

Chapter 24

Assessment and Management of North American Horseshoe Crab Populations, with Emphasis on a Multispecies Framework for Delaware Bay, U.S.A. Populations

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Abstract The horseshoe crab fishery on the US Atlantic coast represents a compelling fishery management story for many reasons, including ecological complexity, health and human safety ramifications, and socio-economic conflicts. Knowledge of stock status and assessment and monitoring capabilities for the species have increased greatly in the last 15 years and permitted managers to make more informed harvest recommendations. Incorporating the bioenergetics needs of migratory shorebirds, which feed on horseshoe crab eggs, into the management framework for horseshoe crabs was identified as a goal, particularly in the Delaware Bay region where the birds and horseshoe crabs exhibit an important ecological interaction. In response, significant effort was invested in studying the population dynamics, migration ecology, and the ecologic relationship of a key migratory shorebird, the Red Knot, to horseshoe crabs. A suite of models was developed that linked Red Knot populations to horseshoe crab populations through a mass gain function where female spawning crab abundance determined what proportion of the migrating Red Knot population reached a critical body mass threshold. These models were incorporated in an adaptive management framework wherein optimal harvest decisions for

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horseshoe crab are recommended based on several resource-based and value-based variables and thresholds. The current adaptive framework represents a true multispecies management effort where additional data over time are employed to improve the predictive models and reduce parametric uncertainty. The possibility of increasing phenologic asynchrony between the two taxa in response to climate change presents a potential challenge to their ecologic interaction in Delaware Bay.

Keywords Red knot • Multispecies management • Population modeling • Delaware Bay • Shorebird migration • Stock assessment • Phenology • Shorebird energetics

24.1 Introduction

The horseshoe crab fishery represents an interesting case study of a resource management program that has progressed from casual indifference to a sophisticated multispecies-based harvest framework, almost all within the twenty-first century. The reasons for this relatively rapid 15-year rise of the horseshoe crab in both public and scientific discussions are multifaceted and compelling. Numerous summaries of the pertinent economic, social, and ecologic issues have been published and continue to be debated today (Berkson and Shuster 1999; Walls et al. 2002; Berkson 2009; Okun 2012). With little recognition prior to the early 2000s, the horseshoe crab has supported important processes involving domestic agriculture, global fishery markets, human health and safety, and trans-continental migratory shorebird populations (Walls et al. 2002). As the various roles of the horseshoe crab have become more understood and more widely publicized, fishery scientists and managers have worked to continually improve management of the multi-user resource.

Harvest of horseshoe crabs along the Atlantic coast has dramatically fluctuated through time. Prior to 1998, harvest of horseshoe crabs was unregulated in most states. In addition to their use as bait in other fisheries and the biomedical industry, they were also commercially harvested for use as fertilizer and livestock feed from the mid-1800s through the mid-1900s. During this time period harvest ranged from approximately one to five million crabs annually (Shuster 1960, 1982; Shuster and Botton 1985; Finn et al. 1991). Harvest numbers dropped to between 250,000 and 500,000 in the 1950s (Shuster 1960), which was followed by a sharp increase in reported harvest in the late 1990s due to the rising demand for bait for the whelk *Busycon* spp fishery (Fig. 24.1). Harvest estimates prior to 1998 should be viewed with caution because harvest reporting was not mandatory prior to 1998 and under-reporting of actual harvest may have been significant.

As described in Smith et al. (2009b), the Atlantic States Marine Fisheries Commission (ASMFC) began formal management measures for horseshoe crabs in 1998 with the establishment of the Interstate Fishery Management Plan (IFMP) for Horseshoe Crab (ASMFC 1998). Specifically, the goal of the management plan is “*management of horseshoe crab populations for continued use by: current and*

