A production modeling approach to the assessment of the horseshoe crab (*Limulus polyphemus*) population in Delaware Bay

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Abstract—Horseshoe crab (*Limulus polyphemus*) is harvested commercially, used by the biomedical industry, and provides food for migrating shorebirds, particularly in Delaware Bay. Recently, decreasing crab population trends in this region have raised concerns that the stock may be insufficient to fulfill the needs of these diverse user groups. To assess the Delaware Bay horseshoe crab population, we used surplus production models (programmed in ASPIC), which incorporated data from fishery-independent surveys, fishery-dependent catch-per-unit-of-effort data, and regional harvest. Results showed a depleted population ($B_{2003}/B_{\mathrm{MSY}}$=0.03–0.71) and high relative fishing mortality ($F_{2002}/F_{\mathrm{MSY}}$=0.9–9.5). Future harvest strategies for a 15-year period were evaluated by using population projections with ASPICP software. Under 2003 harvest levels (1356 t), population recovery to B_{MSY} would take at least four years, and four of the seven models predicted that the population would not reach B_{MSY} within the 15-year period. Production models for horseshoe crab assessment provided management benchmarks for a species with limited data and no prior stock assessment.

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The horseshoe crab (*Limulus polyphemus*) has become a source of controversy on the Atlantic coast of the United States (Berkson and Shuster, 1999; Walls et al., 2002). This species is commercially harvested for use as bait, is used by the biomedical industry, and is an important source of food for a large number of species, including migrating shorebirds. However, population trends in the Delaware Bay region in recent years have indicated a possible decline in horseshoe crab abundance, raising concerns that the population may be unable to fulfill the present and future needs of these diverse user groups.

Horseshoe crabs are harvested commercially for use as bait in the American eel (*Anguilla rostrata*), whelk, and conch (family Melongenidae) pot fisheries (ASMFC[1]). Historically, horseshoe crabs were considered "trash fish" of little commercial value and were used primarily as fertilizer or animal feed. When the bait fishery began, there were few restrictions on harvest and no harvest-reporting requirements. A maximum reported coastwide harvest of about 2 million crabs (3100 metric tons [t]) occurred in 1998 (ASMFC[2]). Commercial harvest has decreased in recent years owing to the adoption of state-by-state quotas in 2000 (ASMFC[3]) and the increased use of bait-saving devices for the eel and conch fisheries, both of which have reduced the demand for crabs.

Horseshoe crabs are also used by the biomedical industry. The blood of horseshoe crabs contains *Limulus* Amebocyte Lysate (LAL), a substance used to detect the presence of endotoxin contamination in injectable and implantable drugs and devices (Novitsky, 1984). The Food and Drug Administration estimated that 260,000 horseshoe crabs were bled for LAL in 1997. After bleeding, the animals were released at the capture site, and

[1] ASMFC (Atlantic States Marine Fisheries Commission). 1998. Interstate fishery management plan for horseshoe crab, 57 p. ASMFC, 1444 Eye Street, NW, Sixth Floor, Washington, DC 20005.

[2] ASMFC. 2004. Horseshoe crab 2004 stock assessment report, 87 p. ASMFC, 1444 Eye Street, NW, Sixth Floor, Washington, DC 20005.

[3] ASMFC. 2000. Addendum I to the fishery management plan for horseshoe crab, 9 p. ASMFC, 1444 Eye Street, NW, Sixth Floor, Washington, DC 20005.

the mortality from the bleeding process was estimated to be 7.5% (Walls and Berkson, 2003). Currently, there is no substitute for LAL that offers comparable speed and sensitivity.

Horseshoe crabs also play an important role in marine and terrestrial food webs (Botton and Shuster, 2003). Shorebirds migrating from South America to Arctic breeding grounds stop in the Delaware Bay to rebuild depleted energy reserves (Botton et al., 1994). The time and place of their stop-over coincides with that of annual horseshoe crab breeding, when the crabs arrive en masse to spawn on sandy beaches during high tides of May and June (Botton and Harrington, 2003). An adult female horseshoe crab lays approximately 88,000 eggs per year (Shuster, 1982), and a single red knot (*Calidris canutus*) can consume an estimated 18,000 crab eggs daily (USFWS[4]).

Horseshoe crabs account for substantial economic value in the Delaware Bay region. Regional economic contribution of the eel and conch fisheries is approximately \$2.2 to \$2.8 million annually. The regional economic value of the horseshoe crab biomedical industry is \$26.7 to \$34.9 million annually. Ecotourism related to migrating shorebirds has become increasingly important to the economy of the Delaware Bay region. An estimated 6,000 to 10,000 recreational bird watchers visit the Delaware Bay in spring and contribute \$6.8 to \$10.3 million to the regional economy.

Recently, there has been concern that the horseshoe crab population can fulfill the current needs of these user groups. These concerns led the Atlantic States Marine Fisheries Commission (ASMFC) to develop a fishery management plan for horseshoe crabs. Unfortunately, very few abundance data are available for this species. Many state and federal trawl surveys record horseshoe crabs caught during sampling, but gear and sampling methods are not designed for horseshoe crabs and catches are not common. Only recently have statistically robust horseshoe crab-specific surveys been initiated: a Delaware Bay spawning survey (Smith et al., 2002) and an offshore trawl survey (Hata and Berkson, 2003).

