

# Horseshoe Crab Spawning Activity in Delaware Bay, USA, After Harvest Reduction: A Mixed-Model Analysis

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**Abstract** A Delaware Bay, USA, standardized survey of spawning horseshoe crabs, *Limulus polyphemus*, was carried out in 1999–2013 through a citizen science network. Previous trend analyses of the data were at the state (DE or NJ) or bay-wide levels. Here, an alternative mixed-model regression analysis was used to estimate trends in female and male spawning densities at the beach level ( $n=26$ ) with the objective of inferring their causes. For females, there was no overall trend and no single explanation applies to the temporal and spatial patterns in their densities. Individual beaches that initially had higher densities tended to experience a decrease, while beaches that initially had lower densities tended to experience an increase. As a result, densities of spawning females at the end of the study period were relatively similar among beaches, suggesting a redistribution of females among the beaches over the study period. For males, there was a positive overall trend in spawning abundance from 1999 to 2013, and this increase occurred broadly among beaches. Moreover, the beaches with below-average initial male density tended to have the greatest increases. Possible explanations for these patterns include harvest reduction, sampling artifact, habitat change, density-dependent habitat selection, or mate selection. The broad and significant increase in male spawning density, which occurred after enactment of harvest controls, is consistent with

the harvest reduction explanation, but there is no single explanation for the temporal or spatial pattern in female densities. These results highlight the continued value of a citizen-science-based spawning survey in understanding horseshoe crab ecology and conservation.

**Keywords** Horseshoe crabs · *Limulus polyphemus* · Citizen science · Trend analysis · Hierarchical model

## Introduction

The American horseshoe crab (*Limulus polyphemus*) spawns at higher densities in Delaware Bay, USA, than anywhere else throughout its range, which extends from Maine to the Yucatan, and higher than any other horseshoe crab species throughout the world (Anderson and Shuster 2003). Much has been written about the reproductive biology of the horseshoe crab, the phenomenal spawning event each spring in Delaware Bay, and the ecological relationships central to horseshoe crab spawning in Delaware Bay (Shuster and Botton 1985; Myers 1986; Berkson and Shuster 1999; Shuster et al. 2003; Tanacredi et al. 2009). In summary, horseshoe crabs spawn on high tides mainly in May and June at Delaware Bay latitudes (Fig. 1). Females bury their externally fertilized eggs in nests within the beach substrate. Subsequent spawning can disturb nests releasing previously buried eggs to the beach surface. The high spawning densities in Delaware Bay result in large quantities of eggs being available for consumption by other species, most notably shorebirds migrating through the bay during their northward spring migration (Myers 1986). High harvests of horseshoe crabs during the 1990s were followed by declines in spawning density and shorebird populations leading to coast-wide restrictions in harvest, a no-harvest sanctuary in federal waters off the mouth of

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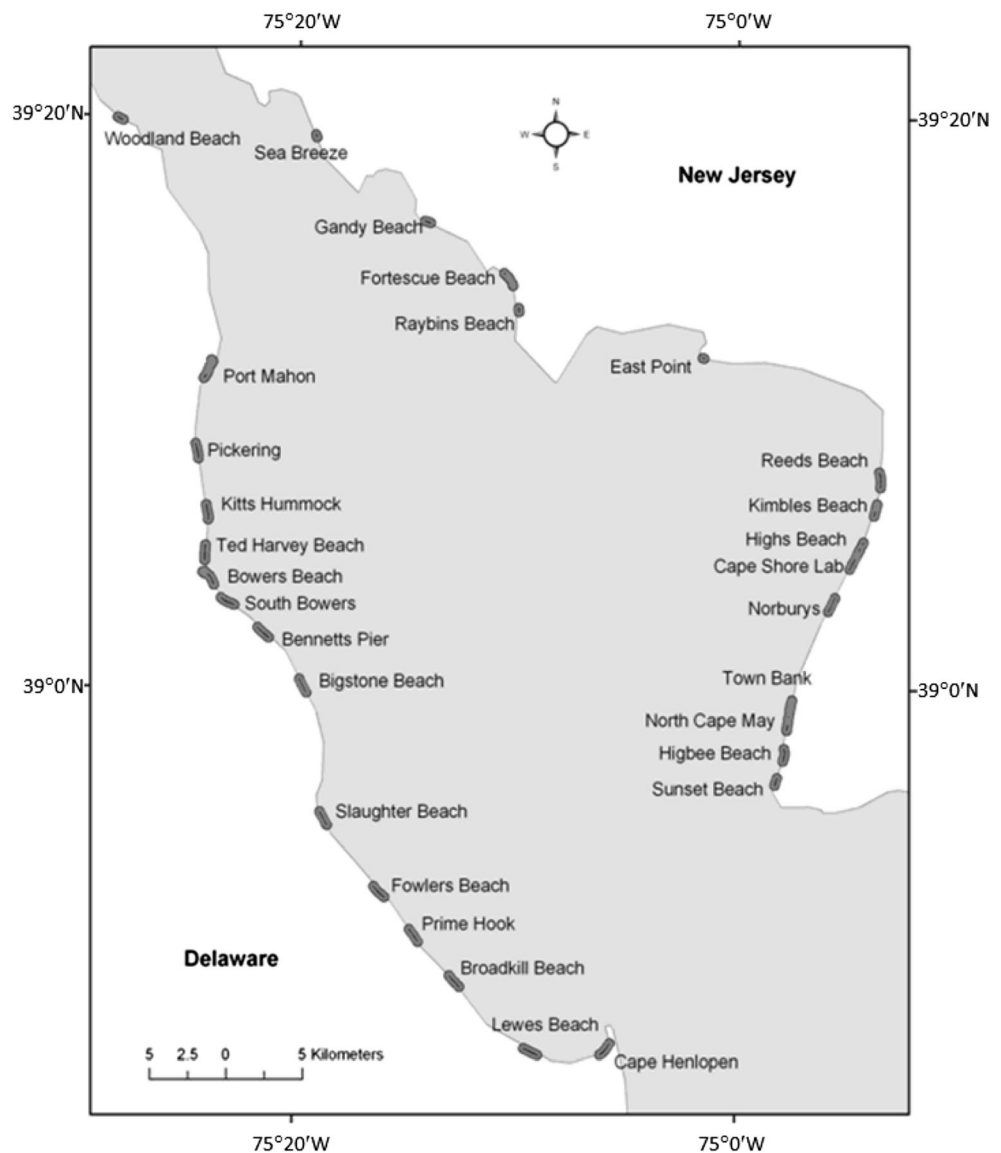
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**Fig. 1** Map of beaches sampled at least once during 1999–2013 in the Delaware Bay spawning survey



the bay, and a moratorium on harvesting female horseshoe crabs in Delaware Bay (Smith et al. 2009). Monitoring horseshoe crab spawning activity helps in understanding the potential effect of those harvest restrictions (Niles et al. 2009).