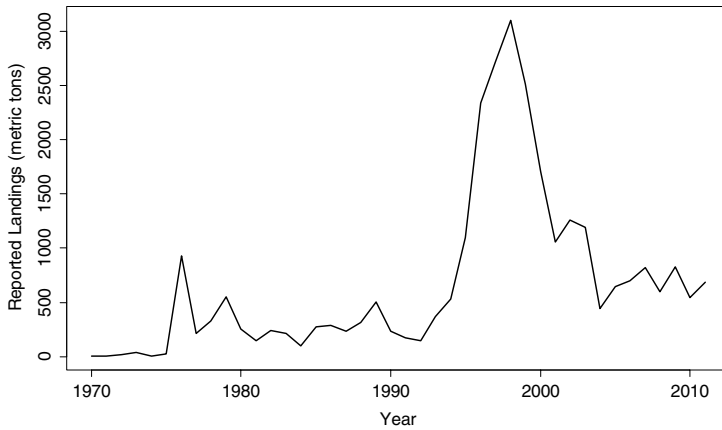


Fig. 24.1 Reported U.S. Atlantic coast horseshoe crab landings (metric tons), 1970–2011 (NMFS Commercial Landings Database August 2013)

future generations of the fishing and non-fishing public (including the biomedical industry, scientific and educational research), migratory shorebirds, and other dependent fish and wildlife (including federally listed sea turtles).” State-by-state reporting of horseshoe crab landings was mandated, with the plan requiring each State to “*continue or initiate mandatory monthly reporting of all harvest (including, but not limited to bait fisheries, bycatch, biomedical industry, and scientific and educational research harvest*” (ASMFC 1998). This IFMP mandate served to codify consistent reporting of coastwide landings data, which up to then had been inconsistent. Addendum I to the FMP established state-by-state reference period landings (RPL) for the bait fishery and implemented a 25 % reduction from each state’s RPL (ASMFC 2000). Subsequent addenda to the IFMP further reduced harvest quotas, implemented seasonal bait harvest closures, and mandated male only fisheries in some or all of the four Delaware Bay states (DE, MD, NJ, and VA) (ASMFC 2004, 2006, 2008). States are allowed to implement more conservative measures than mandated by ASMFC, and New Jersey adopted a moratorium on all bait harvest in 2006. Compared to 1998 when the IFMP was established, landings in 2012 were reduced by 74 % due to the combined cumulative management actions imposed by ASMFC and states. Landings in the four Delaware Bay states decreased 79 % from 1998 to 2012.

Due to a lack of data to support traditional fishery management analyses and identification of reference points for appropriate harvest levels, the initial harvest regulations were implemented primarily with the goal of being precautionary and risk-averse. Managers recognized that management decisions needed to be more scientifically defensible and tasked their technical experts with assembling the relevant data and developing the necessary and appropriate decision support tools, particularly in the Delaware Bay region where the bulk of the harvest occurred. This approach required a greater understanding of horseshoe crab population dynamics

and demographics. Stock assessments within the ASMFC technical group became progressively more insightful, time series of dependable data expanded, and initial efforts to apply traditional fishery assessment models (e.g. surplus production and catch survey) became feasible (ASMFC 2009).

Coincident with the progress towards applying the single-species approach to managing the horseshoe crab fishery was the growing need to include the ecological needs of migratory shorebirds, particularly the Red Knot *Calidrus canutus rufa*, in the fishery's management regime. During spring, northward migrating shorebirds on the Atlantic coast of North America rely heavily on horseshoe crab eggs as a food resource. Red Knots that stopover in Delaware Bay have been dietarily and physiologically linked to horseshoe crab eggs (Niles et al. 2008; Gillings et al. 2009; Fraser et al. 2010; Karpanty et al. 2011). In the early 2000s, following the large increases in horseshoe crab harvest, Red Knot populations in wintering sites in Tierra del Fuego (Argentina and Chile) and stopover sites in Delaware Bay exhibited steep apparent declines in abundance, which raised serious concerns about Red Knot population viability (Baker et al. 2004; Morrison et al. 2004; Niles et al. 2008; Gillings et al. 2009). Some researchers proposed and presented support for the hypothesis that unregulated harvests in the late 1990s caused a decline in horseshoe crab populations in Delaware Bay, which reduced spawning activity and eggs available for migrating shorebirds to consume, which then led to shorebird population collapse (Baker et al. 2004; Niles et al. 2009). As such, identification and refinement of Red Knot population dynamics, as related to the migratory energetic demands supplied during their stopover in the Delaware Bay, was needed to begin framing a multispecies approach to managing the horseshoe crab fishery. As a result, since 2000, significant effort was invested in studying Red Knot population dynamics, their migration ecology, and their ecologic relationship to horseshoe crabs (Morrison et al. 2007; Cohen et al. 2009; Gillings et al. 2009; Karpanty et al. 2011; McGowan et al. 2011a).