Because of the limited data available, previous stock assessments of the Delaware Bay population have been restricted to trend analyses to determine whether a single survey identifies a significant change in the population or whether there is a consensus among data sets. However, many Delaware Bay surveys have high variability and low power to detect population change and would therefore only be able to identify dramatic changes in population size. Also, trend analyses do not provide estimates of stock status (Caddy, 1998) such as relative biomass (B/B_{MSY}) and relative fishing mortality (F/F_{MSY}). The ultimate goal for horseshoe crab assessment employs a stage-based catch-survey methodology (Collie and Sissenwine, 1983; HSC-SAS[5]), incorporating data from harvest and surveys. It will be a number of years before this modeling approach can be implemented, however, since stage-class data from commercial harvest are not currently being collected.

The surplus production modeling approach (Prager, 1994) used in our study is an appropriate bridge between these two methods. Production models allow for the incorporation of harvest data and multiple surveys, improving predictive power over that of a single survey. This technique does not include a stage-structure in the model; instead it focuses on the dynamics of the population as a whole. Similar methods have been successfully applied to horseshoe crab data from Rhode Island (Gibson and Olszewski[6]) and production models have been widely used for assessments of other species (Booth and Punt, 1998; Cadrin and Hatfield, 2002; Vaughan and Prager, 2002). Surplus production models assume a low population growth rate at small population sizes and as the population nears the carrying capacity (Quinn and Deriso, 1999). In the logistic growth form of the model used in the present study, maximum growth rate (and maximum surplus production) occurs at one-half of the carrying capacity. At this point, the maximum surplus population growth can be harvested while still maintaining a stable population size. Surplus production models provide estimates of maximum sustainable yield (MSY; the largest harvest that can continuously be removed from a stock), population biomass, and fishing mortality, as well as allow for the estimation of effects of future management.

We fitted a regional-scale production model to Delaware Bay horseshoe crab data in order to quantify the current status of the Delaware Bay population and to estimate impacts of future management actions. The results from this production model will allow the ASMFC and member states to manage the Delaware Bay population of horseshoe crabs more effectively with the goal of providing a sustainable resource for commercial harvest, the biomedical industry, and migrating shorebirds.

Methods

Production model

We used an age-aggregated production model with the Prager (1994) form of the Graham-Schaefer surplus-production model (i.e., logistic population growth),

[4] USFWS (U.S. Fish and Wildlife Service). 2003. Delaware Bay shorebird-horseshoe crab assessment report and peer review. Migratory Bird Publication R9-03/02, 107 p. USFWS, 4401 N. Fairfax Dr., MBSP 4107, Arlington, VA 22203.

[5] HSC-SAS (Horseshoe crab stock assessment subcommittee). 2000. A conceptual framework for the assessment of horseshoe crab stocks in the mid-Atlantic region, 19 p. ASMFC, 1444 Eye Street, NW, Sixth Floor, Washington, DC 20005.

[6] Gibson, M., and S. Olszewski. 2001. Stock status of horseshoe crabs in Rhode Island in 2000 with recommendations for management, 13 p. RI Division of Fish and Wildlife, 4808 Tower Hill Rd., Wakefield, RI 02879.

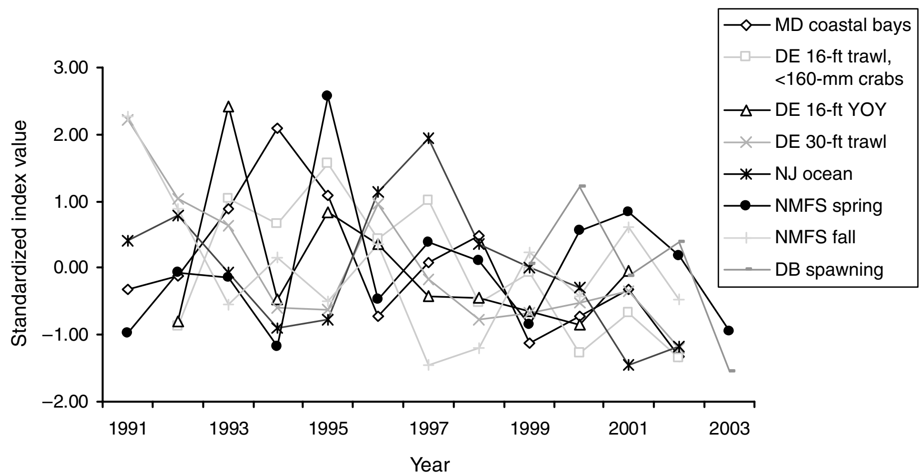

Figure 1

Fishery-independent survey indices for the Delaware Bay (DB) region from 1991 through 2003, standardized by survey for comparison. MD = Maryland; DE = Delaware; NJ = New Jersey; DB=Delaware Bay.

$$\frac{dB_t}{d_t} = (r - F_t)B_t - \frac{rB_t^2}{K},$$

where r = the stock's intrinsic growth rate;
K = the carrying capacity, both of which are assumed to be constant (Prager, 1994); and
F_t and B_t = Fishing mortality and biomass, respectively, at time t.

In addition, the harvest was not assumed to equal surplus production (i.e., the model was a dynamic or nonequilibrium model; Quinn and Deriso, 1999). This model assumes $B_{MSY} = 0.5K$, where B_{MSY} is the spawning biomass that would produce MSY. This form is often used because of its theoretical simplicity and because it is central among possible production model shapes. This production model was conditioned on catch, meaning that landings data were assumed to be more precise than abundance indices. By assuming that abundance indices are correlated measures of population abundance, the model is able to incorporate multiple indices by interpreting differences among indices as sampling error. To fit the production model, we used the ASPIC software (vers. 5.02) of Prager (1994), a program that has been used extensively in stock assessments (Cadrin and Hatfield, 2002; MacCall, 2002). We included data from fishery-independent and fishery-dependent sources in model runs.

