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Article

Recovery of Delaware Bay horseshoe crabs following harvest reductions

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ABSTRACT

Objective: Horseshoe crabs *Limulus polyphemus* play a vital role in the Delaware Bay ecosystem. The migratory stopover of several shorebird species occurs during the horseshoe crab spawning season, and the eggs of horseshoe crabs provide an essential food source to fuel their northward migration to breeding areas. High commercial fishery use of horseshoe crabs as bait during the 1990s coincided with a decline in crabs and shorebirds, particularly the red knot *Calidris canutus rufa*, which has been listed as threatened under the U.S. Endangered Species Act since 2015. In response to the population decline of shorebirds, the Atlantic States Marine Fisheries Commission began reducing the harvest of horseshoe crabs in 2000 with a goal of rebuilding the population of horseshoe crabs and shorebirds that depend upon them. The objective of this analysis was to determine whether horseshoe crab harvest management in the Delaware Bay region has increased the abundance of the species in recent years.

Methods: We analyzed data from fisheries-independent trawl surveys of horseshoe crab relative abundance using a Bayesian hierarchical model to determine whether harvest management has resulted in the rebuilding of the horseshoe crab population to levels seen in 1990—a period before the overuse of horseshoe crabs and the decline in the population of red knots.

Results: Data from multiple surveys showed that the horseshoe crab population in Delaware Bay declined from the 1990s through approximately 2005, was relatively low and stable until 2010, and then increased through 2023, with a 0.38 probability of exceeding the 1990 level.

Conclusions: The results of this analysis support the effectiveness of management decisions related to horseshoe crabs in the Delaware Bay region. In response to harvest restrictions, the abundance of horseshoe crabs has neared levels observed in the early 1990s—a period prior to high commercial use and a decline in both horseshoe crabs and shorebirds that depend on them for food during annual migrations.

KEYWORDS: abundance index, harvest management, horseshoe crab, red knot

LAY SUMMARY

This study examined multiple horseshoe crab abundance indices and determined that the population has increased following harvest restrictions implemented in the early 2000s. By 2023, the population neared abundance levels estimated in 1990.

INTRODUCTION

Delaware Bay supports the largest population of horseshoe crabs *Limulus polyphemus* in the world, with an estimated 16 million adult females and 40 million adult males (Atlantic States Marine Fisheries Commission [ASMFC], 2024), and is an ecologically important stopover site for shorebirds during

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their annual migrations to breeding grounds in arctic and subarctic areas of North America (Botton & Harrington, 2003; Mizrahi & Peters, 2009; Niles et al., 2009). The shorebird migratory stopover occurs each spring and coincides with the timing of horseshoe crab spawning on the sandy beaches of Delaware Bay (Shuster & Botton, 1985). Here, deposited eggs are consumed to support the shorebirds' onward migrations (Gillings et al., 2007; Haramis et al., 2007). Shorebird species—such as red knot *Calidris canutus rufa*, ruddy turnstone *Arenaria interpres*, sanderling *Calidris pusilla*, dunlin *Calidris alpina*, and short-billed dowitcher *Limnodromus griseus*—all stop in Delaware Bay during their northward migrations to feast upon the abundant, nutrient-rich horseshoe crab eggs (Niles et al., 2009). Since the 1980s, the spectacle of shorebird stopover and horseshoe crab spawning has generated an ecotourism industry, with photographers, naturalists, and birdwatchers coming to the area in May and June each year (Burger et al., 1995). Horseshoe crabs are also thought to play a vital role more generally in the ecology of estuarine and coastal communities (Botton, 2009). After hatching, early instars are eaten by surf zone fishes, hermit crabs, and other predators. Although little is known about predator–prey relationships involving older juveniles, adult horseshoe crabs are important as food for the endangered loggerhead sea turtle *Caretta caretta*, especially in the mid-Atlantic region (Keinath, 2003). Horseshoe crabs are dietary generalists, and adult crabs are ecologically important bivalve predators in some locations (Botton & Haskins, 1984). Horseshoe crab shells serve as substrate for a large number of epibionts, such as barnacles and slipper limpets *Crepidula fornicate* (Botton & Ropes, 1988).

In addition to their ecological importance, horseshoe crabs are commercially used as bait in American Eel *Anguilla rostrata* and whelk (knobbed whelk *Busycon carica* and channeled whelk *Busycotypus canaliculatus*) fisheries. They are also used by the biomedical industry in the production of Limulus amebocyte lysate, a compound derived from the hemolymph of horseshoe crabs, to detect Gram-positive bacterial contamination of vaccines, injectable drugs, and implantable medical devices (ASMFC, 1998). As the demand for American Eel and whelk increased in the 1990s, so did the demand for the harvest of horseshoe crabs for use as bait in these fisheries. From 1990 through 1997, reported coastwide landings of horseshoe crabs increased from approximately 454,000 kg to over 2.7 million kg, much of which came from the Delaware Bay region (ASMFC, 1998). The increasing harvest of horseshoe crabs in the 1990s coincided with a decline in their abundance and counts of shorebirds, particularly the red knot, during their stopover in Delaware Bay (Niles et al., 2009). Aerial counts of red knots declined from approximately 50,000 birds in the late 1990s to an average of 25,000 between 2012 and 2018 (New Jersey Department of Environmental Protection, 2020). The ASMFC adopted the first interstate fishery management plan for horseshoe crabs in 1998 (ASMFC, 1998) in efforts to conserve horseshoe crabs and the shorebirds that depend upon their eggs for food during the stopover period. Since then, nine subsequent addenda to the 1998 fishery management plan further curtailed the allowable harvest of horseshoe crabs for bait. In addition, the state of New Jersey instituted a moratorium on commercial horseshoe crab bait harvest in 2008 and Delaware has had a male-only harvest since 1998 (ASMFC, 2019, 2024). Current harvest is <1% of combined-sex abundance (Smith et al., 2025).