The growing body of information on both horseshoe crabs and Red Knots was integrated in an adaptive multispecies management framework designed to recommend harvest management strategies that were consistent with the needs for rebuilding the Red Knot population. Prior to this multispecies framework, the single-species approach for managing horseshoe crab harvest incorporated only conceptual linkages with Red Knots and was frequently mired by conflicting values among various stakeholder groups. The process of developing the adaptive management framework helped the stakeholders reduce conflict by providing the opportunity to incorporate all stakeholder values along with best available science (McGowan et al. 2009; Williams and Brown 2012). In February 2012 under Addendum VII of the Fishery Management Plan, the Atlantic States Marine Fisheries Commission (ASMFC) adopted the resultant multispecies adaptive management framework for sustainable harvest of Delaware Bay horseshoe crabs while maintaining adequate stopover habitat for migrating Red Knots, the focal shorebird species (McGowan et al. 2009; ASMFC 2012).

In the following sections, we describe and summarize the recent research on (1) horseshoe crab status and trends, as well as emerging stock assessment analyses, (2) Red Knot populations with specific focus on Delaware Bay and their interaction with horseshoe crabs, and (3) the adaptive resource management framework that provides for fishery management recommendations in a multispecies context.

24.2 Horseshoe Crab Assessment and Status Along the U.S. Atlantic Coast

Prior to the adoption of the 1998 fisheries management plan for horseshoe crabs, the status of populations along the coast was largely unknown. Quantitative assessments of the population have advanced greatly with implementation of mandatory harvest reporting and the additional fisheries independent data that have become available since 1998. The initial stock assessment (ASMFC 1999) relied on an analysis of trends in relative abundance from fisheries independent surveys (primarily trawl surveys targeting other species). A subsequent stock assessment in 2004 (ASMFC 2004) continued the analysis of trends and also added a meta-analysis (Manly 2001) to examine consistency of trends within geographic regions along the Atlantic Coast. At this time a framework was proposed to utilize a catch-survey model (Collie and Sissenwine 1983) to assess the population in the Delaware Bay region, but sufficient data for the model were not available. The next stock assessment was conducted in 2009 (ASMFC 2009), which continued the meta-analysis of regional trends in fisheries independent data sources and also added analysis of trends with autoregressive integrated moving average (ARIMA) models (Pennington 1986). By 2009, enough data were available to fit the catch-survey model and a surplus production model (Prager 1994) for the Delaware Bay region. These efforts represented the very first estimates of population status of the Delaware Bay relative to fisheries management benchmarks and provided the first quantitative insight into exploitation rates.

Box 24.1: Descriptions of Fisheries Models Applied to Horseshoe Crab Assessment in the 2009 ASMFC Stock Assessment (ASMFC 2009)

Surplus Production Model – A surplus production model is a simple population model that assumes the population grows in a logistic manner and that population growth is maximized at half of the carrying capacity. A surplus production model assesses a population in its entirety with no age-, size-, or stage-structure. It requires a time series of harvest and catch-per-effort data from a fishery independent survey. Results of a surplus production model give a time series of relative biomass and relative fishing mortality.

Catch-Survey Model – A catch survey model is a two-stage stock assessment model with pre-recruits and fully recruited animals. The recruit stage consists of animals that recruit just before or during the current time step of the model and the fully recruited animals consist of all other individuals. The model requires time series of harvest, and relative abundance of pre-recruits and fully recruited animals. Results from a catch-survey model give estimates of abundance and fishing mortality.