Abundance indices

In the Delaware Bay region, there are a number of fishery-independent surveys that collect data on horseshoe crabs (Fig. 1). These include National Marine Fisheries Service (NMFS) trawl (spring, 1968–2003, and fall, 1963–2002), New Jersey (NJ) ocean trawl (1989–2002), Maryland (MD) coastal bays trawl (1988–2002), Delaware (DE) 16-ft trawl (juvenile and young-of-the-year; 1992–2002), DE 30-ft trawl (1990–2002), and Delaware Bay spawning survey (1999–2003). Detailed descriptions of these surveys can be found in ASMFC.[2] We selected 1991–2003 as the modeling timeframe because both harvest data and abundance index data were available for this period.

In spite of the large number of surveys and long time series for some of these surveys, many had high variability and low power to detect a decline. Additionally, many of these surveys were negatively correlated with each other for the years investigated (Table 1). Because an underlying assumption for the model is that each survey is representative of the population being evaluated, total disagreement (i.e., negative correlation) among any pair of surveys cannot be reconciled by the model, resulting in model errors. We therefore used three subsets of fishery-independent surveys in which all pairs were positively correlated for population modeling (Table 2), incorporating six of the eight fishery-independent surveys into production model runs. Fishery-dependent data were also available from 1991 to 2002 from the Delaware hand and dredge fisheries. Abundance indices based on catch-per-unit-of-effort (CPUE) for these fisheries were calculated from the annual number of trips and landings for each fishery (Fig. 2).

Within the models, abundance indices were weighted by the inverse of the coefficient of variation (CV) from regressions, which gave more weight to surveys with less variability. For comparison, we also conducted model runs where surveys were weighted equally within the models. Table 2 lists the three fishery-independent models (referred to as FI) and the four fishery-dependent models (referred to as FD) used in production model applications and the CV and weighting of each survey within the models.

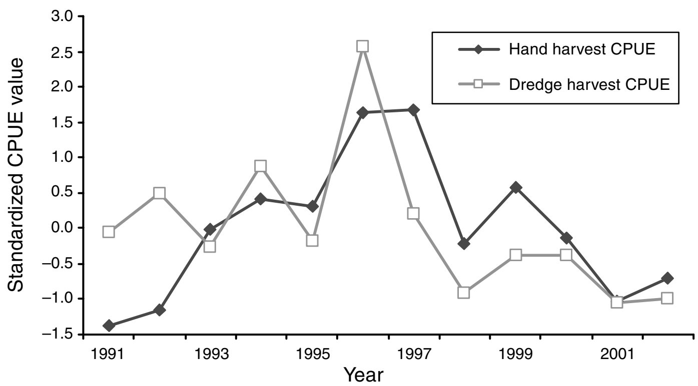

Figure 2

Fishery-dependent abundance indices based on catch-per-unit-of-effort data for the Delaware hand and dredge horseshoe crab (*Limulus polyphemus*) fisheries, 1991–2002, standardized by index for comparison.

Harvest

We obtained horseshoe crab harvest data for Virginia, Maryland, Delaware, Pennsylvania, and New Jersey from 1995 to 2003 (NMFS[7]; Michels[8]). We combined harvests among states for regional-scale production model runs. We estimated the regional harvest from 1991 to 1994 from available Delaware landings data (Fig. 3). Reporting of harvest was not mandatory during this time period, and harvest data

[7] NMFS (National Marine Fisheries Service). 2004. Fisheries Statistics and Economics Division, Silver Spring, MD. Landings data (by state and year) obtained in August 2004 from http://www.st.nmfs.gov/st1/commercial/index.html. Web page was last modified 24 September 2003.

[8] Michels, S. Personal commun. 2004. DE Div. of Fish and Wildlife, 89 Kings Highway, Dover, DE 19901.

Table 1

Correlation matrix for abundance indices derived from 10 surveys, with number of pairwise comparisons (i.e., years) in parentheses for 1991–2003. Negatively correlated indices are shown in bold font. Indices used in production model runs are identified with an asterisk (*).

	1 NMFS fall	2 NMFS spring	3 DE 30-ft trawl	4 DE 16-ft trawl, <160-mm crabs	5 DE 16-ft trawl, YOY	6 NJ ocean	7 MD coast	8 Spawning survey	9 DE dredge	10 DE hand
1 NMFS sall	1.000 (12)									
2 NMFS spring*	**–0.409** (12)	1.000 (13)								
3 DE 30-ft* trawl	0.706 (12)	**–0.370** (12)	1.000 (12)							
4 DE 16-ft trawl, <160-mm* crabs	**–0.261** (11)	0.182 (11)	0.215 (11)	1.000 (11)						
5 DE 16-ft trawl, YOY*	**–0.153** (10)	0.214 (10)	0.341 (10)	0.617 (10)	1.000 (10)					
6 NJ ocean*	**–0.102** (12)	**–0.249** (12)	0.479 (12)	0.252 (11)	**–0.132** (10)	1.000 (12)				
7 MD coastal bays*	**–0.181** (12)	0.086 (12)	**–0.038** (12)	0.639 (11)	0.336 (10)	**–0.116** (12)	1.000 (12)			
8 Spawning survey	**–0.786** (4)	0.211 (5)	**–0.069** (4)	**–0.657** (4)	**–0.781** (3)	0.392 (4)	**–0.087** (4)	1.000 (5)		
9 DE dredge harvest*	0.210 (12)	**–0.329** (12)	0.450 (12)	0.379 (11)	0.031 (10)	0.506 (12)	0.135 (12)	0.509 (4)	1.000 (12)	
10 DE hand harvest*	**–0.536** (12)	0.002 (12)	**–0.214** (12)	0.639 (11)	0.084 (10)	0.485 (12)	0.123 (12)	0.167 (4)	0.564 (12)	1.000 (12)

from other states were unavailable or unreliable. We therefore expanded the Delaware harvest to represent the Delaware Bay region by making the assumption that regional landings were equal to ten times the landings in Delaware, the approximate relationship from 1997 through 2003 when reporting was mandatory. When applicable, we converted numbers to metric tons (t) (Prager and Goodyear, 2001) using the relationship of Gibson and Olszewski[6] (1.8182 kg/horseshoe crab). Commercial harvest of horseshoe crabs has been below the regional quota of 2595 t since 2000 (Fig. 3).