Although the ASMFC reduced the allowable harvest of horseshoe crabs and individual states imposed additional regulations, horseshoe crab harvest values for commercial harvesters were in opposition to the values of shorebird conservation advocates. To address these opposing values, an effort began in 2007 to develop a multispecies adaptive resource management (ARM) framework (Breese et al., 2007) to bring the various stakeholder groups together and formulate a harvest strategy for horseshoe crabs that would support the forage needs of shorebirds, specifically the red knot. This effort culminated in 2012 with the ASMFC adopting the ARM framework as its guiding method for horseshoe crab harvest management in the Delaware Bay region (ASMFC, 2012). To make annual harvest recommendations based on annual abundance estimates of horseshoe crabs and red knots, the ARM framework used population dynamics models of each species, in which the abundance of horseshoe crabs affected the survival and fecundity of red knots (McGowan, 2015; McGowan et al., 2011). These models were largely based on life history parameters taken from the literature because there was a lack of empirical data specific to Delaware Bay for both species. The ARM framework was used to make harvest recommendations for the 2013–2022 harvest seasons, with a consistent annual recommended harvest of 500,000 males and 0 females in the Delaware Bay region. The recommended zero harvest of females was because female abundance was below a threshold level whereby female harvest was valued in the decision framework. After a decade since the initial development of the ARM framework, more horseshoe crab and red knot monitoring data had been collected from the Delaware Bay region, and the ARM framework was revised in 2021 (ASMFC, 2022a), with new underlying population dynamics models based on these local empirical data. The revised ARM framework was adopted for management in 2022 (ASMFC, 2022b). Although the framework recommended a level of female horseshoe crab harvest of <1.5% of female abundance, managers continued the zero female harvest strategy due to an outpouring of public opposition from those concerned about the continued low abundance of red knots and other shorebirds and the belief that horseshoe crabs had not increased in abundance (ASMFC, 2022c).

Recent stock assessments by the ASMFC (ASMFC, 2019, 2024) analyzed trends in relative abundance indices from fishery-independent trawl surveys for the Delaware Bay region. They concluded that recent abundance indices had a high probability of exceeding values observed in 1998—when active management for horseshoe crabs was initiated through a fishery management plan. Despite the apparent increase in abundance since 1998, questions remain as to whether horseshoe crab abundance has returned to the levels present before the decline of shorebird species such as the red knot. Although 1998 was the stock assessment benchmark for measuring the success of fishery management, Niles et al. (2009) suggested that abundance in 1990 was an appropriate benchmark to gauge horseshoe crab's recovery, as this was a time with high counts of red knots (95% confidence intervals ranging from ∼35,000 to 70,000) stopping over in Delaware Bay during their spring migration. It also represents a period prior to the great increase in landings of horseshoe crabs in the commercial fishery.

The objective of this analysis was to determine whether horseshoe crab abundance has increased to levels equivalent to those in 1990 following more than two decades of reduced harvest and no allowable female harvest for the bait industry in the Delaware Bay region since 2012. We used data from multiple fishery-independent trawl surveys to infer an overall index of horseshoe crab abundance with a Bayesian hierarchical model (Conn, 2010) and characterized the probability of the terminal year in our analysis (2023) exceeding abundance in the benchmark year of 1990.

METHODS

The abundance of horseshoe crabs in the Delaware Bay region is assessed using multiple fishery-independent trawl surveys conducted by state agencies and an academic research group (ASMFC, 2019, 2024). Sampling methodologies and gears differ among surveys, and although most do not target horseshoe crabs, they do encounter horseshoe crabs at frequencies adequate to develop indices of relative abundance (indexed as mean annual catch per tow). These trawl surveys have all been deemed acceptable for use in the horseshoe crab stock assessments conducted by the ASMFC and span a range of years from 1988 through the present with broad geographical coverage and adequate sampling protocols (ASMFC, 2019, 2022a, 2022b, 2022c). Their timing covers spring–summer and fall; spatially, they include the nearshore ocean, Delaware Bay, and coastal bays (Figure 1). For trawl surveys that sampled during multiple time periods throughout the year, data were subset to those times of year in which horseshoe crabs occurred most frequently in trawl catches. Filtering the data in this way acknowledged within-year variability in catchability due to variation in the spatial and temporal overlap of the trawl surveys with the migratory distributions of crabs throughout the year. Because sex-specific indices of abundance are not available from the start of the time series, our analysis focused on combined-sex abundance indices.

The Delaware Fish and Wildlife Adult Finfish Trawl Survey (hereafter, referred to as "the DE trawl"; Figure 1) has been conducted continuously since 1990. The survey samples nine fixed stations monthly from March through December, for an annual total of 72 trawl samples. The sampling gear uses a 9.1-m, two-seam otter trawl with a 7.6-cm stretch mesh in the wings and body and a 13-cm stretch mesh in the cod end. The sampling area includes the Delaware waters of Delaware Bay at depths ranging from 7 to 35 m. A standard tow for each sample is 20 min in duration at a speed of 3 knots. Horseshoe crab catch in this survey is mainly comprised of adults. We calculated relative abundance indices for spring–summer (March–August) and fall (September–December) samples using a generalized linear model accounting for covariates of station and salinity (ASMFC, 2022a).

The New Jersey Ocean Trawl Survey (hereafter, referred to as "the NJ trawl"; Figure 1) has been operating continuously since 1988, except in 2020 and 2021 due to the COVID-19 pandemic. The survey collects samples during five survey cruises per year (30 samples in January and 39 samples each month in April, June, August, and October) in the nearshore ocean waters of New Jersey. The NJ Trawl uses a three-in-one-design, two-seam trawl net with forward netting of 12-cm stretch mesh, rear netting of 8 cm, and a 6.4-mm bar mesh liner in the cod end. The survey incorporates a random stratified design with sampling sites selected within 15 strata with longitudinal boundaries consisting of 9.1-, 18.3-, and 27.4-m isobaths. The strata are further divided into blocks of 2 × 2.5 min of longitude and latitude for the midshore and offshore strata and 1 × 1 min for the inshore strata. The standard tow duration is 20 min. The survey catches mainly adult crabs. A spring–summer (April and August) and a fall (October) abundance index were developed because horseshoe crabs were consistently captured in these months. Each seasonal abundance index was calculated using a delta mean catch per tow (Pennington, 1983) to accommodate the number of zero catches of horseshoe crabs.