The Delaware Bay spawning survey has been conducted in a standardized manner since 1999 following a statistical design implemented through a citizen science network (Smith et al. 2002b; Smith and Michels 2006; Zimmerman et al. 2013). Horseshoe crabs spawn on Delaware Bay beaches particularly around the new and full moons when tides are highest (Shuster and Botton 1985; Barlow et al. 1986; Brockmann 1990; Smith et al. 2002b). The survey was designed to take advantage of the spawning crabs' accessibility to be counted. Trends in spawning activity have been evaluated at the state or bay-wide levels by first estimating beach-level density for the whole season, then

combining beach-level estimates to estimate state-level density, and finally combining state-level estimates to estimate bay-wide density (Smith et al. 2002b; Zimmerman et al. 2013). Although the previous trend analysis and estimation procedures are valid and appropriate, additional information might be revealed by examining trend at the beach level and then evaluating variation in beach-specific trends to make inferences at the state or bay-wide levels (Pinheiro and Bates 2000). This alternative analysis would maintain the hierarchical nature of the sampling design but would have the additional advantage of accounting for the repeated measures due to sampling mostly the same beaches each year.

The objectives of the present study were to (1) fit mixed-model regressions to the Delaware Bay spawning survey data after 1999 when harvest was reduced, (2)

assess trends over that period at beach and bay-wide levels, and (3) assess whether trends differed among females and males. Citizen science monitoring can play an important role in describing ecological patterns and generating explanatory hypotheses, which feed into traditional approaches to ecological research and hypothesis testing (Dickinson et al. 2010). We examine patterns in the Delaware Bay spawning survey data and discuss possible explanations for the observed patterns.

## Methods

The yearly survey has been conducted on 12 nighttime high tides during the four spring tides in May and June following the statistical design of Smith et al. (2002b). Volunteers count spawning horseshoe crabs on three nights over the 5-day period centered on the spring tides (i.e., 2 days before, the day of, and 2 days after each of the new and full moons). Because spawning counts have been observed to be consistently higher on nighttime high tides than on daytime high tides and relative change in spawning activity has been observed to be consistent among diurnal tides, only nighttime tides were surveyed in Delaware Bay (Widener and Barlow 1999; Smith et al. 2002b, 2010). Horseshoe crabs spawning at the high tide line are counted within 100 systematically placed 1-m<sup>2</sup> quadrats. The sampling design stratifies sampling effort to ensure coverage of the whole bay (east and western shore as well as upper, middle, and lower bay; Fig. 1) and the whole spawning season (spring tide periods in May and June). Sampled beaches must be safely accessible to the volunteers who conduct the counts often late at night.

Densities spawning horseshoe crabs at the high tide line were estimated for 26 beaches (13 in DE, USA, and 13 in NJ, USA) over 15 years, 1999–2013 (Appendix 1). Densities were averaged over all nights surveyed in May and June each year. Most beaches were sampled in most years, but four beaches (Lewes, East Point, Raybins, and Sunset) were excluded because each was sampled in five or fewer years.

Four linear-mixed models were fit, and in all models, individual beaches were a random effect; time, measured in years, was a fixed effect. The mixed-model analysis allowed for estimation of beach-level, state-level, or bay-wide trends. We assessed multiple candidate models with differing effects on intercept and slope parameters. In model 1, a random intercept was included, which allowed intercepts to be estimated separately for each beach; the slope (trend) was specified to be common to all beaches. In model 2, random intercepts and random slopes were included, which allowed separate intercepts and slopes to be estimated for each beach. Model 3 extended model 2 to include State (DE or

NJ) as a fixed effect adjustment to the intercepts. Model 4 extended model 3 to include State as a fixed effect adjustment to both the intercepts and slopes. The Akaike information criteria (AIC), which measures model parsimony by adjusting maximized likelihood to account for model complexity, was used for model selection (Burnham and Anderson 2002). The model with the smallest AIC was deemed to have the most parsimonious fit and thus to be the most useful for inferential purposes. The analysis was conducted in R version 3.0.2 using the `lme` function in the `nlme` package (Pinheiro and Bates 2000).

Distribution assumptions and influence of outliers were examined (Appendix 2). A square-root transformation effectively met distributional assumptions and reduced the influence of outliers (Pinheiro and Bates 2000). A Poisson mixed model was considered, but the densities analyzed are averages and are thus inappropriate for a Poisson distribution (McCullagh and Nelder 1989).

## Results

The model with beach-level intercepts and slopes (model 2) had the best fit based on AIC for both females and males (Table 1) and that model was the basis for further inference. The best fit of model 2 indicates the existence of significant variation in trends among beaches. However, the beach-level variation in trends could not be explained by the fact that some beaches are on the west side or east side of the bay (i.e., the variation was not associated with the state-level factors included in models 3 and 4).

For females, the estimated trend (i.e., overall slope estimate or the fixed effect for time in years) was 0.002 (SE=0.003,  $t=0.66$ , 318 *df*,  $P=0.51$ ). Beach-level trends (Fig. 2) were split evenly between positive and negative slopes. The beach-level intercepts and slopes were negatively correlated ( $r=-0.58$ , 95 % CI [-0.83, -0.03]; Fig. 3). The negative correlation between intercepts and slopes, the count and direction of trends among initially high and low density beaches, and the insignificant overall trend indicate that beaches with higher densities early in the time series tended to experience a decrease, whereas beaches with lower densities early in the time series tended to experience an increase. Of the seven beaches in the upper quartile of initial density (initial densities were those recorded in 1999, the first year of the study), six had negative trends and one had a positive trend. In contrast, of the seven beaches in the lower quartile of initial density, two had negative trends and five had positive trends (Fisher's exact one-tailed test:  $P=0.051$ ).