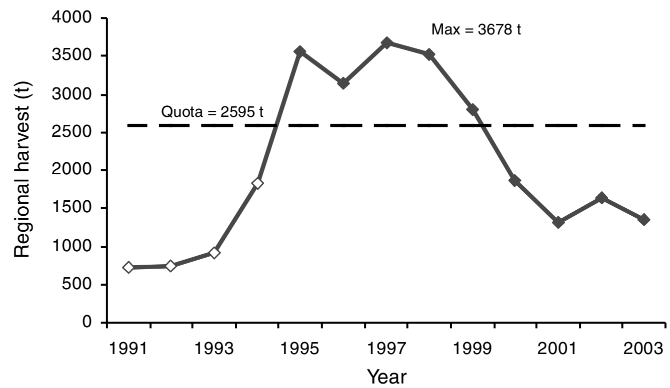

Figure 3

Delaware Bay regional horseshoe crab (*Limulus polyphemus*) harvest (in t). Regional harvest, 1991–1994 (open diamonds), was estimated to be ten times the Delaware harvest. The current regional quota of 2595 t is shown by the horizontal line.

Assumptions associated with the production models

There were a number of general assumptions associated with production models (Quinn and Deriso, 1999). We assumed that productivity (change in biomass over time) responded instantaneously to changes in population size. Changes in the biotic and abiotic environments were ignored, and r (the intrinsic rate of population growth) and K (the carrying capacity) were assumed to be constant. Because production models combine all age classes, it was assumed that size or age structure of the population would not have major effects on population dynamics.

Specific assumptions about population values were also required by the model. All starting values of MSY and K were based on the maximum harvest in the Delaware Bay from 1991 through 2003. The initial guess for MSY was 1850 t (half of the largest catch), and the initial guess for K was 37,000 t (ten times the largest catch). For fishery-independent model runs, we had the model freely estimate initial biomass in relation to carrying capacity (B_1/K), with our start-

Table 2

Description of production model runs, including the data sources, years, and coefficient of variation (CV) from regression analyses. The weighting of surveys within the models is the inverse of the CV. The starting estimate of B_1/K for each model is also shown. FI refers to models that include fishery-independent abundance indices, and FD identifies models where fishery-dependent indices from CPUE data were used.

Model	Data sources	Years	CV	Relative weighting	Initial B_1/K value
FI-1	NMFS spring	1991–2003	0.636	0.241	0.5
	DE 16-ft trawl, <160-mm crabs	1992–2002	0.517	0.296	
	DE 16-ft trawl YOY	1992–2001	0.928	0.165	
	MD coastal bays	1991–2002	0.515	0.297	
FI-2	DE 30-ft trawl	1991–2002	0.524	0.388	0.5
	DE 16-ft trawl, <160-mm crabs	1992–2002	0.517	0.393	
	DE 16-ft YOY	1992–2001	0.928	0.219	
FI-3	DE 30-ft	1991–2002	0.524	0.283	0.5
	DE 16-ft trawl, <160-mm crabs	1992–2002	0.517	0.287	
	NJ ocean trawl	1991–2002	0.345	0.430	
FD-1	DE hand CPUE	1991–2002	0.449	0.553	Fixed at 0.1
	DE dredge CPUE	1991–2002	0.555	0.447	
FD-2	DE hand CPUE	1991–2002	0.449	0.553	Fixed at 0.2
	DE dredge CPUE	1991–2002	0.555	0.447	
FD-3	DE hand CPUE	1991–2002	0.449	0.553	Fixed at 0.3
	DE dredge CPUE	1991–2002	0.555	0.447	
FD-4	DE hand CPUE	1991–2002	0.449	0.553	Fixed at 0.4
	DE dredge CPUE	1991–2002	0.555	0.447	

ing estimate of this value equal to 0.5. In the absence of other information about starting biomass, B_1/K = 0.5 (i.e., B_1=B_{MSY}) is an appropriate default value (Punt, 1990; Prager, 1994). In some cases B_1/K was poorly estimated, and we employed a common solution of fixing the value of B_1/K (Vaughan and Prager, 2002). For model runs based on fishery-dependent indices, we fixed B_1/K at 0.1, 0.2, 0.3, and 0.4 (Table 2). The CPUE value for the Delaware hand fishery was relatively low in 1991; therefore we assumed that the population biomass was below B_{MSY}, i.e. B_1/K was less than 0.5.