The Northeast Area Monitoring and Assessment Program (NEAMAP; Figure 1) began sampling the Atlantic coast from Martha's Vineyard, Massachusetts, to Cape Hatteras, North Carolina, in the fall of 2007, with sampling occurring in both the spring (April–May) and fall (October). The survey area is stratified by both latitudinal–longitudinal region and depth, and the program uses a four-seam, three-bridle, 400- × 12-cm bottom trawl outfitted with a 2.54-cm knotless nylon liner. The trawl is towed for 20 min at 3 knots at each sampling location. To index the Delaware Bay population of horseshoe crabs, survey strata in the Delaware Bay area were subset from the entire data set and the fall seasonal sampling was selected. Relative abundance was calculated as the delta mean catch per tow (Wong, 2024).

The Virginia Polytechnic Institute and State University Trawl Survey (hereafter, referred to as "the VT trawl"; Figure 1) is the only trawl survey specifically designed to assess the relative abundance of the horseshoe crab population in the Delaware Bay region (Hata & Berkson, 2004) and is conducted in the fall (September–November). The survey operated from 2002 to 2011 and then again from 2016 to 2023 due to a lapse of funding from 2012 to 2015. The survey samples the coastal Delaware Bay area of the Atlantic Ocean from shore out to 22.2 km and extends from Atlantic City, New Jersey, southward to approximately Wachapreague, Virginia. Since 2016, the survey has also sampled the lower Delaware Bay, but data from this area were not included because they did not extend back to 2002. The survey area is stratified by distance from shore (0–5.5 km, 5.5–22.2 km) and bottom topography (trough, nontrough). The sampling gear consists of a two-seam flounder trawl with an 18.3-m headrope and 24.4-m footrope, rigged with a Texas Sweep of 13-mm link chain and a tickler chain. The net body consists of 15.2-cm stretch mesh, and the bag consists of 14.3-cm stretch mesh. Standard tow duration is 15 min. A stratified delta-lognormal mean is calculated to estimate the average catch-per-tow abundance index (Wong, 2024).

The Maryland Coastal Bays Trawl (hereafter, referred to as "the MD trawl"; Figure 1) has operated since 1990 in coastal embayments from Delaware's northern border southward to Virginia's border. The survey uses a 14.9-m otter trawl towed at 20 fixed sites. The survey is conducted monthly (April through October), but only the spring survey was used to calculate a relative abundance index due to infrequent catches of horseshoe

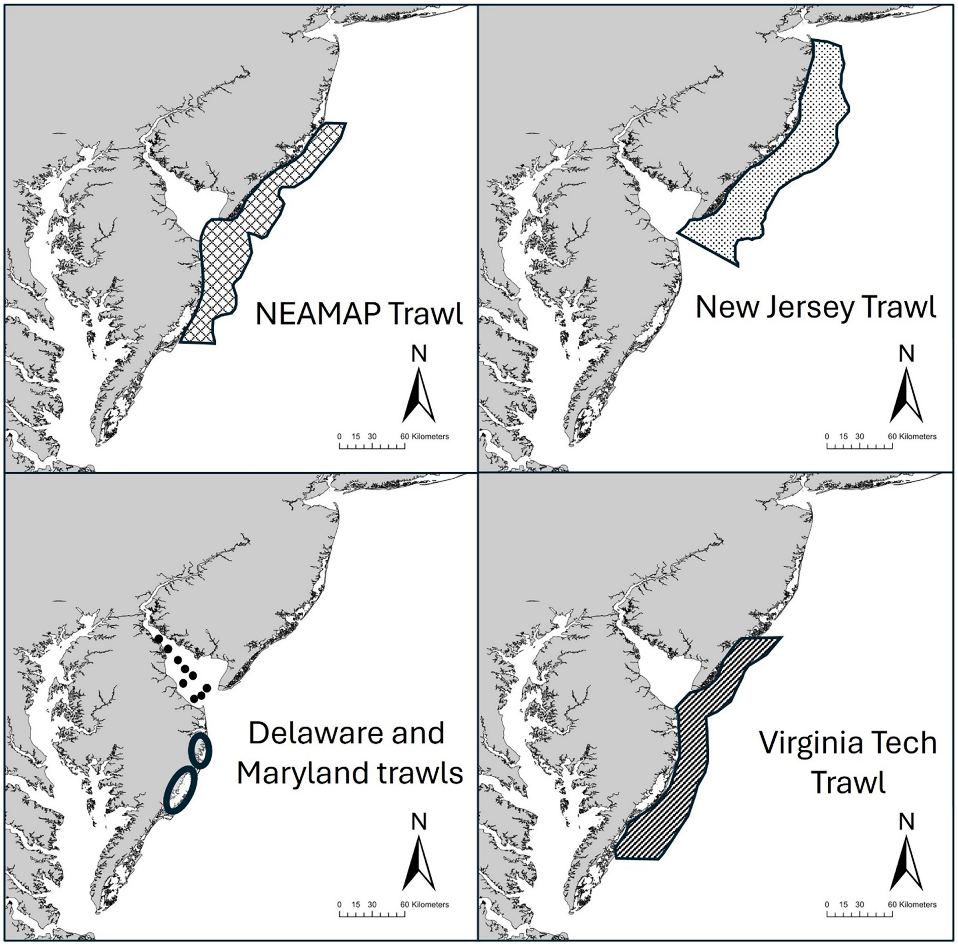

Figure 1. Spatial coverage of the respective trawl surveys used to assess horseshoe crab relative abundance in the Delaware Bay region. The Northeast Area Monitoring and Assessment Program (NEAMAP), New Jersey, and Virginia Tech trawls are conducted along the coast, whereas the Maryland Trawl is conducted in coastal embayments (circles on the map) and the Delaware Trawl is conducted at fixed stations within Delaware Bay (points on the map). Base map courtesy of the National Oceanic and Atmospheric Administration, the National Ocean Service, Office of Coast Survey, and the Strategic Environmental Assessments Division of the Office of Ocean Resources Conservation and Assessment.

crabs in the fall. Annual mean catch per tow was estimated by applying a generalized linear model to catch data. The model included year and site and had a negative binomial error structure (ASMFC, 2022a).