**Table 1** Model selection statistics for the four mixed model fit to beach-level estimates of spawning density in Delaware Bay 1999–2013

Model	Parameters	Females		Males	
		AIC	Log likelihood	AIC	Log likelihood
1	Separate intercept estimated for each beach but slope common to all beaches	-125.17	66.58	424.69	-208.35
2	Separate intercepts and slopes estimated for each beach	-135.18	73.59	413.59	-200.79
3	Separate intercepts and slopes estimated for each beach and State included as a fixed-effect adjustment to the intercepts	-120.19	66.09	426.77	-207.38
4	Separate intercepts and slopes estimated for each beach and State included as a fixed-effect adjustment to the intercepts and slopes	-117.32	68.66	434.37	-209.18

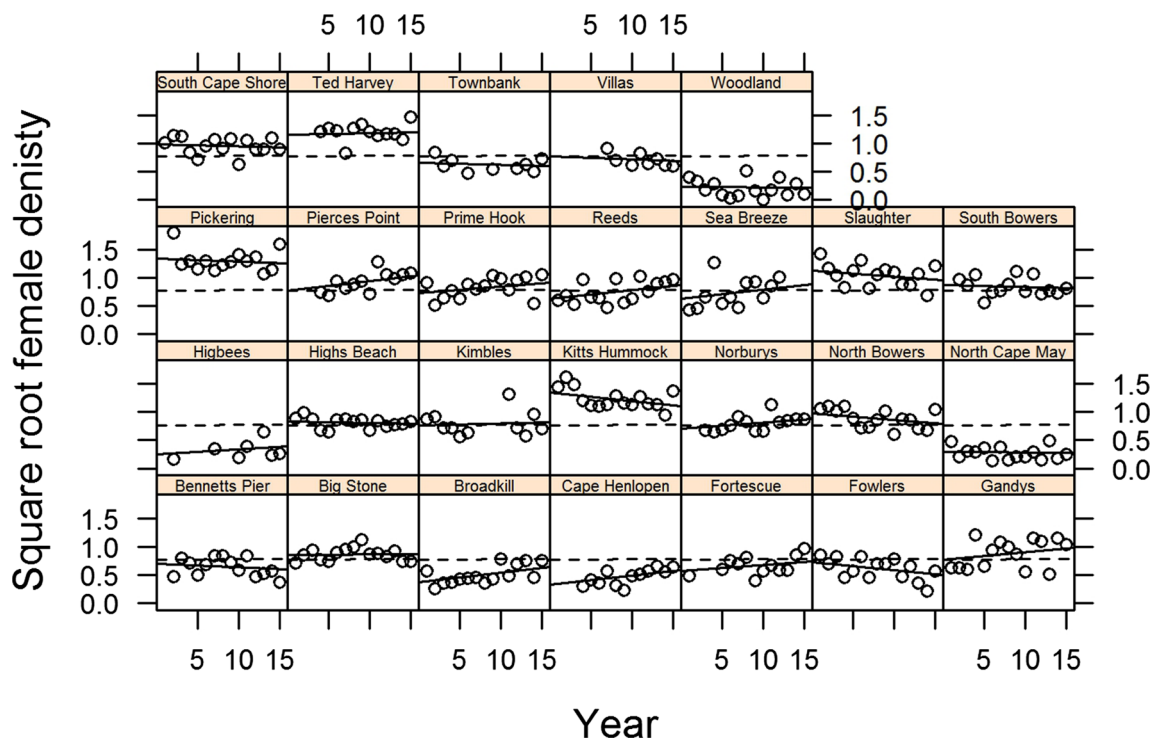
For males, the estimated trend (i.e., overall slope estimate or the fixed effect for time in years) was 0.02 (SE=0.008,  $t=2.52$ , 317 *df*,  $P=0.01$ ). Beach-level trends are plotted in Fig. 4; most of the beach-level trends were positive (18 out of 26). The beach-level intercepts and slopes were negatively correlated ( $r=-0.44$ ; Fig. 5). The highest increases in density were observed in beaches with below-average initial densities, modest declines in density were observed only in beaches with at or above average initial densities, and increases in densities were observed broadly among beaches (Fig. 4).

Predicted trends in male and female densities were positively related ( $t=10.1$ , 24 *df*,  $P<0.001$ ; Fig. 6). Beaches ( $n=13$ ) with positive slopes for females also had positive slopes for males. Beaches ( $n=8$ ) with negative slopes for males also had negative slopes for females. A few beaches ( $n=5$ ) had

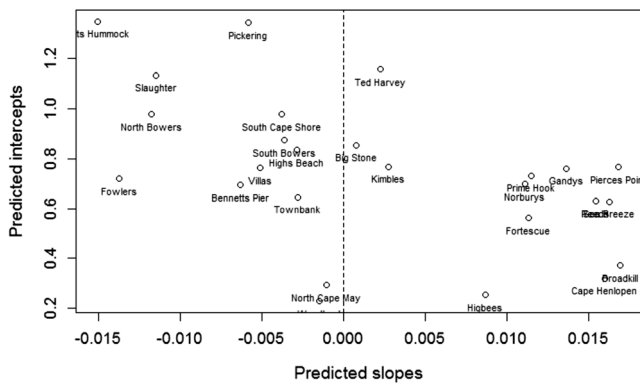
positive slopes for males but negative slopes for females. No beaches had positive slopes for females but negative slopes for males.

## Discussion

This mixed-model analysis adds new information regarding beach-level variation to previous trend analyses (Zimmerman et al. 2013). Here, we present long-term patterns in horseshoe crab spawning in Delaware Bay that include variation in trends among beaches. In contrast, previous trend analyses exemplified by Zimmerman et al. (2013) and following Smith et al.



**Fig. 2** Fit of model 2 to beach-level female densities (square-root transformed). Mixed model fit shown in *solid lines*. Pooled regression fit is shown as *dashed lines*



**Fig. 3** Predicted intercepts and slopes from mixed-model regression of female spawning density in Delaware Bay over the period of 1999–2013