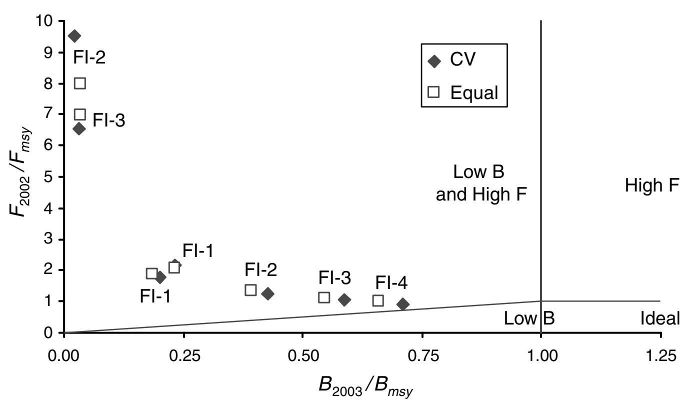

Figure 4

Relative 2003 biomass ($B_{2003}/B_{\mathrm{MSY}}$) and relative 2002 fishing mortality (F_{2002}/F_{MSY}) of Delaware Bay horseshoe crab (*Limulus polyphemus*) for each of the seven model runs presented, with abundance indices weighted equally or inversely to CV within the models.

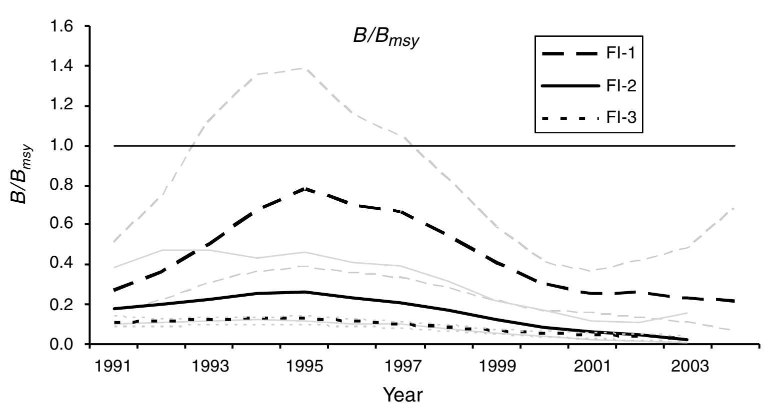

Figure 5

Production model estimates of relative biomass (B/B_{MSY}) of horseshoe crabs (*Limulus polyphemus*) in the Delaware Bay region, 1991–2004. Results from fishery-independent model runs are shown, and the horizontal line represents B/B_{MSY}=1. 80% confidence intervals each model run are the same line pattern in gray.

Quantities estimated by the model

The production model estimated several benchmarks and status indicators useful in understanding horseshoe crab biology and in improving management. These quantities included relative biomass (B/B_{MSY}), relative fishing mortality (F/F_{MSY}), population biomass (B), and maximum sustainable yield (MSY). Point estimates and 80% confidence intervals for each of these quantities were calculated for each model run.

Population projections

We used the Delaware Bay population estimates calculated by the surplus production model to project the population forward in time for a period of 15 years to evaluate potential harvest levels. We conducted projections using ASPICP (Prager, 1994), with annual landings specified for each year of the projections. We selected a 15-year time period because this is the longest projection period that can be programed in ASPICP, and confidence in projection model results decreases at longer time intervals. We evaluated trends in biomass over time for a range of harvest levels, including harvest at 2003 levels and proportional reductions of that harvest. These harvests were 0% of 2003 catch (no harvest), 25% (339 t annually), 50% (678 t), 75% (1017 t), and 100% (1356 t). We identified the number of years under each harvest scenario required for the population (and 80% confidence intervals) to rebuild to B_{MSY}. We also compared relative biomass (with 80% confidence intervals) in the final year of projections (2018) for each harvest level.

Results

Results differed little between model simulations for surveys weighted inversely to CV and for simulations with equally weighted surveys (Fig. 4).

B/B_{MSY}

Production model runs showed that B/B_{MSY} in the Delaware Bay region increased in the early 1990s and has declined steadily since 1995 (Figs. 5 and 6). Slight increases since 2001 were evident in some model runs. Relative biomass in 2003 was estimated to be low, with point estimates ranging from 0.03 to 0.20 for models with fishery-independent data and 0.20 to 0.71 for models with fishery-dependent data (Table 3). Eighty-percent confidence intervals for B_{2003}/B_{MSY} ranged from 0.005 to 1.16.

Table 3

Status indicators and management benchmarks for horseshoe crabs in the Delaware Bay region, estimated from production model runs with fishery-independent (FI) or fishery-dependent (FD) indices weighted by the inverse of the CV. Point estimates and lower (L) and upper (U) 80% confidence intervals (CIs) are shown for each model run. The objective function is a measure of how well the model was able to fit the data using a lognormal error structure—a lower value representing a better fit.

	FI-1	FI-2	FI-3	FD-1	FD-2	FD-3	FD-4
B_{2003}/B_{MSY}	0.232	0.022	0.030	0.201	0.427	0.588	0.710
80% CI (L)	0.109	0.005	0.008	0.127	0.238	0.319	0.388
80% CI (U)	0.479	0.154	0.041	0.347	0.762	1.015	1.157
F_{2002}/F_{MSY}	2.156	9.501	6.560	1.795	1.269	1.034	0.911
80% CI (L)	1.442	6.005	3.999	1.258	0.770	0.588	0.513
80% CI (U)	3.299	18.320	21.300	2.592	2.069	2.112	2.184
B_{2003} (t)	2197	1084	4098	2579	3653	5035	6604
80% CI (L)	1319	524	2295	1423	1853	2955	4340
80% CI (U)	4603	4306	9379	4372	5012	7778	12,080
MSY (t)	3064	5082	7220	3768	2628	2354	2196
80% CI (L)	2550	2985	5340	3274	2566	1905	1372
80% CI (U)	4475	8713	9577	4499	2787	2505	2501
Objective function	16.05	12.40	9.57	2.62	2.93	3.39	3.85

F/F_{MSY}

Although harvest of horseshoe crabs has decreased in recent years (Fig. 3), fishing mortality remains high (Figs. 7 and 8). F_{2002}/F_{MSY} point estimates ranged from 2.3 to 9.5 for models with fishery-independent data and from 0.9 to 1.8 for models with fishery-dependent data (Table 3).

