bay beaches during the first two-thirds of the horseshoe crab spawning period. To account for this temporal factor, we derived the number of eggs available to shorebirds during each year as

$$E^*_t = N^*_{.,t} f 0.7 \left[1 \Big/ \left(a + \frac{B}{N^*_{.,t}} \right) \right] \tag{9}$$

where f is the average fecundity of females, 0.7 was a constant used to correct for differences in timing between shorebird and horseshoe crab migrations, and a and B are parameters from the nest disturbance models in Fig. 2. Based on the Delaware Bay spawning survey, approximately 70% of spawning occurs during the first two spring tides of May

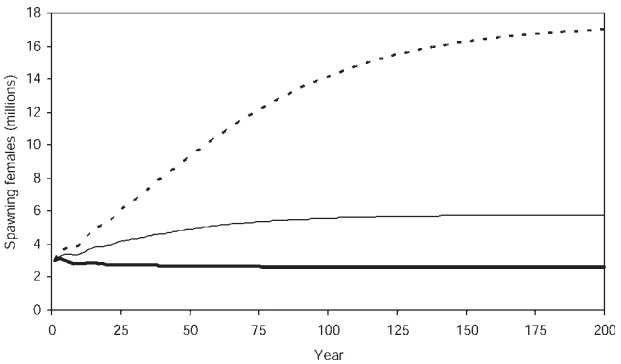

Fig. 3. Spawning female abundance projected for 200 yr from the deterministic model in the absence of harvest for each level of egg mortality given in Fig. 1.

and June, which coincides with the shorebird stopover in Delaware Bay (Smith and Michels 2006). Simulations were conducted for each level of eggs brought to the surface in conjunction with all levels of egg mortality, harvest, and timing of harvest.

Results

The deterministic model showed that in the absence of harvest, the density-dependent egg mortality functions would prevent the population from growing to infinity (Fig. 3). The spawning female population asymptotes at 17.0×10^6, 5.8×10^6, and 2.6×10^6 for low, medium, and high egg mortality curves, respectively.

The mean projected population increased from the initial number of spawning females in year 1 ($N^*_{\cdot,t}$ = 3,000,000) by year 15 in nearly all cases of low and medium egg mortality (Table 3). Under high egg mortality the mean projected population decreased by year 15 regardless of harvest timing and harvest level. By year 30, the mean projected population of female spawners exceeded the initial population in nearly all scenarios of low and medium egg mortality. The exception was when harvest occurred before spawning with a harvest level of 200,000 females per year and medium egg mortality. Under the high egg mortality case, the mean projected population of spawning females decreased from year 1 to year 30 regardless of harvest level. Overall, abundance was consistently higher when harvest occurred after spawning compared to before spawning, but these differences were slight and 90th percentile ranges overlapped (Table 3).

The probability of population increase [$P(r > 0)$] was dependent upon egg mortality (Fig. 4). Under low egg mortality, this probability was > 90% for all levels of female harvest. With medium egg mortality, this probability was < 80% when annual female harvest was 200,000. The probability of population increase under the high egg mortality case was < 50% even in the absence of any female harvest and

TABLE 3. Mean projected spawning female abundance (millions) in years 15 and 30 under various combinations of egg mortality, female harvest, and timing of harvest. The model started with 3.00 million mature females in year 1.

			Year 15			Year 30		
Harvest Timing	Egg Mortality	Harvest	Mean	5th percentile	95th percentile	Mean	5th percentile	95th percentile
After Spawning	Low	0	4.80	2.86	7.16	6.58	3.90	9.83
		50,000	4.64	2.73	6.91	6.26	3.64	9.47
		100,000	4.46	2.58	6.72	5.96	3.44	9.12
		200,000	4.20	2.30	6.46	5.43	2.93	8.59
	Medium	0	3.76	2.33	5.45	4.24	2.64	6.11
		50,000	3.61	2.20	5.22	4.01	2.42	5.87
		100,000	3.47	2.07	5.07	3.81	2.26	5.63
		200,000	3.19	1.82	4.81	3.35	1.84	5.14
	High	0	2.84	1.85	3.95	2.69	1.74	3.79
		50,000	2.72	1.73	3.82	2.52	1.58	3.58
		100,000	2.60	1.62	3.72	2.33	1.41	3.38
		200,000	2.35	1.39	3.45	1.97	1.09	2.99
Before Spawning	Low	0	4.79	2.86	7.15	6.55	3.93	9.79
		50,000	4.54	2.65	6.83	6.12	3.54	9.33
		100,000	4.27	2.40	6.52	5.66	3.11	8.79
		200,000	3.79	1.94	5.98	4.77	2.35	7.78
	Medium	0	3.76	2.34	5.43	4.24	2.64	6.16
		50,000	3.53	2.12	5.14	3.89	2.33	5.76
		100,000	3.30	1.92	4.90	3.54	2.01	5.34
		200,000	2.84	1.51	4.41	2.81	1.35	4.56
	High	0	2.85	1.84	3.99	2.69	1.75	3.78
		50,000	2.63	1.66	3.76	2.41	1.49	3.44
		100,000	2.44	1.47	3.55	2.12	1.25	3.15
		200,000	2.04	1.11	3.10	1.50	0.65	2.49