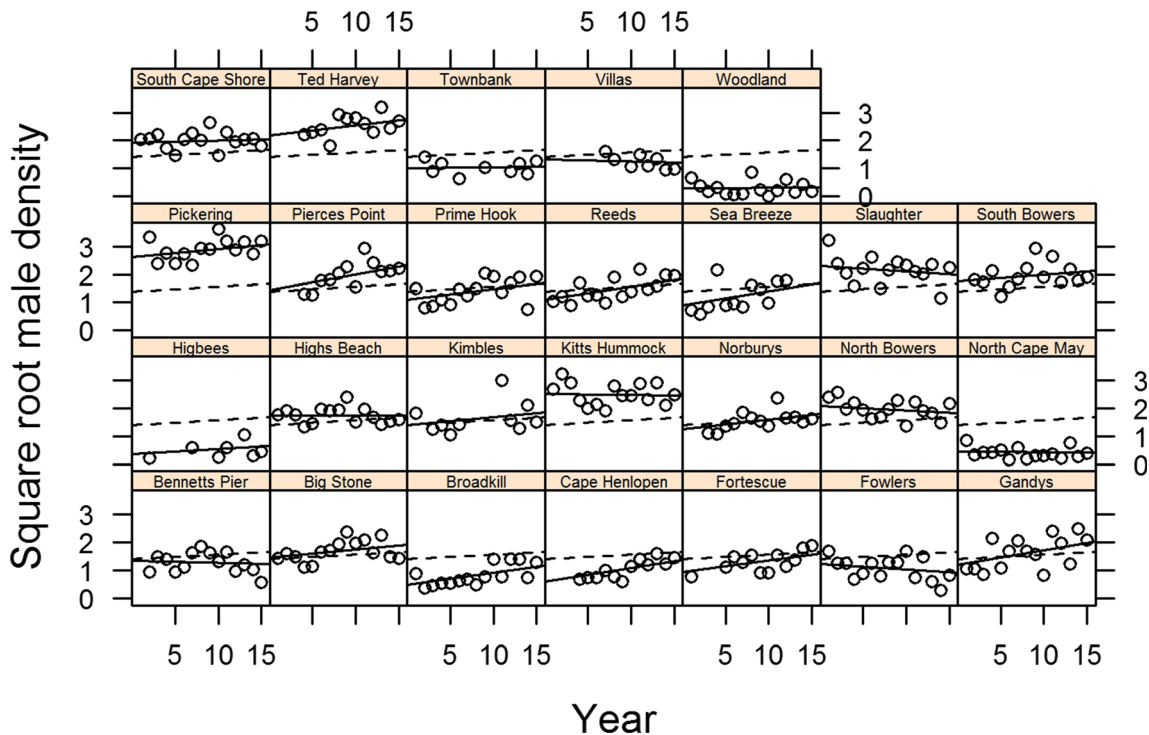
(2002b) presented only state and bay-wide trends. As we show, the beach-level information is important in understanding how changes in spatial distribution have contributed to overall trends.

The mixed-model analysis indicates that while female density did not change overall, females redistributed among beaches causing spawning to be more evenly distributed. Specifically, beaches with initially high density of females tended to experience decreases and beaches with initially low density tended to experience increases. At the same time, overall male density

increased significantly during 1999 to 2013 in Delaware Bay. Whereas density of males increased broadly among beaches, the highest rates of increase in male spawning activity were observed at beaches with initially low density. Beach-level trends for females and males were positively correlated. However, for the five beaches where direction of trend differed between males and females, the slopes were negative for females and positive for males.

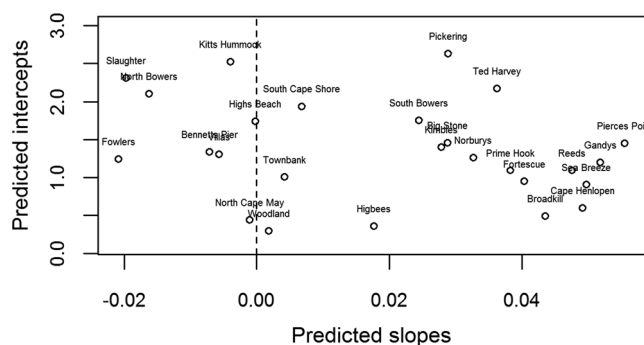
There are a number of possible explanations for these patterns involving harvest reduction, sampling artifact, habitat change, density-dependent habitat selection, or mate selection. The list of possible explanations is not exhaustive, but it represents those explanations that we deem plausible given current knowledge. Although the explanations are post hoc, they can serve as hypotheses for future tests and comparative analyses (Dickinson et al. 2010).

Harvest reduction is the most obvious possible explanation for recent trends in spawning activity. Coast-wide harvest reduction, which began in 2000 and continued with enactment of a series of restrictive quotas including establishment of a marine reserve (Smith et al. 2009), could explain some of the observed patterns. Prior to 2000, harvest was biased toward take of females. Since 2000, harvest shifted toward the take of males, and since 2005, harvest of females in Delaware



**Fig. 4** Fit of model 2 to beach-level male densities (square-root transformed). Mixed model fit shown in *solid lines*. Pooled regression fit is shown as *dashed lines*

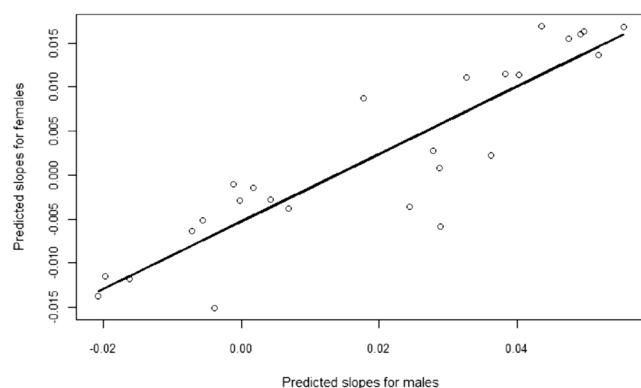




**Fig. 5** Predicted intercepts and slopes from mixed-model regression of male spawning density in Delaware Bay over the period of 1999–2013

Bay states has been banned. The expectation is that spawning activity of males and females would increase after harvest was reduced, which is consistent with the observed trends in male densities. However, the significant increase observed in male densities was not observed in female densities despite the ban on harvest of females and the male-biased harvest ongoing since 2005.

Aspects of the survey design offer another possible explanation for observed patterns. The spawning survey samples were only 1 m from the high tide line even though the zone over which spawning occurs across the beach can be wider than 1 m (Weber and Carter 2009), which could limit the survey's capacity to detect increases in density, especially in females. During the spawning survey, 1-m<sup>2</sup> quadrats are placed at the high tide line. There is typically low wave energy during spawning; however, spawning beyond 1 m from the high tide is submerged and not safely accessible to volunteers for reliable counting. The maximum count within 1 m of the shoreline for females is much less than for males. Simultaneously nesting females tend not to overlap, and



**Fig. 6** Predicted slopes for female and male spawning densities in Delaware Bay over the period of 1999–2013

given the typical prosomal width of a Delaware Bay female, at most eight to nine can fit within 1 m<sup>2</sup> without overlapping (Smith 2007). Spawning males surround and cover females during fertilization. The 99.9th percentile for individual quadrat counts was 8 for females and 32 for males. Furthermore, the spawning survey is conducted only on high tides within the 5-day period centered on the spring tides in May and June. Substantial spawning also occurs outside of the spring tide periods. Smith et al. (2010) reported that 55 % of spawning activity occurred within the 5-day period centered on the spring tide, which was just slightly higher than the 46 % that would be expected if spawning was uniformly distributed. The assumption is that as population abundance increases, spawning activity will spread across the foreshore (a wider zone over which spawning occurs), along the beach (a greater percent along the beach covered with spawning on a given night), and over time (more tides when spawning occurs). The spawning survey would not pick up increases across the foreshore but should record increases along the beach and, to a limited extent, over time.