Biomass

Biomass of horseshoe crabs in the Delaware Bay region has decreased substantially since 1995, such that the 2003 biomass was less than 56% of the 1995 biomass. This equates to an annual decline of greater than 7% during this period. Point estimates for 2003 biomass ranged from 1084 t (596,000 crabs) to 6604 t (3,632,000 crabs). As is characteristic of production models (Prager, 1994), absolute biomass was estimated much less precisely than relative biomass (B/B_{MSY}). The range of 80% confidence intervals for 2003 biomass across all seven model runs was 524 t (288,000 crabs) to 12,080 t (6,644,000 crabs).

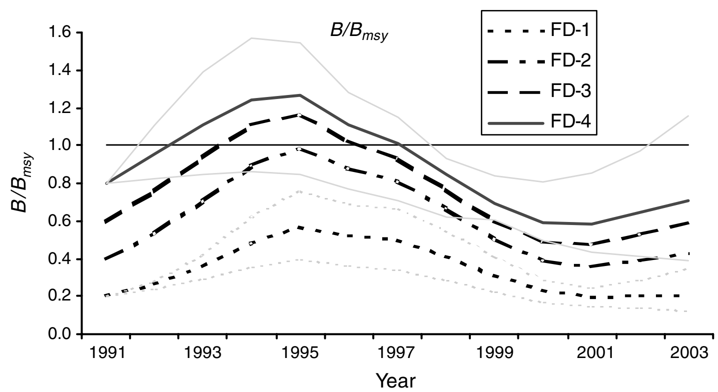

Figure 6

Production model estimates of relative biomass (B/B_{MSY}) of horseshoe crabs (*Limulus polyphemus*) in the Delaware Bay region, 1991–2003. Results from fishery-dependent model runs are shown, and the horizontal line represents B/B_{MSY}=1. 80% confidence intervals for models FD-1 and FD-4 are shown in gray.

Population projections

We used results from production model runs to project the horseshoe crab population forward in time to evaluate potential management options. Figure 9 shows the trajectory of B/B_{MSY} over time for model FI-1 under each harvest scenario. The number of years required to rebuild the population to B_{MSY} varied substantially among models (Table 4). At 2003 harvest levels (i.e., 100%), projections showed population recovery in a minimum of four years, although four of the seven models did not reach B_{MSY} in the 15-year projection period. In the absence of harvest (i.e., 0%), recovery could occur in as few as 2 years, but two models did not reach B_{MSY} in the projection period. Estimates of B/B_{MSY} in the final year of projections (2018) also differed among model applications (Table 5).

Discussion

According to surplus production model runs and corresponding projections, the horseshoe crab population in the Delaware Bay region has been depleted and current harvest levels may be too high to allow the population to rebuild to B_{MSY} within 15 years. Biomass in this region has decreased steadily since 1995 and is currently well below B_{MSY}. This decline was evident in models that incorporated regional fishery-independent surveys and Delaware fishery-dependent indices. Figure 4 shows current relative biomass and relative fishing mortality for each of the model applications. All model runs indicated a depleted population with high fishing mortality, although the estimated extent differed among models (Fig. 4). Projections for some of the model runs predicted a relatively fast population recovery. In the absence of harvest, five of the seven model applications predicted rebuilding to B_{MSY} in five or fewer years. However, two of the model runs estimated such low population biomass that rebuilding the Delaware Bay population to B_{MSY} would take greater than 15 years, even with no harvest. A precautionary management strategy may therefore be appropriate for this population in the short term as more data are being collected.

Population model results may have been affected by assumptions that we made during the modeling process. In order to extend the time period of the model back to 1991, we had to estimate regional harvest based on Delaware harvest data for the early years of the model. Because harvest data from most states were not available prior to 1995, we assumed that regional harvest was equal to ten times the Delaware harvest for the years 1991–94. This was the approximate relationship between Delaware and regional harvest from 1997 through 2003 when reporting was mandatory. Actual regional harvest for 1991–94 was unknown because there were no harvest-reporting requirements. We conducted sensitivity analyses which showed very little difference among runs with 1991–94 harvest equal to Delaware landings, 10 times Delaware landings, or 20 times the Delaware landings (the mean difference for B_{2003}/B_{MSY} from these runs was 0.011). If the actual harvest was substantially greater than 20 times Delaware landings, differences in results may occur.

Results were also influenced by the data sources that were included. We based the inclusion of fishery-independent surveys on positive correlations among surveys, incorporating the largest number of data sources possible into model runs. However, two fishery-independent surveys were not included: the NMFS fall trawl and the Delaware Bay spawning survey. The NMFS fall trawl was negatively correlated with seven of the nine other data sources (Table 1), and we therefore assumed that it was not a reliable index of horseshoe crab abundance. The spawning survey was negatively correlated with five of the nine other data sources (Table 1). This survey also had a very short time series because it was redesigned in 1999 to improve statistical power (Smith et al., 2002). With so few data points, the production model would be unable to distinguish population trends from survey variability; therefore spawning survey data were excluded. However, as one of only two horseshoe crab-specific surveys currently in place, the Delaware Bay spawn-