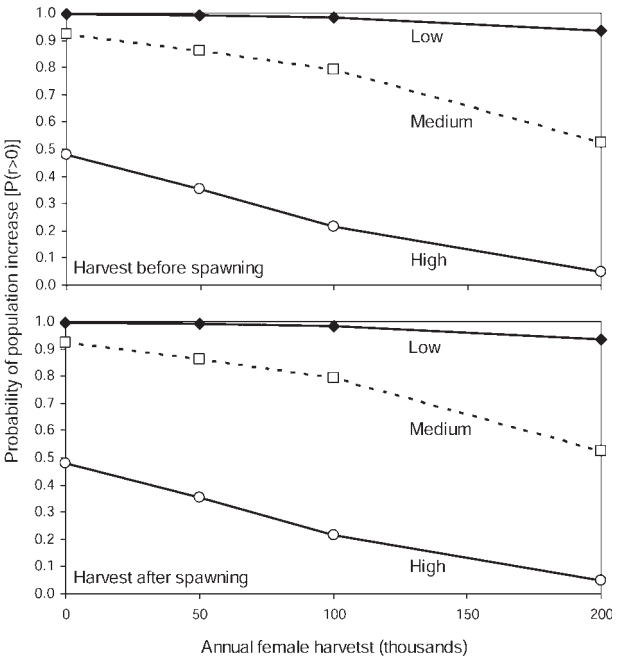

Fig. 4. Effect of harvest on the probability of the intrinsic rate of population increase being greater than 0, P ($r \geq 0$), for various levels of egg mortality and timing of harvest.

decreased steadily as harvest increased. Overall, the probability of population growth tended to be somewhat higher when harvest occurred after spawning compared to when it occurred before spawning.

Although the population projections showed that high harvest levels could have the potential to cause a population decline, especially under the high egg mortality case (Table 3), the sensitivity and elasticity analyses indicated that other life history parameters have a much greater influence on population growth (Table 4). The sensitivity values for survival decreased with age, and sensitivity values for age 0 survival were orders of magnitude greater than those of any other life history parameter. Under the case of low egg mortality, if age 0 survival were increased by a very small amount, say 1×10^{-6}, we would expect an increase in λ of approximately $(2.79 \times 10^{3})(1 \times 10^{-6}) = 2.8 \times 10^{-3}$. In comparison, the same change in age 13 survival would only result in a change in λ of approximately $(1.77 \times 10^{-2})(1 \times 10^{-6}) = 1.77 \times 10^{-8}$. Sensitivity values for fecundity were highest for ages 9 and 10 and decreased in older ages. Elasticity values for survival were equivalent for pre-reproductive age classes (ages 1–8), and quickly decreased in older ages. Increasing age 0 survival by 1% would increase λ by 0.0813%. Our elasticity values for pre-reproductive ages (ages 0–8) were equal, and then sharply decreased with increasing ages. Elasticity values for fecundity increased from age 9 to 10, as new females recruit to the spawning population, and then decreased in older ages. Changing levels of egg mortality had minor influence on sensitivity and elasticity values, and overall patterns of sensitivity and elasticity remained the same across egg mortality levels (Table 4).

Harvest affected simulated horseshoe crab age structure slightly (Fig. 5). Increasing harvest from 0 to 200,000 females per year increased the proportion of the spawning population in younger age classes and decreased the proportion in older age classes by < 3 percentage points. The most extreme differences occurred under the high egg mortality scenario, but the difference between no harvest and harvest of 200,000 for ages 16–20 was only 1.9% (Fig. 5). Differences were less with lower egg mortalities.