Horseshoe crabs in the surveyed areas are genetically similar and linked by migration (Hallerman et al., 2022; King et al., 2015), and therefore, we assumed that the respective surveys were indexing a single overall population. Commonalities in trends in abundance from the seven trawl surveys were first examined through visual comparison of plots of annual indices of abundance from each survey. A Spearman rank correlation analysis was then conducted to further examine how closely high and low abundance years tracked across the respective surveys.

The seven time series of horseshoe crab relative abundance were then analyzed using a Bayesian hierarchical model as described by Conn (2010) to develop a single time series of relative abundance. Conn (2010)'s hierarchical model assumed the typical relationship between relative and absolute abundance: $U_{it} = q_{it} N_t + \varepsilon_{it}$, where U_{it} is the relative abundance index of survey *i* in year *t*, *q* is catchability, *N* is the absolute abundance, and ε is a random error term, with relative and absolute abundance expressed on the log scale. Inferences based on measures of relative abundance are concerned with proportional changes in abundance through time, and multiple indices of relative abundance support estimation of appropriate error and scaling terms for each index. Thus, $\log(U_{it}) \sim \text{Normal}(\log[\mu_t] + \log[q'_{it}], [\sigma^p_{it}]^2 + [\sigma^s_{it}]^2)$, where μ_t is a scaled abundance reflective of changes in abundance at the population scale; σ^p_{it} and σ^s_{it} are the standard deviations associated with process and sampling errors, respectively; and q'_{it} is a scaling factor for index *i* in year *t*. The sampling error is a function of the estimated coefficient of variation (CV) of index *i* on the absolute scale $\sigma^s_{it} = \sqrt{\log([\text{CV}\{U_{it}\}]^2 + 1)}$. The process error is the remaining error attributable to variation in catchability or spatial distributions of individuals caught. The model was fit to all time series of relative abundance by performing a Bayesian analysis with WinBUGS (Lunn et al., 2000) accessed by the R2WinBUGS package (Sturtz et al., 2005). Prior distributions for $\log(\mu_t)$, $\log(q'_i)$, and σ^p_i were set to those used by Conn (2010) as Normal(log[100], 1), Normal(log[0.01], 0.5), and Uniform(0, 5), respectively. Markov chain–Monte Carlo simulations progressed with four chains of 60,000 samples, of which the first 10,000 were discarded as burn-in. The thinning rate was 1.0 or no thinning, as the literature indicates it can reduce precision and may be unnecessary (Link & Eaton, 2012).

Assuming that the horseshoe crab abundance in 1990 is a suitable reference point for assessing the recovery of horseshoe crabs (Niles et al., 2009), we estimated the probability that abundance in 2023 exceeded that in 1990. This probability was equal to the proportion of total Markov chain–Monte Carlo iterations ($n = 200{,}000$) in which 2023 estimated abundance was greater than that in 1990.

We conducted a sensitivity analysis to determine the influence of each survey on the final combined index of relative abundance. This analysis was done by dropping one of the seven surveys and refitting the model to the remaining surveys. For each one of the sensitivity model runs, we recalculated the probability that the predicted abundance in 2023 was greater than that in 1990. We also conducted a sensitivity run in which both VT and NEAMAP trawl surveys were dropped because these two surveys did not extend back in time to 1990. Finally, a sensitivity run was conducted in which 2022 was considered the terminal year (dropping 2023 data) because of a very large increase in the catches in the VT trawl survey in 2023. This large increase was due to some tows in 2023 that captured an extraordinarily large number of crabs that when incorporated into the estimation of a stratified mean for 2023 resulted in a large increase in mean catch per tow (and a much larger than usual coefficient of variation for that year).

RESULTS

Relative abundances of horseshoe crabs in the seven fisheries-independent surveys were quite variable over time (Figure 2). However, several surveys, particularly the spring DE trawl and the NJ trawl surveys, showed their lowest relative abundance index values during the 2005–2010 period, with a general increasing trend thereafter. The MD trawl showed relatively large fluctuations over its time series without a consistent trend. The VT trawl survey had a shorter time series than the DE, NJ, and MD trawl surveys and showed some large yearly variation, but four out of its five highest abundance indices occurred in the most recent 4 years (2020–2023).

Visual observations of the commonalities in trends among surveys were supported by the Spearman rank correlation