Beach habitat characteristics can affect spawning activity (Botton et al. 1988; Penn and Brockmann 1994; Smith et al. 2002a), and spawning activity can affect beach characteristics (Jackson et al. 2005). For example, geochemistry of beach sediments contributes to egg viability (Penn and Brockmann 1994; Jackson et al. 2008), and wave energy affects both beach morphology and beach selection (Smith et al. 2002a, 2011). Further, horseshoe crab spawning can change beach morphology and sediment characteristics especially in the mid to upper foreshore (Jackson et al. 2005). Thus, it is conceivable that heavy spawning can make beaches less suitable over time. The expectation is that beaches with initially high spawning density would see decreased habitat suitability and, in turn, decreased spawning activity. Although this is a reasonable explanation, there currently is no indication that habitat suitability has decreased at beaches with high spawning activity (e.g., Kitts Hummock, Pickering, North Bowers). Periodic beach nourishment would replenish eroded sediment and restore the eroded beach profile.

Density-dependent habitat selection can cause shifts in habitat use (Rosenzweig 1991). Density-dependent egg development has been proposed as a primary control on population growth (Sweka et al. 2007). Density-dependent bioturbation, which is caused when horseshoe crab nests are physically disturbed by subsequent spawning, is the primary mechanism for exhumation of eggs to the beach surface where eggs develop poorly or are consumed by scavengers (Castro and Myers 1993; Jackson et al. 2002). The expectation is that as

population abundance increases, densities on the best beaches would approach a carrying capacity (which could vary with habitat quality) and spawning activity would shift onto other beaches. Following this expected model, spawning densities would reach asymptotes at beaches with most suitable habitat first followed by increasing densities at beaches with less suitable habitat. However, this specific pattern was not observed for either males or females. For males, increases were observed broadly including at previously high-density beaches. For females, the broad pattern was that previously high-density beaches tended to decrease while previously low-density beaches tended to increase.

Mate selection by male horseshoe crabs has been studied and found to involve visual and chemical cues (Schwab and Brockmann 2007; Brockmann and Smith 2009). The study of selection of spawning beaches by horseshoe crabs has focused on habitat characteristics (Botton et al. 1988; Smith et al. 2002a; Avissar 2006) and has not considered sex-specific mechanisms. However, Lucas et al. (1996) modeled and cited evidence for female arrival rate in anurans to be an increasing function of the number of calling males. Horseshoe crab males arrive early along the shoreline at spawning beaches to intercept later-arriving females (Brockmann 1990; Smith et al. 2010). The expectation is that female arrival rate at spawning beaches would follow a density-dependent strategy and as male density increased broadly among beaches, female arrival rate would also increase broadly. The pattern of increased female density at beaches with initially low densities and the positive correlation between trends in females and males corresponds to this expectation, but the observation of declines in female density at initially high-density beaches coupled with broad increases among beaches in male density does not match the expectation. Alternatively, males could be distributing among beaches in response to their search for females. However, under that hypothesis, the overall increase in male density would have been observed in females, which was not the case. Also, the hypothesis that males select beaches based on the presence of females is contrary to observations that males arrive at beaches before females (Brockmann 1990; Smith et al. 2010).

The broad and significant increase in male spawning density, which occurred after enactment of harvest controls, is consistent with the explanation that harvest reduction caused a population increase. While this is a post hoc explanation, harvest reduction is an obvious candidate for explaining the observed pattern in male densities. However, there is currently no single explanation that is consistent with the observed pattern in female densities. Female spawning has become more

evenly distributed, but female spawning density has not increased overall because increased density at some beaches was offset by decreased density at other beaches. A combination of explanations involving harvest reduction, survey design, and habitat and mate selection warrants further study.

The Delaware Bay horseshoe crab spawning survey has served as an example of a well-coordinated citizen science effort involving hundreds of volunteers each year (Smith and Michels 2006). Citizen science and community-based monitoring have been increasing internationally (Conrad and Hilchey 2011; Tulloch et al. 2013). Such programs have the benefit of being cost-effective and contribute to public education and support (Conrad and Hilchey 2011). In many cases, volunteers make it possible to achieve the geographic and temporal coverage needed to describe ecologically meaningful patterns and avoid the blind men and the elephant syndrome (Smith and Michels 2006; Bonney et al. 2009; Tulloch et al. 2013). For example, simultaneous coverage of dozens of beaches throughout Delaware Bay has relied on volunteers (Smith and Michels 2006). Well-designed, longitudinal surveys conducted with the help of volunteers can be an effective investment for measuring management impacts (Tulloch et al. 2013). However, the full potential of any monitoring effort regardless of volunteer involvement depends on use and publication of the data (Bonney et al. 2009; Biber 2013). Descriptions of ecological patterns and subsequently generated hypotheses based on citizen science efforts can contribute to and complement hypothesis-testing research (Dickinson et al. 2010). The statistical design of the Delaware Bay survey in combination with substantial volunteer effort has made it possible to analyze variation of spawning activity at multiple scales. Results from this paper provide new insights into temporal and spatial variation in spawning activity and indicate the continued value of the spawning survey to understanding horseshoe crab ecology and conservation.