24.2.1 *Regional Trends*

Assessment of horseshoe crabs has adopted a regional approach as information from tagging (ASMFC 2009, 2013) and genetic analysis (King et al. 2003, 2005) found evidence for population structure. These regions include: New England (Rhode Island and areas north of Cape Cod), New York (embayments of Long Island and Long Island Sound), Delaware Bay (areas from the New Jersey Coast southward to Virginia), and the Southeast (areas south of Virginia). The most recent stock assessment for horseshoe crabs was conducted in 2013 (ASMFC 2013) and was an update of the 2009 stock assessment (ASMFC 2009). The 2013 stock assessment update relied primarily on the use of ARIMA models. Time series of horseshoe crab relative abundance indices, like other fisheries data, reflect two sources of variation: (1) measurement error arising from sampling variation; and (2) process error arising from actual changes in population abundance (Pennington 1986). The ARIMA approach filters the measurement error from the process variability and derives fitted estimates of abundance over the entire time series whose variance is less than the variance of the observed time series (Pennington 1986). An extension of the ARIMA models was used to infer population status relative to an index-based reference point (Helser and Hayes 1995) in the 2013 stock assessment. An index-based reference point is a reference point equivalent to some value within the observed range of values for the relative abundance index. This bootstrapping method of Helser and Hayes (1995) gave the probability of a fitted index value of a particular year (e.g. the terminal year of the survey) being less than the reference point. Chosen reference points were the 25th percentile (Q_{25}) of the fitted abundance index and the 1998 fitted abundance index. The 25th percentile was chosen because it provides a reasonable reference point for comparison for data with relatively high and low abundance over a range of years, and the 1998 fitted abundance index was chosen because that was the year when the fisheries management plan was adopted by ASMFC.

The 2013 stock assessment fit ARIMA models to a total of 39 horseshoe crab survey (primarily trawl surveys) indices of relative abundance (ASFMC 2013). Of these, 9 surveys were from the New England region, 6 from the New York Region, 19 from the Delaware Bay region, and 5 from the Southeast region (Table 24.1). Trends in the fitted abundance indices for these surveys showed much variation among surveys. Surveys with time series extending back into the mid-1990s generally showed decreasing trends through the early 2000s, but showed mixed results from the mid 2000s through the end of their time series in 2011 or 2012. For example, the Southeast Area Monitoring and Assessment Program (SEAMAP) trawl survey increased, the Delaware Bay 30 ft trawl survey remained stable, and the New York Peconic Bay trawl survey continued to decrease (Fig. 24.2).

With the exception of the New England Region, typically less than half of the surveys were less than their reference points with a probability greater than 0.50. For surveys which had adequate ARIMA model fits (normal distributions of residuals), 9 out of 33 surveys coast-wide (27 %) had 2011 or 2012 indices that were less

Table 24.1 Fisheries-independent surveys to which ARIMA models were fit in the 2013 stock assessment (ASMFC 2013)