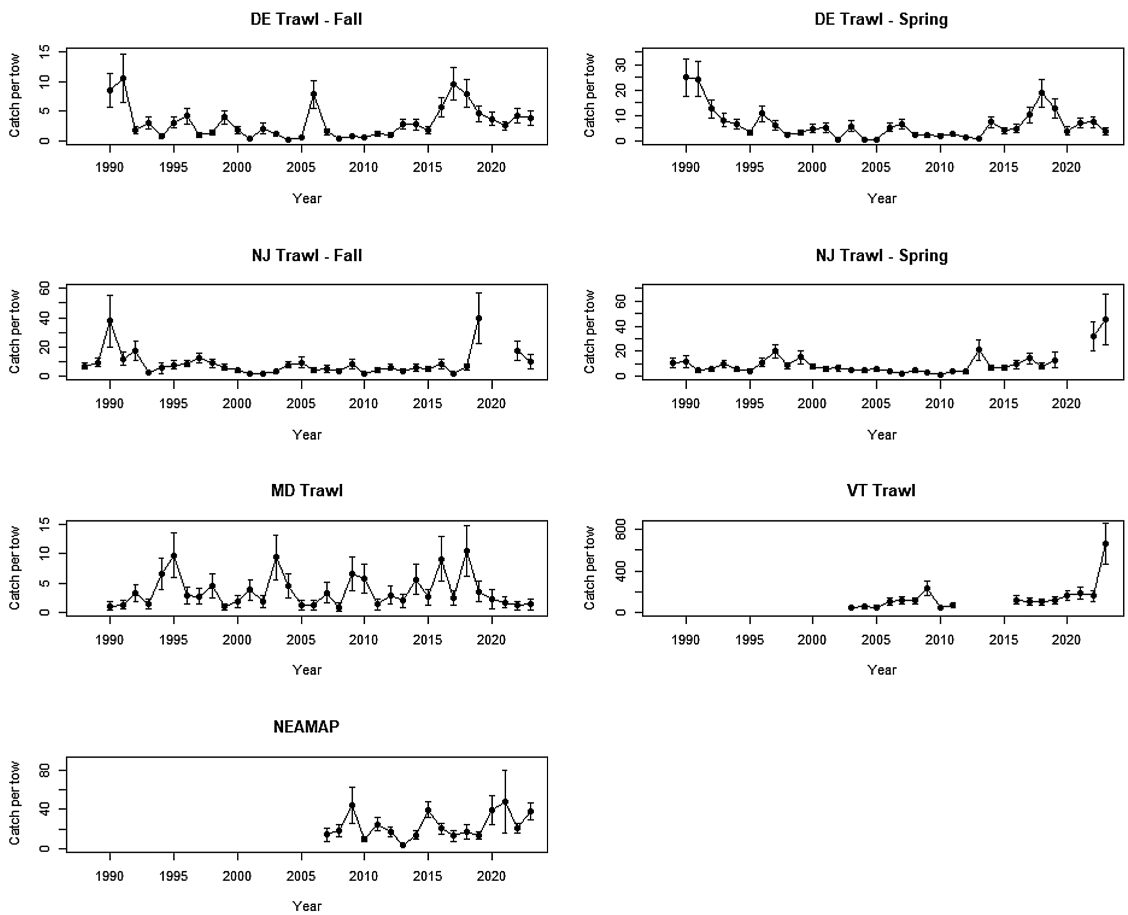

Figure 2. Time series of horseshoe crab relative abundance indices from seven fisheries-independent trawl surveys conducted in the Delaware Bay region. Error bars correspond to standard deviations on relative abundance estimates. Abbreviations are as follows: DE Trawl = Delaware Fish and Wildlife Adult Finfish Trawl Survey, NJ Trawl = New Jersey Ocean Trawl Survey, MD Trawl = Maryland Coastal Bays Trawl, VT Trawl = Virginia Polytechnic Institute and State University Trawl Survey, and NEAMAP = Northeast Area Monitoring and Assessment Program.

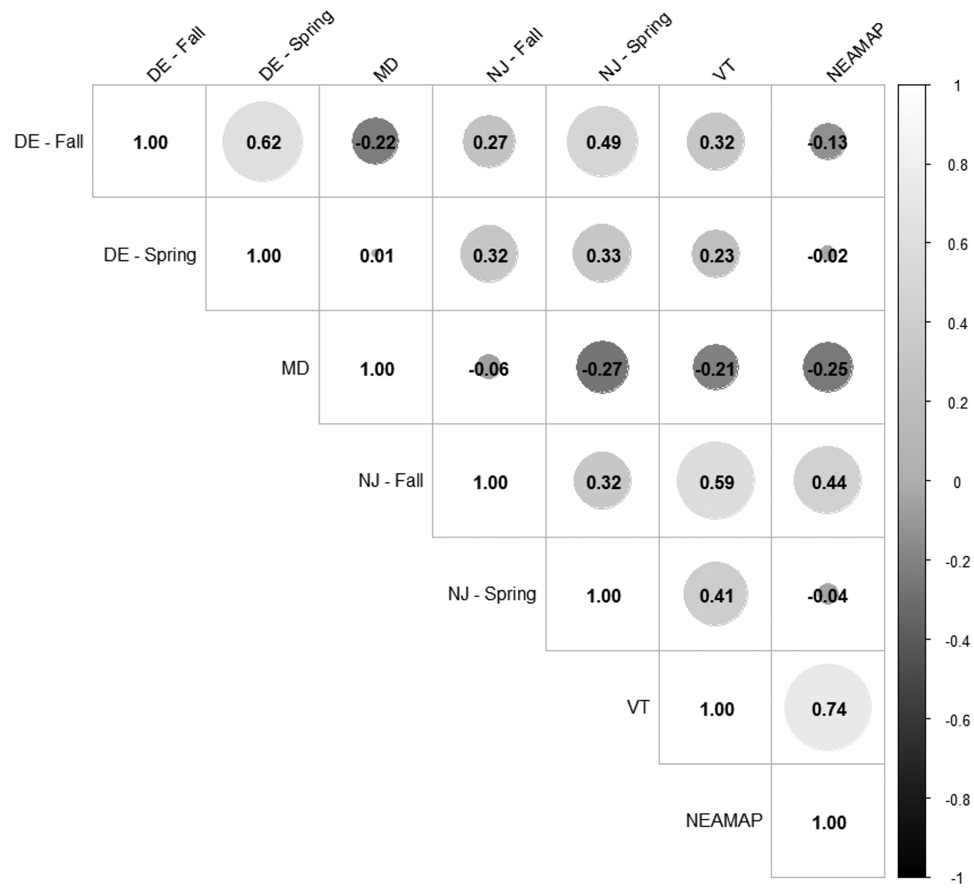

Figure 3. Spearman rank correlation coefficients among the time series of annual relative abundance estimates from trawl surveys of horseshoe crabs in the Delaware Bay region. Abbreviations are as follows: DE = Delaware Fish and Wildlife Adult Finfish Trawl Survey, NJ = New Jersey Ocean Trawl Survey, MD = Maryland Coastal Bays Trawl, VT = Virginia Polytechnic Institute and State University Trawl Survey, and NEAMAP = Northeast Area Monitoring and Assessment Program.

analysis (Figure 3). In most cases, correlation coefficients were positive, with the strongest correlations occurring when paired with the VT trawl survey (correlation coefficients ranging from 0.23 to 0.74). An exception was the MD trawl survey, which showed low or negative correlation coefficients with the other surveys (correlation coefficients ranging from −0.27 to 0.01), likely because of an absence of temporal trends in the coastal bays of Maryland.