The simulated number of eggs available to shorebirds varied across the simulation cases. As harvest and total egg mortality increased, the number of spawning females declined and the number of eggs available to shorebirds declined (Fig. 6). The simulated data shown in Fig. 6 illustrates the most optimistic cases in terms of eggs available to shorebirds when the proportion of eggs brought to the surface was highest.

Discussion

Debate on the management of the horseshoe crab fishery has centered on harvest levels that will allow stock rebuilding to the level required to support shorebird populations. There is concern that shorebird populations will significantly decline in the absence of restrictive harvest regulations (Berkson and Shuster 1999; USFWS 2003; Baker et al. 2004). The Interstate Fishery Management Plan for Horseshoe Crab (ASMFC 1998) and subsequent amendments to the plan have reduced harvest of horseshoe crabs since the late 1990s. Our modeling encompassed the historic harvest levels of females and explored the effects of a moratorium on the fishery. The results indicated a high probability (> 80%) of population increase under the low to medium egg mortality cases when annual female harvest is < 200,000 per year. Delaying harvest until after the spawning season increased the probability of population growth. These simulations illustrated that juvenile age-specific mortality could have large effects on the population of spawning females even in the absence of harvest (Table 3).

Population growth combined with exhumation rates of horseshoe crab eggs could have important implications for food availability to migrating shorebirds in Delaware Bay. The USFWS Shorebird Technical Committee (USFWS 2003) modified an earlier model by Castro and Meyers (1993) to derive

TABLE 4. Results of the sensitivity and elasticity analyses under the three levels of egg mortality. S and F denote age-specific survival and fecundity, respectively. Sensitivity values represent the slope of λ as a function of the life history parameter while elasticity values represent the proportional contribution of the life history parameter to λ.