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## Appendix 1

**Table 2** Densities of female and male spawning horseshoe crabs (no. m<sup>-2</sup>) at the high tide line on beaches in Delaware Bay from 1999 to 2013

State	Beach	Year														
		1999	2000	2001	2002	2003	2004	2005	2006	2007	2008	2009	2010	2011	2012	2013
<b>A. Density of female spawning horseshoe crabs (no. m<sup>-2</sup>) at the high tide line on beaches in Delaware Bay from 1999 to 2013</b>																
DE	Bennetts Pier		0.22	0.64	0.51	0.24	0.47	0.71	0.70	0.52	0.34	0.70	0.22	0.28	0.32	0.13
DE	Big Stone	0.50	0.73	0.88	0.60	0.54	0.79	0.92	1.00	1.27	0.75	0.77	0.67	0.86	0.54	0.54
DE	Broadkill	0.32	0.07	0.13	0.14	0.18	0.19	0.21	0.12	0.18	0.61	0.23	0.49	0.57	0.20	0.56
DE	Cape Henlopen				0.09	0.16	0.13	0.32	0.10	0.05	0.23	0.27	0.32	0.42	0.30	0.42
DE	Fowlers	0.72	0.48	0.67	0.21	0.32	0.69	0.20	0.49	0.48	0.60	0.22	0.42	0.13	0.04	0.32
DE	Kitts Hummock	2.11	2.62	2.23	1.46	1.24	1.23	1.27	1.66	1.35	1.28	1.62	1.30	1.27	0.89	1.91
DE	North Bowers	1.13	1.23	1.03	1.21	0.78	0.53	0.55	0.75	1.05	0.36	0.76	0.75	0.49	0.46	1.08
DE	Pickering		3.21	1.55	1.69	1.33	1.69	1.28	1.49	1.64	1.99	1.67	1.87	1.14	1.29	2.55
DE	Prime Hook	0.84	0.26	0.42	0.59	0.39	0.78	0.65	0.73	1.08	0.98	0.61	0.92	1.03	0.30	1.12
DE	Slaughter	2.02	1.36	1.09	0.69	1.26	1.71	0.65	1.12	1.32	1.21	0.78	0.75	1.14	0.47	1.47
DE	South Bowers		0.94	0.75	1.11	0.31	0.56	0.59	0.78	1.25	0.57	1.13	0.50	0.60	0.54	0.66
DE	Ted Harvey				1.47	1.61	1.49	0.68	1.59	1.77	1.47	1.30	1.35	1.35	1.12	2.13
DE	Woodland	0.16	0.10	0.03	0.08	0.01	0.00	0.01	0.25	0.02	0.00	0.03	0.16	0.01	0.08	0.01
NJ	Fortescue	0.24				0.35	0.58	0.49	0.65	0.16	0.33	0.44	0.34	0.34	0.73	0.93
NJ	Gandys	0.40	0.38	0.36	1.45	0.42	0.88	1.17	0.99	0.75	0.31	1.33	1.21	0.25	1.34	1.08
NJ	Higbees		0.03					0.12			0.04	0.16		0.42	0.06	0.07
NJ	Highs Beach	0.79	0.99	0.76	0.46	0.43	0.74	0.76	0.69	0.75	0.46	0.73	0.56	0.61	0.63	0.71
NJ	Kimbles	0.77	0.85	0.51	0.51	0.32	0.40	NA	NA	NA	NA	1.73	0.51	0.33	0.93	0.49
NJ	Norburys			0.46	0.42	0.47	0.59	0.84	0.69	0.45	0.44	1.27	0.68	0.71	0.78	0.77
NJ	North Cape May	0.23	0.04	0.10	0.09	0.13	0.02	0.15	0.02	0.04	0.04	0.09	0.02	0.24	0.03	0.06
NJ	Pierces Point				0.56	0.47	0.89	0.67	0.79	0.88	0.51	1.65	1.11	0.96	1.13	1.19
NJ	Reeds	0.35	0.47	0.28	0.94	0.43	0.42	0.22	0.97	0.31	0.41	1.07	0.57	0.82	0.86	0.95
NJ	Sea Breeze	0.18	0.21	0.43	1.63	0.30	0.43	0.22	0.84	0.86	0.41	0.73	1.02			
NJ	South Cape Shore	1.01	1.30	1.28	0.70	0.51	0.90	1.04	0.82	1.17	0.38	1.10	0.79	0.80	1.19	0.80
NJ	Townbank		0.71	0.36	0.49		0.21			0.29			0.31	0.39	0.24	0.52
NJ	Villas							0.82	0.48		0.37	0.67	0.41	0.53	0.38	0.35
<b>B. Density of male spawning horseshoe crabs (no. m<sup>-2</sup>) at the high tide line on beaches in Delaware Bay from 1999 to 2013</b>																
DE	Bennetts Pier		0.91	2.26	1.99	0.91	1.24	2.69	3.42	2.65	1.70	2.79	0.95	1.41	1.08	0.34
DE	Big Stone	2.09	2.58	2.26	1.28	1.30	2.78	2.93	3.77	5.64	3.86	4.40	2.65	5.13	2.25	2.08
DE	Broadkill	0.78	0.14	0.22	0.30	0.30	0.39	0.46	0.22	0.60	1.94	0.60	1.97	1.97	0.54	1.66
DE	Cape Henlopen				0.47	0.57	0.54	1.02	0.60	0.36	1.34	1.94	1.47	2.55	1.53	2.18
DE	Fowlers	2.86	1.58	1.58	0.46	0.81	1.60	0.62	1.68	1.65	2.81	0.54	2.19	0.35	0.08	0.69
DE	Kitts Hummock	7.28	10.44	8.59	5.18	4.03	4.56	3.65	7.84	6.02	6.08	8.33	5.39	8.51	4.45	6.14
DE	North Bowers	5.81	6.65	3.93	4.88	3.78	2.62	2.80	3.90	5.29	1.88	4.93	3.70	3.32	2.16	4.67
DE	Pickering		11.23	5.78	7.64	5.67	7.46	5.51	8.68	8.41	13.06	10.29	8.32	10.09	7.45	10.22
DE	Prime Hook	2.24	0.66	0.76	1.22	0.83	2.18	1.51	2.24	4.18	3.73	1.82	2.91	3.58	0.57	3.72
DE	Slaughter	10.33	5.67	4.19	2.51	4.93	6.94	2.25	4.65	6.01	5.50	4.38	4.02	5.63	1.32	5.08
DE	South Bowers		3.34	2.96	4.55	1.49	2.46	3.42	4.89	8.61	3.60	7.00	2.99	4.75	3.25	3.65
DE	Ted Harvey				4.91	5.26	5.73	3.25	8.50	7.72	7.86	6.83	5.33	10.16	5.98	7.21
DE	Woodland	0.43	0.13	0.03	0.09	0.01	0.00	0.01	0.74	0.05	0.00	0.04	0.36	0.02	0.17	0.03
NJ	Fortescue	0.59				1.22	2.19	1.64	2.36	0.86	0.86	2.41	1.30	1.87	3.28	3.61
NJ	Gandys	1.15	1.09	0.75	4.60	1.19	2.89	4.30	2.89	2.48	0.69	5.77	3.93	1.48	6.24	4.44