Survey	Years of data	P (<1998)	P (< Q ₂₅)
<i>New England Region</i>			
Massachusetts Inshore Bottom Trawl (fall)	1978–2012	0.91	0.72
Massachusetts Inshore Bottom Trawl (spring)	1978–2012	0.96	0.55
New Hampshire Spawning Survey (spring)	2001–2012		0.34
New Hampshire Spawning Survey (spring – summer)	2001–2009		0.47
Rhode Island – Marine Research Inc.	1988–2012	0.87	0.53
Rhode Island – Marine Research Inc. Providence River Impingement	1992–2012	0.86	0.52
Rhode Island – Stout Survey	1975–2002	0.01	0.25
Rhode Island DFW Trawl	1998–2012	0.18	0.69
University of Rhode Island – Graduate School of Oceanography	1959–2012	1.00	1.00
<i>New York Region</i>			
CT Long Island Sound Trawl (fall)	1992–2012	0.22	0.11
CT Long Island Sound Trawl (spring)	1992–2012	0.11	0.08
NY Peconic Bay Trawl Survey	1987–2012	1.00	0.93
NY Western Long Island Beach Seine – Jamaica Bay	1987–2012	0.03	0.01
NY Western Long Island Beach Seine – Little Neck Bay	1987–2012	0.93	0.44
NY Western Long Island Beach Seine – Manhasset Bay	1987–2012	0.82	0.24
<i>Delaware Bay Region</i>			
Delaware 16 ft trawl (Juvenile)	1992–2012	0.42	0.26
Delaware 16 ft trawl (YOY)	1992–2012	0.38	0.04
Delaware 30 ft trawl (all HSC)	1990–2012	0.76	0.20
Delaware 30 ft trawl (female)	1990–2012	1.00	0.61
Delaware 30 ft trawl (male)	1990–2012	0.77	0.21
Delaware Bay Spawning Survey (female)	1999–2012		0.54
Delaware Bay Spawning Survey (male)	1999–2012		0.05
Maryland Coastal Bay	1990–2012	0.15	0.08
NJ Delaware Bay Trawl (female)	1998–2012	0.99	0.19
NJ Delaware Bay Trawl (male)	1998–2012	0.08	0.02
NJ Delaware Bay Trawl (all HSC)	1998–2012	0.09	0.04
NJ Delaware Bay Trawl (Juvenile)	1998–2012	0.15	0.08
NJ Ocean Trawl	1988–2012	0.87	0.28
NJ Surf Clam Dredge	1998–2012	0.00	0.00
NMFS bottom trawl survey (fall)	1988–2008	0.05	0.14
NMFS bottom trawl survey (spring)	1988–2008	0.17	0.05
Virginia Tech Trawl (all HSC)	2002–2011		0.10
Virginia Tech Trawl (female)	2002–2011		0.19
Virginia Tech Trawl (male)	2002–2011		0.06

(continued)

Table 24.1 (continued)

Survey	Years of data	P (<1998)	P (< Q ₂₅)
<i>Southeast Region</i>			
Florida Seahorse Key (Gulf) Spawning Survey ^a	1993–2010		0.00
Georgia Shrimp Trawl	1999–2012		0.06
NC Pamlico Sound Neuse River Gill Net	2001–2012		0.00
SEAMAP Trawl Survey	1995–2012	0.00	0.00
South Carolina Trawl	1995–2012	0.29	0.69

P (<1998) is the probability that the terminal year of the survey was less than the 1998 fitted index value and P (Q₂₅) is the probability that the terminal year of the survey was less than the 25th percentile of fitted index values. Some surveys did not have an associated P (<1998) because they began after 1998. See ASMFC (2013) for a full description of each of the surveys

^aThe Florida Seahorse Key (Gulf) Spawning survey was not conducted in 1998 or 1999, and a fitted value for P(<1998) could not be calculated

than the Q₂₅ reference point and 13 out of 24 surveys (54 %) were less than the 1998 reference point. The number of surveys available to compare to the 1998 reference point was less than the number available to compare to the Q₂₅ reference point because several surveys were not initiated until after 1998. In the New England region six out of seven surveys (86 %) were less than the Q₂₅ reference point and five out of six (83 %) were less than the 1998 reference point. In the New York region, one out of five surveys (20 %) was less than the Q₂₅ and three out of five (60 %) were below the 1998 reference point. Within the Delaware Bay region, 2 out of 16 (13 %) had 2011 or 2012 indices that were less than Q₂₅ and 4 out of 11 (36 %) were less than the 1998 reference point. In the Southeast region, only one out of five surveys (20 %) was less than the Q₂₅ reference point (Table 24.2).

The differences among regions in the proportion of surveys that were below their reference points in the 2013 stock assessment emphasizes the importance of management, regulation, and monitoring of horseshoe crabs on a regional or localized scale. In general, abundance indices suggest increases in the Southeast region, possible increases or at least stabilization in the Delaware Bay region, and continued population declines in the New York and New England region. Although harvest of horseshoe crabs for the bait industry has declined coast-wide since the late 1990s, the current level of harvest in the New York and New England regions may still be in excess of what those populations can sustain. The data and models necessary to quantitatively determine sustainable levels of harvest (e.g. maximum sustainable yield) in any of the regions are not yet available.