	Low egg mortality		Medium egg mortality		High egg mortality	
	$\lambda = 1.0287$		$\lambda = 1.0141$		$\lambda = 0.9963$	
Parameter	Sensitivity	Elasticity	Sensitivity	Elasticity	Sensitivity	Elasticity
S_0	2.79×10^{3}	8.13×10^{-2}	2.73×10^{3}	8.09×10^{-2}	2.67×10^{3}	8.04×10^{-2}
S_1	8.58×10^{-2}	8.13×10^{-2}	8.42×10^{-2}	8.09×10^{-2}	8.23×10^{-2}	8.04×10^{-2}
S_2	8.58×10^{-2}	8.13×10^{-2}	8.42×10^{-2}	8.09×10^{-2}	8.23×10^{-2}	8.04×10^{-2}
S_3	8.58×10^{-2}	8.13×10^{-2}	8.42×10^{-2}	8.09×10^{-2}	8.23×10^{-2}	8.04×10^{-2}
S_4	8.58×10^{-2}	8.13×10^{-2}	8.42×10^{-2}	8.09×10^{-2}	8.23×10^{-2}	8.04×10^{-2}
S_5	8.58×10^{-2}	8.13×10^{-2}	8.42×10^{-2}	8.09×10^{-2}	8.23×10^{-2}	8.04×10^{-2}
S_6	8.58×10^{-2}	8.13×10^{-2}	8.42×10^{-2}	8.09×10^{-2}	8.23×10^{-2}	8.04×10^{-2}
S_7	8.58×10^{-2}	8.13×10^{-2}	8.42×10^{-2}	8.09×10^{-2}	8.23×10^{-2}	8.04×10^{-2}
S_8	8.58×10^{-2}	8.13×10^{-2}	8.42×10^{-2}	8.09×10^{-2}	8.23×10^{-2}	8.04×10^{-2}
S_9	8.28×10^{-2}	6.43×10^{-2}	8.19×10^{-2}	6.46×10^{-2}	8.09×10^{-2}	6.49×10^{-2}
S_{10}	6.59×10^{-2}	5.12×10^{-2}	6.56×10^{-2}	5.17×10^{-2}	6.54×10^{-2}	5.24×10^{-2}
S_{11}	5.06×10^{-2}	3.07×10^{-2}	5.11×10^{-2}	3.15×10^{-2}	5.17×10^{-2}	3.24×10^{-2}
S_{12}	3.01×10^{-2}	1.83×10^{-2}	3.08×10^{-2}	1.90×10^{-2}	3.17×10^{-2}	1.99×10^{-2}
S_{13}	1.77×10^{-2}	1.08×10^{-2}	1.84×10^{-2}	1.13×10^{-2}	1.92×10^{-2}	1.20×10^{-2}
S_{14}	1.02×10^{-2}	6.18×10^{-3}	1.07×10^{-2}	6.58×10^{-3}	1.13×10^{-2}	7.09×10^{-3}
S_{15}	5.59×10^{-3}	3.40×10^{-3}	5.93×10^{-3}	3.65×10^{-3}	6.36×10^{-3}	3.99×10^{-3}
S_{16}	2.81×10^{-3}	1.17×10^{-3}	3.01×10^{-3}	1.85×10^{-3}	3.27×10^{-3}	2.05×10^{-3}
S_{17}	1.11×10^{-3}	6.77×10^{-4}	1.20×10^{-3}	7.42×10^{-4}	1.32×10^{-3}	8.31×10^{-4}
S_{18}	6.73×10^{-4}	5.23×10^{-5}	7.38×10^{-4}	5.82×10^{-5}	8.26×10^{-4}	6.63×10^{-5}
S_{19}	4.86×10^{-5}	3.78×10^{-6}	5.40×10^{-5}	4.26×10^{-6}	6.14×10^{-5}	4.93×10^{-6}
S_{20}	0	0	0	0	0	0
F_9	1.53×10^{-6}	1.69×10^{-2}	1.73×10^{-6}	1.63×10^{-2}	2.02×10^{-6}	1.55×10^{-2}
F_{10}	1.19×10^{-6}	2.04×10^{-2}	1.36×10^{-6}	2.03×10^{-2}	1.62×10^{-6}	2.00×10^{-2}
F_{11}	9.23×10^{-7}	1.24×10^{-2}	1.08×10^{-6}	1.25×10^{-2}	1.30×10^{-6}	1.25×10^{-2}
F_{12}	5.61×10^{-7}	1.24×10^{-2}	6.63×10^{-7}	1.25×10^{-2}	8.15×10^{-7}	1.25×10^{-2}
F_{13}	3.41×10^{-7}	7.55×10^{-3}	4.09×10^{-7v}	7.69×10^{-3}	5.11×10^{-7}	7.87×10^{-3}
F_{14}	2.07×10^{-7}	4.58×10^{-3}	2.52×10^{-7}	4.74×10^{-3}	3.21×10^{-7}	4.94×10^{-3}
F_{15}	1.26×10^{-7}	2.79×10^{-3}	1.55×10^{-7}	2.92×10^{-3}	2.01×10^{-7}	3.10×10^{-3}
F_{16}	7.64×10^{-8}	1.69×10^{-3}	9.56×10^{-8}	1.80×10^{-3}	1.26×10^{-7}	1.94×10^{-3}
F_{17}	4.64×10^{-8}	1.03×10^{-3}	5.89×10^{-8}	1.11×10^{-3}	7.91×10^{-8}	1.22×10^{-3}
F_{18}	2.82×10^{-8}	6.25×10^{-4}	3.63×10^{-8}	6.84×10^{-4}	4.96×10^{-8}	7.64×10^{-4}
F_{19}	2.19×10^{-9}	4.86×10^{-5}	2.87×10^{-9}	5.40×10^{-5}	3.99×10^{-9}	6.14×10^{-5}
F_{20}	1.70×10^{-10}	3.78×10^{-6}	2.26×10^{-10}	4.26×10^{-6}	3.20×10^{-10}	4.93×10^{-6}

an estimate of 107 billion horseshoe crab eggs required to support a population of 423,000 migrating shorebirds in the Delaware Bay region. Under our modeling assumptions, the mean number of eggs available to shorebirds only reached this

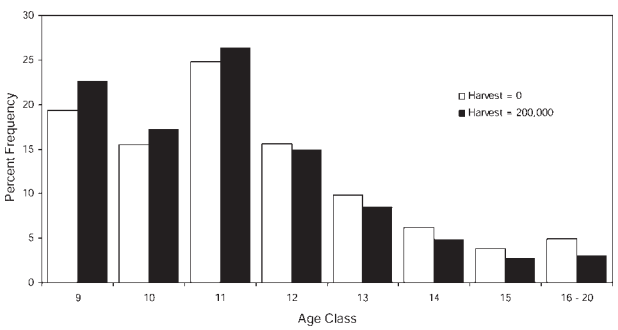

Fig. 5. Effect of harvest on the age structure of the simulated spawning female horseshoe crab population. This figure depicts the results for the highest level of egg mortality and harvest occurring prior to spawning.