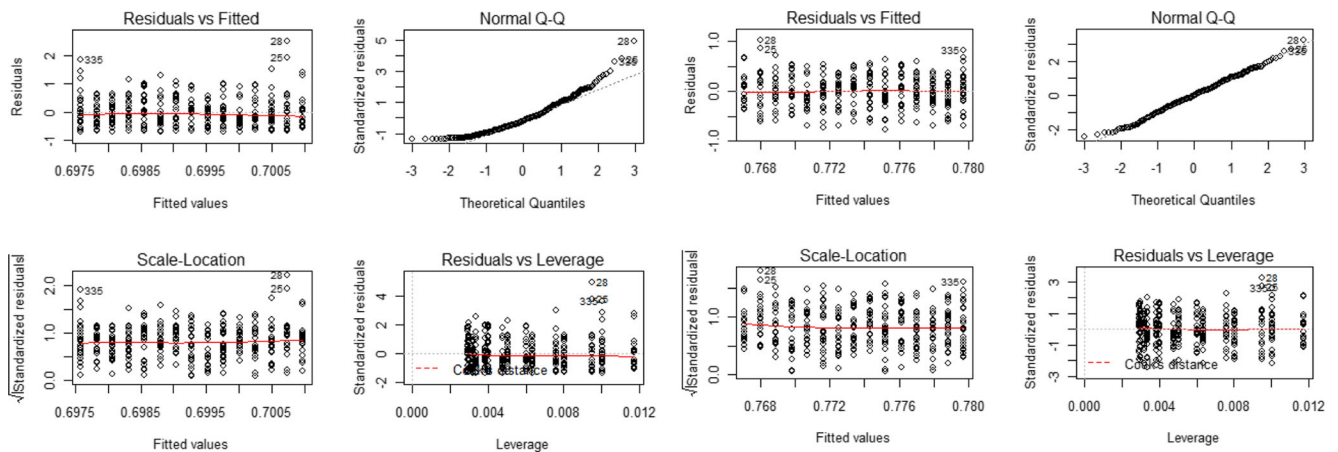


**Table 2** (continued)

State	Beach	Year															
		1999	2000	2001	2002	2003	2004	2005	2006	2007	2008	2009	2010	2011	2012	2013	
NJ	Higbees		0.05					0.34			0.06	0.36		1.13	0.10	0.20	
NJ	Highs Beach	3.16	3.63	3.13	1.75	2.09	3.85	3.71	3.81	5.70	2.26	3.92	2.82	1.99	2.34	2.57	
NJ	Kimbles	3.30		1.59	1.93	1.12	2.01					9.03	2.43	1.63	4.43	2.27	
NJ	Norburys			1.26	1.15	1.89	2.14	3.44	2.75	2.36	1.87	5.56	2.70	2.81	2.29	2.64	
NJ	North Cape May	0.73	0.11	0.19	0.17	0.26	0.02	0.36	0.04	0.10	0.09	0.14	0.05	0.59	0.08	0.15	
NJ	Pierces Point				1.72	1.64	3.21	3.28	4.19	5.15	2.42	8.69	5.88	4.47	4.51	4.97	
NJ	Reeds	1.06	1.45	0.83	2.95	1.53	1.63	0.96	3.64	1.50	1.95	4.81	2.13	2.56	3.98	3.83	
NJ	Sea Breeze	0.52	0.35	0.72	4.68	0.81	0.92	0.69	2.57	2.19	0.99	3.13	3.23				
NJ	South Cape Shore	4.13	4.28	4.91	2.92	2.11	4.10	5.13	4.02	7.03	2.13	5.24	3.84	4.10	4.28	3.23	
NJ	Townbank		1.99	0.81	1.37		0.39			1.04			0.79	1.35	0.62	1.61	
NJ	Villas							2.59	1.78		1.14	2.20	1.21	1.82	0.89	0.97	

Densities are averages over all 1-m<sup>2</sup> quadrats per night and all sample nights within a year from the Delaware Bay Horseshoe Crab Spawning Survey

**Appendix 2**



**Fig. 7** Comparison of residuals from regressions with untransformed and square-root-transformed female density as dependent variable. Similar patterns were seen for modeling of male density