24.2.2 Biomedical Harvest

Despite the advances in assessment of horseshoe crab along the Atlantic Coast over the years, accounting for the mortality induced by the biomedical industry during the bleeding process remains problematic. The biomedical industry returns many of

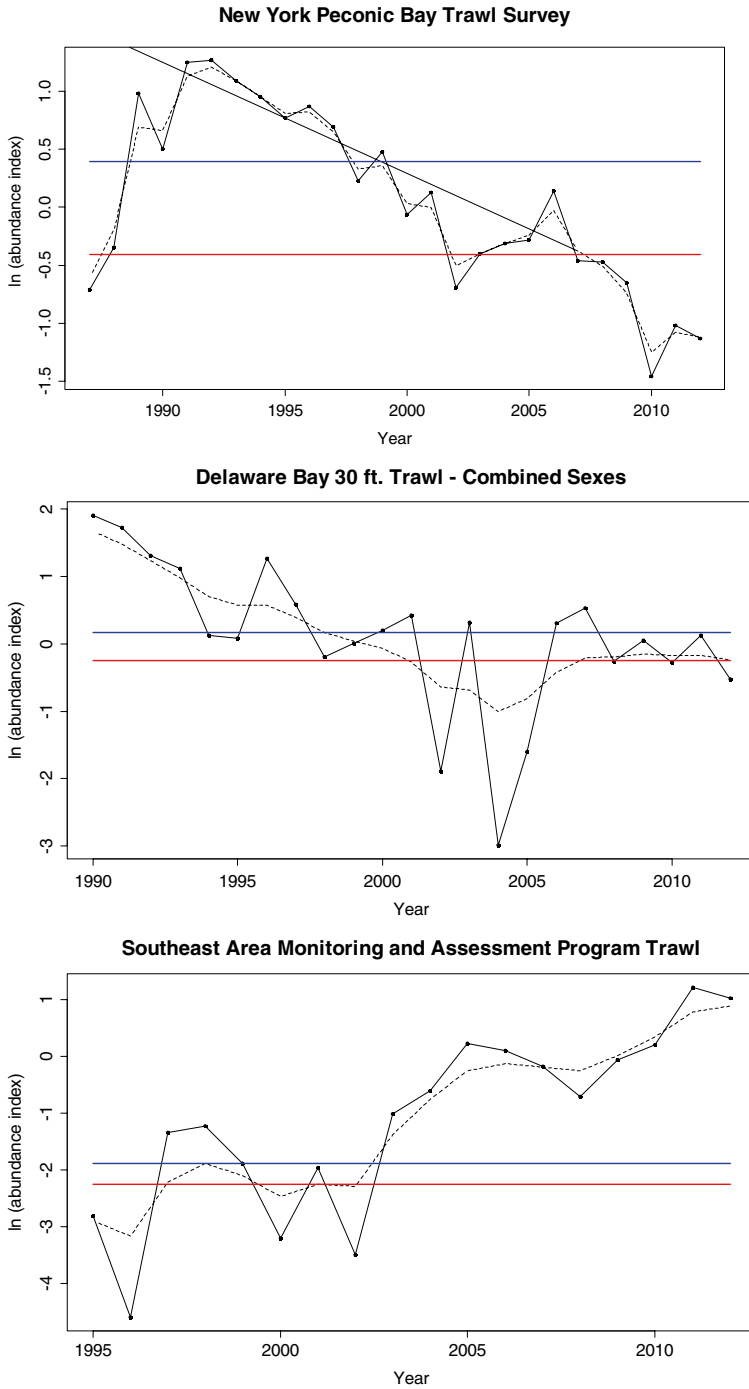


Fig. 24.2 Examples of autoregressive integrated moving average (ARIMA) model fits to horseshoe crab indices of abundance. The *solid lines* are the observed abundance indices, the *dashed line* is the ARIMA fit, the *blue horizontal lines* represent the 1998 reference points, and the *red horizontal lines* represent the 25th percentile reference points

Table 24.2 Summary of ARIMA model results from the 2013 ASMFC horseshoe crab assessment (ASMFC 2013)

Region	P (<1998) >0.50	P (<Q ₂₅) >0.50
New England	5 out of 6	6 out of 7
New York	3 out of 5	1 out of 5
Delaware Bay	4 out of 11	2 out of 16
Southeast	0 out of 2	1 out of 5
Coast-wide	12 out of 24	10 out of 33