The combined relative abundance index from the hierarchical model supported general observations of trend across individual surveys (Figure 4) with adequate model convergence as indicated by the potential scale reduction ($\hat{R} = 1.0$) . There was a decrease in abundance from the beginning of the time series in the early 1990s, followed by a relatively stable, but low, abundance between 2000 and 2010. After 2010, there was a consistent increase in abundance through the terminal year of 2023. The 95% confidence intervals on the combined index were larger for the start and end of the time series compared with the middle years. The abundance index in 2023 approached the level in 1990 and possibly exceeded that level with a 0.38 probability.

The hierarchical model also gave estimates of the process error variance associated with each of the surveys (Figure 5). The VT trawl survey had the lowest standard deviation of process error among the seven surveys, whereas the DE trawl and MD trawl had the highest. The NJ trawl and NEAMAP had intermediate standard deviations of process error. These results suggest that the VT trawl survey best represents the abundance trends of horseshoe crabs relative to the other surveys.

Sensitivity analysis showed that the combined abundance index was generally robust to the inclusion/exclusion of each time series (Figure 6). In all cases, the general pattern of a decreasing abundance through the 1990s to early 2000s and then an increase after 2010 remained. However, the degree of increase by the terminal year in 2023 was somewhat dependent upon which survey was excluded from the model. The greatest increase by the terminal year occurred with the exclusion of the fall NJ trawl survey, resulting in a probability of exceeding the 1990 abundance of 0.65. At the other extreme, the lowest increase by the terminal year occurred with the exclusion of the spring NJ trawl survey, resulting in a 0.22 probability of exceeding the 1990 abundance. Excluding surveys that did not extend back to the 1990 reference point (VT and NEAMAP trawls) resulted in a probability of exceeding the 1990 level of abundance of 0.28 and, excluding all survey data from 2023, also resulted in a probability of 2022 abundance exceeding 1990 abundance of 0.28.

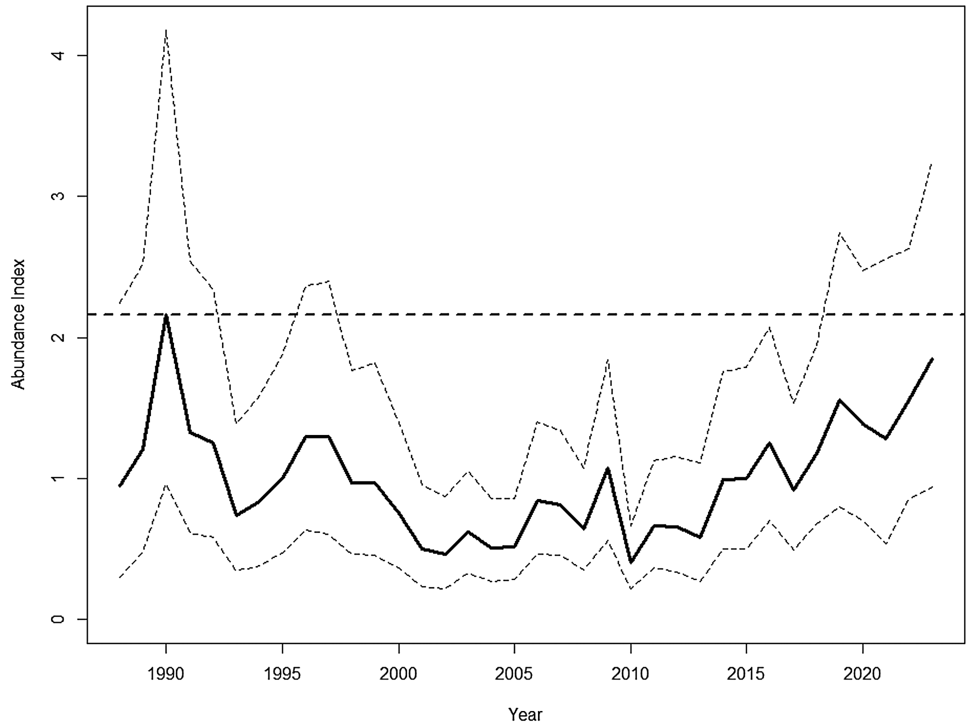

Figure 4. Time series of horseshoe crab relative abundance in the Delaware Bay region as estimated by the hierarchical model (Conn, 2010). The solid line gives the posterior mean, and the dotted lines represent the 95% credible intervals. The dashed horizontal line represents the 1990 relative abundance for comparison with the rest of the time series. The probability of the relative abundance in the terminal year (2023) being greater than that in 1990 was 0.38.