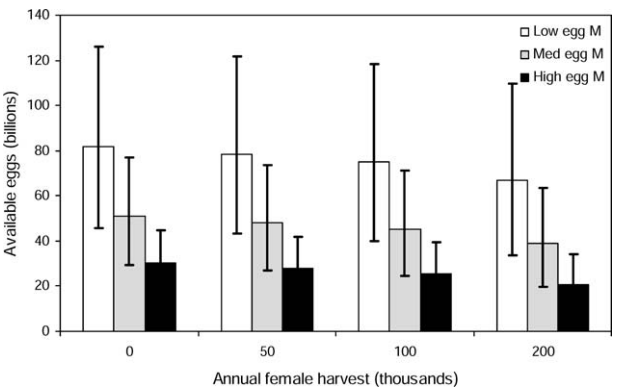

Fig. 6. Simulated mean number of eggs available to shorebirds by year 30 under the case of harvest occurring after spawning and 30% of the eggs being brought to the surface given nest disturbance by subsequent spawning females. The data shown in this figure represent the most liberal case for egg availability under each level of egg mortality and harvest. Other simulation combinations showed similar patterns with respect to the effect of harvest, but with lower numbers of available eggs. Error bars correspond to 90th percentile ranges.

level when using our lowest level of egg mortality and highest rate of egg exhumation given nest disturbance (Fig. 6). If egg mortality was higher, egg exhumation lower, or abundance of spawning females lower, then it appears unlikely that this number of eggs would be available regardless of horseshoe crab harvest levels. Of course, not all of the exhumed eggs (Fig. 6) would be available to shorebirds because shorebirds do not utilize all horseshoe crab spawning habitat and exhumed eggs are removed from the beach by wave action or consumed by other egg predators.

The USFWS (2003) report did not provide any measure of uncertainty in their estimate and our model is based on limited data. Our modeling is the first attempt to link the population dynamics of horseshoe crab with the availability of eggs for shorebirds. Managers should view the difference between this estimate of shorebird food requirements and our simulated egg availability with caution when making management decisions. Until more refined bioenergetic models for shorebirds are developed and more quantitative research on the availability of horseshoe crab eggs to shorebirds is conducted, managers are justified in being risk-averse to ensure rebuilding of horseshoe crab populations and food resources for migrating shorebirds.

Although harvest levels and timing influenced rates of population growth and potential food availability to shorebirds, sensitivity and elasticity analyses indicated that early life stage survival was most important to population growth. Sensitivity values for age 0 survival were much larger than those for any other age-specific survival indicating that slight changes in age 0 survival will have a greater effect on population growth than changes in any other life history parameter, including removals by harvest. The pattern of decreasing sensitivities with increasing age classes is a general property of age-structured population models (Caswell 2001). The decrease of over four orders of magnitude from age 0 survival to age 1 survival illustrates the importance of age 0 survival in the population dynamics of horseshoe crabs.

Harvest would influence subadult and adult survival, but perturbations at adult stages are minor in comparison to perturbations at the early juvenile stages. Botton et al. (2003) estimated that only 3 trilobites per 100,000 survived to 4th instars. If under the case of high egg mortality age 0 survival increased to 5 trilobites per 100,000, the population of spawning females by year 30 in our model could increase from an average of 1.5 to 6.6 million, and the number of eggs available to shorebirds could increase from an average of 15 to 82 billion (assuming 30% of disturbed eggs reach the surface). This is even at the highest simulated levels of harvest (200 thousand females annually) occurring before the spawning period. The causes of larval mortality in Delaware Bay have not been quantified, but could involve factors such as adverse environmental conditions and predation by shorebirds and small fishes. There also is insufficient data to determine if larval survival is density dependent (Botton et al. 2003). It seems likely that density-independent factors such as the severity of spring storms play a critical role in annual variability in survival of early life stages.