The values represent the number of surveys with terminal year having a greater than 0.50 probability of being less than the reference point (i.e. likely less than the reference point). Time series were only included in this summary if the terminal year was 2011 or 2012 and residuals from ARIMA model fits were normally distributed. Those that ended earlier are not included. Also, those surveys that did not begin until after 1998 were not included in the $P(i_f < i_{1998}) > 0.50$ summary

the bled crabs to the wild following blood collection and also transfers some bled crabs to the bait industry where they are then accounted for in the bait harvest. For those that are released to the wild, ASMFC assumes 15 % suffer mortality (ASMFC 2013). This mortality rate is applied to the total number of crabs reported as bled and released by the biomedical companies coast-wide. The coast-wide estimated mortality of crabs by the biomedical industry has increased 78 %, from approximately 46,000 individuals in 2004 to approximately 80,000 in 2012. In 2012, 10 % of the total coast-wide reported mortality of horseshoe crabs came from the biomedical industry (ASMFC 2013). Although the mortality due to the biomedical industry is small compared to bait industry, we consider it significant for quantitative assessments. The limited number of biomedical companies along the Atlantic coast and policies regarding confidential proprietary information prevent the inclusion of company-specific biomedical mortality in regional assessments. The use of biomedical mortality in coast-wide analyses is permissible, but analysis on a regional scale would violate data confidentiality with individual companies. This policy prevented the application of the catch-survey model and the surplus production model, developed during the 2009 stock assessment in the Delaware Bay region (ASMFC 2009), from being included in the 2013 stock assessment (ASMFC 2013). While the mortality from the biomedical industry was ignored during initial applications of these models, including this mortality in current models would increase their applicability. Because of the data confidentiality policy precluding use of the biomedical mortality, the utility of these models was compromised such that they were not included in the 2013 assessment (ASMFC 2013). To date, no biomedical company has granted ASMFC permission to disclose individual company data. The advancement of horseshoe crabs assessment on a regional scale would benefit greatly with the availability of regional biomedical mortality data (Novitsky 2015).

24.3 Migratory Red Knots and Their Relationship to Horseshoe Crabs in Delaware Bay

Red Knots are migratory shorebirds, and the Atlantic flyway population in the western hemisphere is classified as a distinct subspecies *C. c. rufa*. The *rufa* population historically spent the majority of the non-breeding season in the Tierra del Fuego region of Argentina and Chile (Baker et al. 2013). Additional birds were known to overwinter in northern Brazil and the southeastern U.S., primarily in Florida (Baker et al. 2013). From March through May each year, the birds migrate from their wintering locations to the breeding grounds in the central Arctic regions of Canada, periodically stopping at several sites along the way (Baker et al. 2013). In Delaware Bay, Red Knots and a variety of other migratory shorebird species gather in vast numbers to exploit seasonally available horseshoe crab eggs deposited on the beach by spawning female crabs (Gillings et al. 2009; Karpanty et al. 2011). Researchers have shown that Red Knot behavior and spatial distribution is strongly associated with horseshoe crab spawning and egg availability in the bay (Gillings et al. 2009; Cohen et al. 2009; Fraser et al. 2010; Karpanty et al. 2011).

Using physiological models and flight and fuel requirements, Baker et al. (2004) proposed that Red Knots departing Delaware Bay and migrating to the arctic need to weigh at least 180 g at the time of departure in order to survive the transition to the arctic (Kvist et al. 2001, as cited by Baker et al. 2004). Studies of the Icelandic sub-species of Red Knot, *C. c. islandica*, indicate that in years of extreme cold weather late in the spring, birds that arrive in the Arctic breeding grounds at low weights have lower survival rates (Morrison 2006; Morrison et al. 2007). Studies have reported that the proportion of birds in Delaware Bay achieving the 180 g mass threshold greatly declined between 2000 and 2008 following the heavy, unregulated horseshoe crab harvests in the late 1990s (Baker et al. 2004; Atkinson et al. 2007; Niles et al. 2009). Baker et al. (2004) further proposed that the primary reason for the *rufa* Red Knot population decline was that too few birds were achieving that mass threshold during stopover in Delaware Bay and were therefore suffering mortality during their subsequent migratory flight to the Arctic.