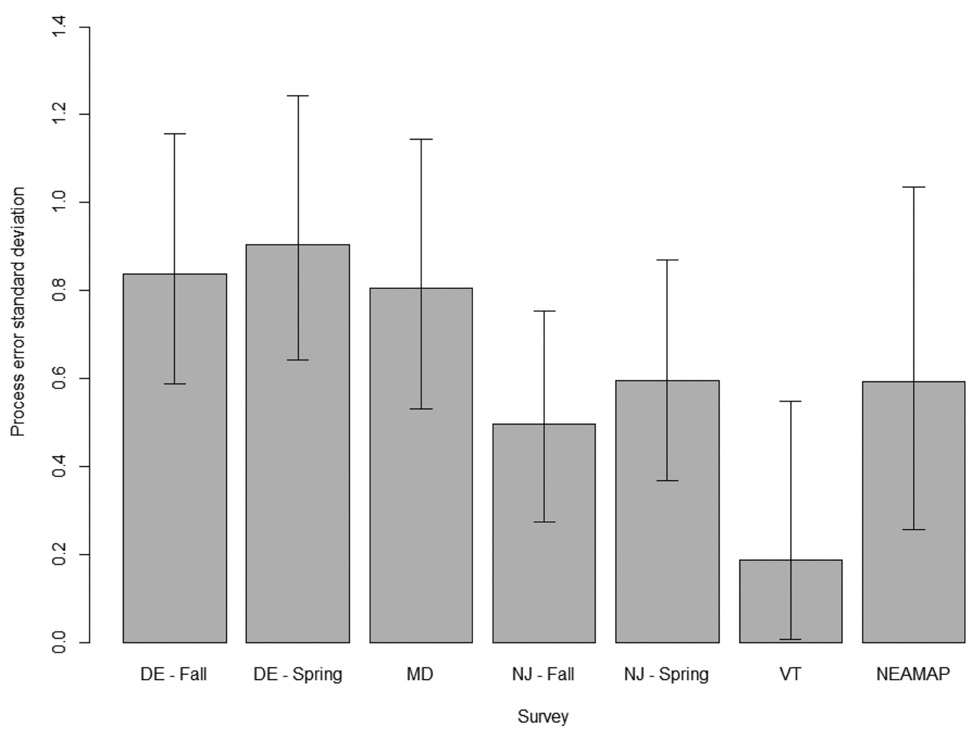

Figure 5. Posterior means and 95% credible intervals for the standard deviation of the process error (σ^p) for the seven trawl surveys used to estimate horseshoe crab relative abundance in the Delaware Bay region. Abbreviations are as follows: DE = Delaware Fish and Wildlife Adult Finfish Trawl Survey, NJ = New Jersey Ocean Trawl Survey, MD = Maryland Coastal Bays Trawl, VT = Virginia Polytechnic Institute and State University Trawl Survey, and NEAMAP = Northeast Area Monitoring and Assessment Program.

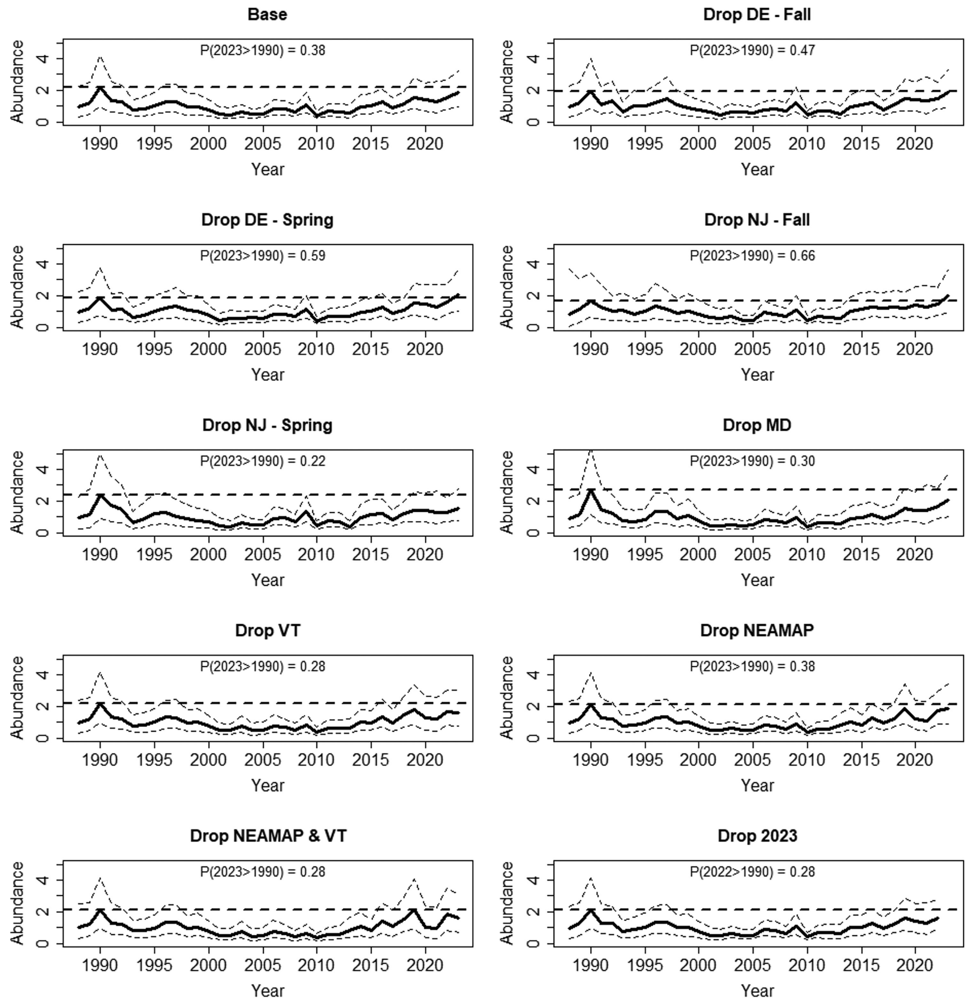

Figure 6. Results of the sensitivity analyses on the predicted relative abundance index from the hierarchical model for horseshoe crabs in the Delaware Bay region. The "Base" graph depicts the model including all seven trawl surveys. The solid line gives the posterior mean, and the dotted lines represent the 95% credible intervals. The horizontal dashed line indicates the 1990 level of relative abundance for comparison through the time series, and the $P(2023 > 1990)$ gives the probability of the relative abundance in the terminal year (2023 or 2022 in the case where 2023 data were dropped) being greater than that in 1990. Abbreviations are as follows: DE = Delaware Fish and Wildlife Adult Finfish Trawl Survey, NJ = New Jersey Ocean Trawl Survey, MD = Maryland Coastal Bays Trawl, VT = Virginia Polytechnic Institute and State University Trawl Survey, and NEAMAP = Northeast Area Monitoring and Assessment Program.