We acknowledge uncertainty in our modeling with respect to the parameters used and the variability around these parameters. We used subadult and adult survival parameters from Pleasant Bay, Massachusetts (Carmichael et al. 2003), instead of those specific to Delaware Bay. Environmental differences between Delaware Bay and Pleasant Bay would likely produce different life history parameters, but until such data become available for the Delaware Bay population, the Pleasant Bay data provide the best available estimates. While Botton et al. (2003) and Carmichael et al. (2003) provided estimates of survival, these studies were temporally limited and did not provided any estimates of interannual variability in survival. As such, we made assumptions about what this variability may be. Also, horseshoe crab fecundity recently has been shown to be size specific (Leschen et al. 2006). Leschen et al. (2006) modeled the size-specific fecundity of horseshoe crabs from Pleasant Bay, Massachusetts. In Delaware Bay, the median prosomal width of adult females was 265 mm (25th and 75th percentiles were 255 and 280 mm, respectively) based on 9,756 adult females captured during 2003 to 2005 for a tagging study (Smith et al. 2006). The median size from Delaware Bay was found on the upper end of the size-fecundity relationship described in Leschen et al. (2006: page 59, Fig. 3). Leschen et al. (2006) predicted that realized fecundity for a female with prosomal width of approximately 265 mm was lower than the 80,000 eggs per female that we used in this study, perhaps closer to 60,000 eggs per female (cf., Leschen et al. 2006: page 59, Fig. 4).

The largest uncertainty in our modeling was density-dependent egg mortality. If egg mortality is actually near the highest level that we modeled, then the probability of population growth is only approximately 50% even in the absence of any harvest. If egg mortality is actually closer to our simulated low level, then the probability of population growth is high even with harvest levels exceeding 100,000 females per year. The ranges of egg mortality we used appear reasonable, as Botton et al. (2003) estimated survival from live egg to

hatch at 50% and our scenarios encompassed this estimate. The egg mortality curves (Fig. 1) represent total egg mortality over the entire spawning season, which was a simplification in our modeling. In reality, egg mortality likely changes throughout the spawning season as the cumulative number of spawning females on the beaches increases.

We believe our model projections and results of the sensitivity and elasticity analyses are useful for indicating where research and monitoring of horseshoe crabs in the Delaware Bay regions should focus. Estimates of subadult and adult mortality specific to the Delaware Bay population, and estimates of the interannual variation of mortality for all life stages are needed. The relationship between female size and fecundity for Delaware Bay horseshoe crabs needs to be quantified. Future research should further quantify the relationships between spawning female density, nest disturbance, egg exhumation, and egg mortality. These data will add realism and specificity to modeling the population dynamics of the Delaware Bay horseshoe crab population and to predicting eggs available to migratory shorebirds. Our results suggest that management actions that are directed at reducing mortality in the early juvenile stages may have a greater effect on horseshoe crab and shorebird population dynamics than adjusting harvest levels alone. Such actions may include beach preservation and restoration in order to increase the amount of available spawning area and reduce density-dependent egg mortality. Assessing and monitoring spawning and nursery habitats within Delaware Bay could be critical in increasing and sustaining horseshoe crab populations. The most effective management strategy will involve a combination of harvest management and actions to increase early juvenile survival.

The population projections from our age-structured model were quite different from the projections of Davis et al. (2006). Davis et al. (2006) predicted population recovery to MSY biomass in as few as 2 yr from a depleted population. The age-structured models indicated a lag in population growth of 10 yr corresponding to the years required for horseshoe crabs to reach sexual maturity. Two critical assumptions of surplus production modeling, in part, could explain the difference. Surplus production modeling assumes that productivity responds instantaneously to changes in spawning biomass and that age structure of the population does not affect population dynamics (Prager 1994). We believe both assumptions are violated in the Davis et al. (2006) application because they did not account for horseshoe crab's long time to maturity (9–10 yr) and they mixed juvenile and adult indices as numbers rather than as biomass. We believe equating juvenile numbers with adult numbers presents a problem when these numbers are used as input into a biomass-based model.

Although there is much uncertainty in our model predictions, our model is useful for evaluating qualitative relationships between harvest levels and population growth, determining relative effects of horseshoe crab life history parameters on population growth, and assessing potential for egg availability for shorebird requirements. Our results are intended to help identify areas where future research is needed for scientifically based management decisions. This work should serve as a starting point for continued development of multispecies models in a multiple use environment.

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MICHELS, S. personal communication. Delaware Division of Fish and Wildlife, 3010 Bayside Drive, Dover, Delaware 19901

YOUNG, J. personal communication. U.S. Geological Survey, Leetown Science Center, 11649 Leetown Road, Kearneysville, West Virginia 25430

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