## References

- Anderson, L.I., and C.N. Shuster Jr. 2003. Throughout geologic time: Where have they lived? In *The American Horseshoe Crab*, ed. C.N. Shuster Jr., R.B. Barlow, and H.J. Brockman, 189–223. Cambridge: Harvard University Press.
- Avissar, N.G. 2006. Modeling potential impacts of beach replenishment on horseshoe crab nesting habitat suitability. *Coastal Management* 34: 427–441.
- Barlow Jr., R.B., M.K. Powers, H. Howard, and L. Kass. 1986. Migration of *Limulus* for mating: Relation to lunar phase, tide height, and sunlight. *Biological Bulletin* 171: 310–329.
- Berkson, J., and C.N. Shuster Jr. 1999. The horseshoe crab: The battle for a true multiple-use resource. *Fisheries* 24: 6–10.
- Biber, E. 2013. The challenge of collecting and using environmental monitoring data. *Ecology and Society* 18: 68.
- Bonney, R., C.B. Cooper, J. Dickinson, S. Kelling, T. Phillips, K.V. Rosenberg, and J. Shirk. 2009. Citizen science: A developing tool for expanding science knowledge and scientific literacy. *BioScience* 59: 977–984.
- Botton, M.L., R.E. Loveland, and T.R. Jacobsen. 1988. Beach erosion and geochemical factors: Influence on spawning success of horseshoe crabs *Limulus polyphemus* in Delaware Bay. *Marine Biology* 99: 325–332.
- Brockmann, H.J. 1990. Mating behavior of horseshoe crabs, *Limulus polyphemus*. *Behavior* 114: 206–220.
- Brockmann, H.J., and M.D. Smith. 2009. Reproductive competition and sexual selection in horseshoe crabs. In *Biology and conservation of horseshoe crabs*, ed. J.T. Tanacredi, M.L. Botton, and D.R. Smith, 199–221. New York: Springer.
- Burnham, K.P., and D.R. Anderson. 2002. *Model selection and multimodel inference*, 2nd ed. New York: Springer.
- Castro, G., and J.P. Myers. 1993. Shorebird predation on eggs of horseshoe crabs during spring stopover on Delaware Bay. *Auk* 110: 927–930.
- Conrad, C.C., and K.G. Hilchey. 2011. A review of citizen science and community-based environmental monitoring: Issues and opportunities. *Environmental Monitoring and Assessment* 176: 273–291.
- Dickinson, J.L., B. Zuckerman, and D.N. Bonter. 2010. Citizen science as an ecological research tool: Challenges and benefits. *Annual Review of Ecology, Evolution, and Systematics* 41: 149–172.
- Jackson, N.L., K.F. Nordstrom, and D.R. Smith. 2002. Geomorphic—biotic interactions on beach foreshores in estuaries. *Journal of Coastal Research* 36: 414–424.
- Jackson, N.L., K.F. Nordstrom, and D.R. Smith. 2005. Influence of waves and horseshoe crab spawning on beach morphology and sediment grain-size characteristics on a sandy estuarine beach. *Sedimentology* 52: 1097–1108.
- Jackson, N.L., D.R. Smith, and K.F. Nordstrom. 2008. Physical and chemical changes in the foreshore of an estuarine beach: Implications for viability and development of horseshoe crab *Limulus polyphemus* eggs. *Marine Ecology Progress Series* 355: 209–218.
- Lucas, J.R., R.D. Howard, and J.G. Palmer. 1996. Callers and satellites: Chorus behaviour in anurans as a stochastic dynamic game. *Animal Behaviour* 51: 501–518.
- McCullagh, P., and J.A. Nelder. 1989. *Generalized linear models*, 2nd ed. Cambridge: Chapman & Hall.
- Myers, J.P. 1986. Sex and gluttony on Delaware Bay. *Natural History* 95: 68–77.
- Niles, L.J., J. Bart, H.P. Sitters, A.D. Dey, K.E. Clark, P.W. Atkinson, A.J. Baker, K.A. Bennett, K.S. Kalasz, N.A. Clark, J. Clark, S. Gillings, A.S. Gates, P.M. Gonzalez, D.E. Hernandez, C.D.T. Minton, R.I. Guy Morrison, R.R. Porter, R.K. Ross, and C.R. Veitch. 2009. Effects of horseshoe crab harvest in Delaware Bay on Red Knots: Are harvest restrictions working? *Bioscience* 59: 153–164.
- Penn, D., and H.J. Brockmann. 1994. Nest-site selection in the horseshoe crab, *Limulus polyphemus*. *Biological Bulletin* 187: 373–384.
- Pinheiro, J.C., and D.M. Bates. 2000. *Mixed-effects models in S and S-PLUS*. New York: Springer.
- Rosenzweig, M.L. 1991. Habitat selection and population interactions: The search for mechanism. *American Naturalist* 137: S5–S28.
- Schwab, R.L., and H.J. Brockmann. 2007. The role of visual and chemical cues in the mating decisions of satellite male horseshoe crabs, *Limulus polyphemus*. *Animal Behaviour* 74: 837–846.
- Shuster Jr., C.N., and M.L. Botton. 1985. A contribution to the population biology of horseshoe crabs, *Limulus polyphemus* (L.), in Delaware Bay. *Estuaries* 8: 363–372.
- Shuster Jr., C.N., R.B. Barlow, and H.J. Brockmann (eds.). 2003. *The American horseshoe crab*. Cambridge: Harvard University Press.
- Smith, D.R. 2007. Effect of horseshoe crab spawning density on nest disturbance and exhumation of eggs: A simulation study. *Estuaries and Coasts* 30: 287–295.
- Smith, D.R., and S.F. Michels. 2006. Seeing the elephant: Importance of spatial and temporal coverage in a large-scale volunteer-based program to monitor horseshoe crabs. *Fisheries* 31: 485–491.
- Smith, D.R., P.S. Pooler, R.E. Loveland, M.L. Botton, S.F. Michels, R.G. Weber, and D.B. Carter. 2002a. Horseshoe crab (*Limulus polyphemus*) reproductive activity on Delaware Bay Beaches: Interactions with beach characteristics. *Journal of Coastal Research* 18: 730–740.
- Smith, D.R., P.S. Pooler, B.L. Swan, S.F. Michels, W.R. Hall, P.J. Himchak, and M.J. Millard. 2002b. Spatial and temporal distribution of horseshoe crab (*Limulus polyphemus*) spawning in Delaware Bay: Implications for monitoring. *Estuaries* 25: 115–125.
- Smith, D.R., M.J. Millard, and R.H. Carmichael. 2009. Comparative status and assessment of *Limulus polyphemus* with emphasis on the New England and Delaware Bay populations. In *Biology and conservation of horseshoe crabs*, ed. J.T. Tanacredi, M.L. Botton, and D.R. Smith, 361–386. New York: Springer.
- Smith, D.R., L.J. Brousseau, M.T. Mandt, and M.J. Millard. 2010. Age and sex specific migration timing and frequency of horseshoe crab spawning in Delaware Bay: Insights from a large-scale radio telemetry array. *Current Zoology* 56: 563–574.
- Smith, D.R., N.L. Jackson, K.F. Nordstrom, and R.G. Weber. 2011. Beach characteristics mitigate effects of onshore wind on horseshoe crab spawning: Implications for matching with shorebird migration in Delaware Bay. *Animal Conservation* 14: 575–584.
- Sweka, J.A., D.R. Smith, and M.J. Millard. 2007. An age-structured population model for horseshoe crabs in the Delaware Bay area to assess harvest and egg availability for shorebirds. *Estuaries and Coasts* 30: 277–286.
- Tanacredi, J.T., M.L. Botton, and D.R. Smith (eds.). 2009. *Biology and conservation of horseshoe crabs*. New York: Springer.
- Tulloch, A.I., H.P. Possingham, L.N. Joseph, J. Szabo, and T.G. Martin. 2013. Realising the full potential of citizen science monitoring programs. *Biological Conservation* 165: 128–138.
- Weber, R.G., and D.B. Carter. 2009. Distribution and development of *Limulus* egg clusters on intertidal beaches in Delaware Bay. In *Biology and conservation of horseshoe crabs*, ed. J.T. Tanacredi, M.L. Botton, and D.R. Smith, 249–266. New York: Springer.
- Widener, J.W., and R.B. Barlow. 1999. Decline of a horseshoe crab population on Cape Cod. *Biological Bulletin* 197: 300–302.
- Zimmerman, J., S. Michels, D. Smith, and S. Bennett. 2013. *Horseshoe crab spawning activity in Delaware Bay: 1999–2012. Report to the ASMFC Horseshoe Crab Technical Committee*. Arlington: Atlantic States Marine Fisheries Commission.