DISCUSSION

There is mounting evidence from multiple data sources that the horseshoe crab population has increased in the Delaware Bay region since approximately 2010. Anstead et al. (2023) used a catch-multiple-survey analysis model to estimate the population size of horseshoe crabs from 2003 to 2021, and the ASMFC (2024) continued to estimate the population through 2022 using this same model. Population sizes of males and females were stable from 2003 to 2012, with approximately 5 million adult females and 10 million adult males. The population of each sex began increasing after 2012, and by 2022, there were an estimated 16 million females and 40 million males (ASMFC, 2024).

It is difficult to compare absolute abundance estimates from Anstead et al. (2023) and the ASMFC (2024) in contemporary times to those in the early 1990s, when the population was believed to have started a decline due to use as bait in commercial fisheries. Before 1998, when active management for horseshoe crabs began, trawl surveys did not differentiate sexes of horseshoe crabs in their catches, and there is no means by which to estimate sex-specific population sizes around the beginning of the time series examined here. However, if we assume that relative abundance indices from the trawl surveys and our resulting index of abundance are proportional to population size, we get a sense of how the population has fluctuated through time and how it has responded to commercial fishery management changes.

Harvest of horseshoe crabs for the bait industry was largely unregulated prior to the adoption of the 1998 fisheries management plan by the ASMFC (1998). Although the fisheries management plan and subsequent addenda reduced allowable quotas in the Delaware Bay region during the 2000s, the population showed a delayed response to these regulatory changes. Horseshoe crabs have a relatively long life history, taking 9–10 years to reach sexual maturity (Shuster, 1950; Smith et al., 2009; Sweka et al., 2007). Given this long time to maturity, a consistent increase in abundance was not expected until approximately 2010, about a decade following the initiation of harvest regulations (Sweka et al., 2007). In a theoretical age-structured simulation model for horseshoe crabs, Sweka et al. (2007) predicted it would take at least 10 years to see a population response to reductions in horseshoe crab harvest, and empirical data now support that prediction.

The Delaware Bay horseshoe crab abundance index, as predicted by our combined index of relative abundance, suggests that the population has responded positively to harvest management and is nearing levels observed in 1990, with a modest probability (0.38) of exceeding it. Credible intervals on the 1990 and 2023 relative abundance indices appeared large relative to their posterior means with a high degree of overlap (Figure 4). To put the probability of abundance in 2023 exceeding that in 1990 into context, if posterior means from 1990 and 2023 were equal and credible intervals were equivalent, we would have expected the probability of 2023 exceeding 1990 to be near 0.50. Thus, direct comparison of 2023 and 1990 model predictions suggests that although there is a nonnegligible chance that abundance now exceeds the 1990 reference period, abundance in 2023 may still be somewhat less than in 1990.

The combined relative abundance index was not overly influenced by any single trawl time series of relative abundance. The leave-one-out sensitivity analysis did not show any large deviation from predictions from the base model that included all trawl survey time series. In all cases, the predicted abundance index declined through the early 2000s, remained low until 2010, and thereafter increased. The greatest deviation occurred when the NJ trawl from the spring was dropped from the overall model. The spring NJ trawl had the two highest abundance indices over its entire time series in the final 2 years (2022 and 2023). These two final high data points had some influence on the combined index. However, when this survey was dropped during the sensitivity analysis, the general pattern of a decrease followed by stability and subsequent increase remained but the probability of exceeding the 1990 level of abundance decreased to 0.22.

The results of this analysis support the effectiveness of management decisions related to horseshoe crabs in the Delaware Bay region. The consensus among the abundance index time series indicates that the horseshoe crab population in the region has increased, as expected, in response to restrictive harvest management. Abundance in 2023 neared that in 1990, which Niles et al. (2009) suggested as a benchmark needed to produce the density of eggs necessary for adequate red knot stopover foraging habitat along the shores of Delaware Bay. With increasing abundance and a likely increase towards 1990 levels, we would expect egg resources for shorebird foraging to also increase. Smith et al. (2022) showed a recent increasing trend in egg densities along Delaware Bay beaches. However, those densities were still well below egg densities estimated in the early 1990s (Botton et al., 1994). These contradictory findings are likely an artifact of differences in egg sampling methodologies between the studies of Botton et al. (1994) and Smith et al. (2022) (ASMFC, 2022a) and substantial habitat loss at New Jersey beaches (Botton et al., 2022). Also, the stopover population of red knots in Delaware Bay has been stable but has not shown signs of increase during the period when horseshoe crabs have increased (Lyons, 2023). In the Delaware Bay region, fisheries managers have some control over horseshoe crab population levels through harvest management. However, they have much more limited control over the response of other species to the population size of horseshoe crabs. The lack of a concurrent increase in red knot abundance despite the increase in horseshoe crabs suggests either a delayed response by red knots to increasing horseshoe crab abundance or that other factors, such as conditions during migration, breeding, or overwintering, are limiting their population dynamics (McGowan et al., 2015). Continued population monitoring and regulation of harvest could ensure that use of the horseshoe crabs as bait does not once again result in declining abundance in the region. However, the long-term threat to high horseshoe crab abundance in Delaware Bay may be loss of quality spawning habitat (Botton et al., 2022; Smith et al., 2025).

DATA AVAILABILITY

Data supporting this study's findings are available from the authors representing their respective agencies upon reasonable request. The R scripts used in this analysis are available upon reasonable request to the primary author.

ETHICS STATEMENT

Data used in this analysis were provided by the agencies and institutions represented by the authors, and collection and handling of animals was conducted in accordance with agency and institutional protocols.

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CONFLICTS OF INTEREST

The authors have no conflicts of interest to report related to this analysis.

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