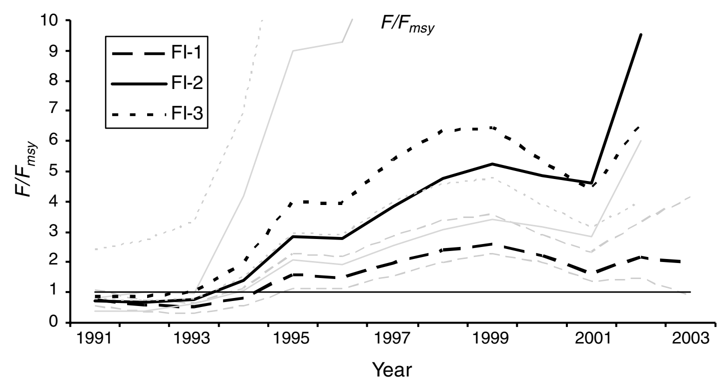

Figure 7

Production model estimates of relative fishing mortality (F/F_{MSY}) of horseshoe crabs (*Limulus polyphemus*) in the Delaware Bay region, 1991–2003. Results from fishery-independent model runs are shown, and the horizontal line represents F/F_{MSY}=1. 80% confidence intervals for each model run are the same line pattern in gray.

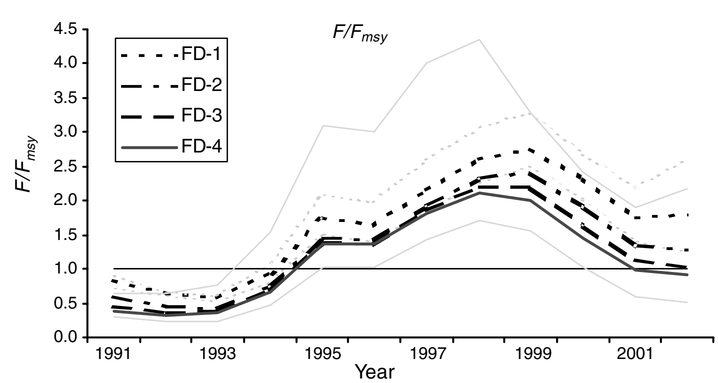

Figure 8

Production model estimates of relative fishing mortality (F/F_{MSY}) of horseshoe crabs (*Limulus polyphemus*) in the Delaware Bay region, 1991–2002. Results from fishery-dependent model runs are shown, and the horizontal line represents F/F_{MSY}=1. 80% confidence intervals for models FD-1 and FD-4 are shown in gray.

ing survey will likely prove to be a valuable source of information in the future.

Negative correlations were present among a relatively large number of Delaware Bay surveys (Table 1) which are assumed to be sampling the same population. This is a common problem in fisheries stock assessments (Richards, 1991; Schnute and Hilborn, 1993). The observed differences among these surveys could be attributed to a number of factors. Catches of horseshoe crabs are not common, leading to small sample sizes and high variability. Also, these surveys may differ in location, time of year, and gear selectivity. Future studies could employ an analysis of variance (ANOVA) to attempt to separate these factors from underlying horseshoe crab abundance trends.

The data sources included in individual model runs also led to differing results. Models incorporating fishery-dependent data tended to present a slightly more optimistic view of the population and the fishery, predicting higher relative biomass and lower relative fishing mortality. Although harvest data often have the benefit of having been derived from large sample sizes (and have resulting low variance estimates), there is often a bias associated with fishery-dependent data. Fisheries do not sample randomly because they target areas of highest abundance, and thus biased indices are produced (Quinn and Deriso, 1999). In addition, the use of fishery-dependent abundance indices is often complicated by changes in gear, regulations, or sampling methods over time, any of which could affect catch rates. Fishery-independent surveys are usually more appropriate for assessments, assuming there is high consistency in sampling methods among years (Chen et al., 2003).

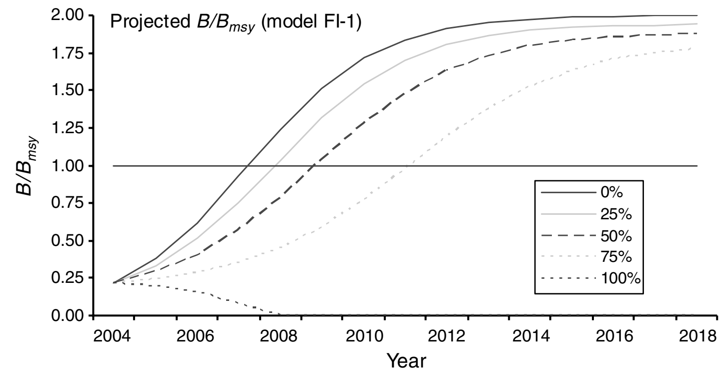

Figure 9

Example of projection results. Projected relative biomass (B/B_{MSY}) in shown for model FI-1, with each line representing a harvest level applied annually in the 15-year projections. The percentage refers to the percent of the 2003 Delaware Bay regional landings of 1356 t (i.e., 50%=678 t).

Differences also existed among fishery-independent surveys. Models FI-2 and FI-3 predicted a much lower population size than FI-1 or the fishery-dependent models. Projections with these runs predicted that the population was too depleted to recover in 15 years, even in the absence of harvest. The models differed only in the abundance indices included. In the trend analyses conducted for ASMFC,[2] the most significant population declines since 1997 were identified in the NJ ocean

Table 4

Results of Delaware Bay population projections from production model runs from fishery-independent (FI) and fishery-dependent (FD) indices. Projections were conducted for 15 years, with a constant harvest (in t) applied annually. Harvest levels were based on 2003 harvest and are listed in the left column. The time period (and 80% confidence intervals) shown represent the number of years (starting in 2003) required for the population biomass to reach B_{MSY}. "n/a" indicates that the biomass did not reach B_{MSY} during the 15-year projection period.

Harvest level in relation to that of 2003	Years to rebuild to B_{MSY}						
	FI-1	FI-2	FI-3	FD-1	FD-2	FD-3	FD-4
0% (0 t)	5 years	n/a	n/a	4 years	3 years	2 years	2 years
80% CI	(2, 12)	(3, n/a)	(n/a, n/a)	(3, 7)	(1, 6)	(0, 8)	(0, 15)
25% (339 t)	5	n/a	n/a	5	3	2	2
80% CI	(2, n/a)	(3, n/a)	(n/a, n/a)	(3, 8)	(1, 8)	(0, 9)	(0, n/a)
50% (678 t)	6	n/a	n/a	6	4	3	2
80% CI	(2, n/a)	(n/a, n/a)	(8, n/a)	(3, 11)	(1, 10)	(0, 14)	(0, n/a)
75% (1017 t)	9	n/a	n/a	7	4	3	3
80% CI	(3, n/a)	(n/a, n/a)	(5, n/a)	(4, 15)	(1, n/a)	(0, n/a)	(0, n/a)
100% (1356 t)	n/a	n/a	n/a	n/a	6	5	4
80% CI	(3, n/a)	(n/a, n/a)	(n/a, n/a)	(5, n/a)	(2, n/a)	(0, n/a)	(0, n/a)

Table 5

Results of Delaware Bay population projections from production model runs from fishery-independent (FI) and fishery-dependent (FD) indices. Projections were conducted for 15 years, with a constant harvest (in t) applied annually. Harvest levels were based on 2003 harvest and are listed in the left column. The relative biomass (B/B_{MSY}) in the final year of projections (2018) and 80% confidence intervals are shown for each model simulation.

Harvest level in relation to that of 2003	B_{2018}/B_{MSY}						
	FI-1	FI-2	FI-3	FD-1	FD-2	FD-3	FD-4
0% (0 t)	2.00	0.41	0.14	2.00	2.00	2.00	2.00
80% CI (L)	1.49	0.02	0.04	1.91	1.87	1.63	1.05
80% CI (U)	2.00	1.97	0.28	2.00	2.00	2.00	2.00
25% (339 t)	1.94	0.00	0.06	1.95	1.93	1.92	1.91
80% CI (L)	0.00	0.00	0.00	1.95	1.90	1.42	0.86
80% CI (U)	1.96	1.94	0.42	1.95	1.93	1.93	1.93
50% (678 t)	1.87	0.00	0.00	1.90	1.86	1.84	1.82
80% CI (L)	0.00	0.00	0.00	1.89	1.80	1.07	0.61
80% CI (U)	1.93	0.00	1.76	1.90	1.86	1.86	1.86
75% (1017 t)	1.78	0.00	0.00	1.83	1.78	1.74	1.71
80% CI (L)	0.00	0.00	0.00	1.66	0.86	0.57	0.26
80% CI (U)	1.85	0.00	1.74	1.85	1.78	1.78	1.77
100% (1356 t)	0.00	0.00	0.00	0.76	1.67	1.62	1.58
80% CI (L)	0.00	0.00	0.00	0.00	0.00	0.00	0.00
80% CI (U)	1.72	0.00	0.00	1.77	1.69	1.69	1.68

trawl and the DE 16-ft 160-mm survey, both of which were included in model FI-3, and possibly explain the low population estimates.

In other trend analyses conducted during the previous assessment, a population decline in the Delaware Bay was less evident. Using data from 1997 through 2003, we found that only four of eight fishery-independent surveys showed a significant decline, partially owing to high variability and low power. By incorporating a number of these surveys into a production model, we also found that the decreasing biomass in recent years becomes more apparent. These production model runs provide the added benefit of estimating stock status and management benchmarks, as well as the benefit of evaluating future management options.

Although interpretation of absolute biomass or population size from a surplus production model can be somewhat problematic, our estimates are roughly comparable to estimates from previous studies. Hata and Berkson (2003) calculated a mean 2001 population size of 4.4 million adults (95% confidence intervals of 2.1 million and 6.8 million) in the Delaware Bay from daytime trawl survey data. Botton and Ropes (1987) estimated 2.3 to 4.5 million adults in this region. In the present study, our estimates of the 2003 population size ranged from 0.6 million to 3.6 million crabs, and the mean of the seven model runs equaled 2.0 million crabs. Eighty percent confidence intervals ranged from 0.3 million to 6.6 million crabs for all model applications. Although within the range of results from the other studies, these wide confidence intervals provide little information for management. It will therefore be more appropriate to interpret relative biomass (B/B_{MSY}) and relative fishing mortality (F/F_{MSY}) for use in management decisions (Prager, 1994).

It is important to understand the spatial scale and population represented by these models and analyses. This regional model is a compilation of a number of localized fishery-independent surveys, most of which encompassed a relatively small spatial area. However, the model results should not be interpreted at a more localized scale because landings data are combined for the region. Similarly, interpretation of results should not be expanded to represent other Atlantic horseshoe crab populations outside the Delaware Bay region because neither survey nor harvest data in this model extend to other regions. Nevertheless, the Delaware Bay is believed to be the center of abundance and spawning activity for Atlantic horseshoe crabs; therefore population trends in this region may have significant implications for adjacent populations.

In analyses conducted for ASMFC,[2] trend analyses identified dramatic regional differences in horseshoe crab population trends. Although the Delaware Bay, eastern Long Island Sound, and New England populations have experienced declines in recent years, the southeast population and the western Long Island population have remained stable or have increased. Future production models applied to these other regions will hopefully clarify these trends and allow managers to determine regional harvest regulations. By identifying appropriate management for each region, we will improve our ability to rebuild the Atlantic horseshoe crab population and provide a sustainable resource for the diverse user groups.

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