More recent research by McGowan et al. (2011a) strongly support the hypothesis that Red Knot mass gain during stopover in Delaware Bay was closely associated with adult female horseshoe crab abundance. Using capture-mark-recapture/resight data from Delaware Bay collected between 1998 and 2008, they developed a multi-state mark recapture/resight model that tracked bird arrival, departure, annual survival, and used a multi-state structure to establish mass classes for birds in the Bay, i.e. birds above and below 180 g. The analysis estimated the probability of transition between mass classes as a function of horseshoe crab abundance covariates (McGowan et al. 2011a). The analysis demonstrated a strong association between estimated adult female horseshoe crab abundance and the probability of transitioning from the lower mass class to the higher mass class. However, McGowan et al. (2011a) reported weak associations between departure mass class and subsequent annual survival, i.e., survival of lighter weight birds was slightly lower than that of

heavy birds, and all birds survived greater than 90 % annually on average across years. They found that annual adult survival was closely associated with snow depth in the arctic in early June, where survival rates were higher in years with more snow on the ground on June 10th (McGowan et al. 2011a).

Recent Red Knot mass data suggest improved stopover conditions; the proportion of birds achieving the 180 g threshold between May 26th and 28th has steadily increased from 2006 to 2010 (Dey et al. 2011). As horseshoe crab eggs have increased on the beaches of Delaware Bay, Red Knot mass at the end of the stop over season has improved (Dey et al. 2011). However, the metric of proportion of birds over the 180 g threshold at the end of the stopover season has limited inferential capacity since birds that achieved that mass threshold may have already departed the Bay or may not be actively foraging. Cannon netting (trapping) efforts tend to target foraging flocks because their movement patterns are more predictable, but cannon netting can lead to biased catches and limited inferences (Clark 1980; Pienkowski and Dick 1976). Additionally McGowan et al. (2011a) found very limited survival consequences of the mass threshold in their multi-state survival analysis. McGowan et al. (2011b) demonstrated through simulation modeling that if underweight birds fail to breed, significant population decline is possible, but there is a paucity of data on *rufa* Red Knot reproductive biology (Baker et al. 2013).

24.3.1 *Red Knot Population Estimates and Trends*

Infrequent and unstandardized surveys in the 1980s and 1990s indicated that there may have been over 120,000 Red Knots using Delaware Bay in the early 1990s (Niles et al. 2008). Aerial surveys are riddled with error and uncertainty (Pollock and Kendall 1987; Frederick et al. 2003) and have extensive limitations as a shorebird monitoring method. However, in the 1980s and 1990s there were years with greater than 70,000 Red Knots counted in Delaware Bay (Clark et al. 1993; Niles et al. 2008), and counts in the Tierra del Fuego wintering area regularly encountered more than 50,000 birds (Morrison et al. 2004; Niles et al. 2008). Between 2000 and 2008, aerial counts of stopover sites in Delaware Bay were variable but generally declined and have since stabilized (Niles et al. 2009). Between 2009 and 2011, peak aerial counts in Delaware Bay showed signs of increasing (Dey et al. 2011). Mark-recapture based estimates of abundance for Red Knots that stopover in Delaware Bay indicate that their population abundance has been very stable since 2011 (Lyons et al. in review, see below). The Tierra del Fuego populations exhibited significant declines in the early 2000s and subsequently stabilized at approximately 10,000–15,000 birds with annual variation (Dey et al. 2011; Baker et al. 2013).

24.3.2 *Population Projection Models*

Baker et al. (2004) presented the first population projection model, and they predicted rapid and continued decline for *rufa* Red Knots in the 2000s and the potential for extinction as early as 2010. Baker et al. (2004) estimated survival rates of ~0.50 for Red Knots that did not make the 180 g mass threshold during stopover and included very low annual average survival rates in their projections. While Red Knots in Delaware Bay did decline significantly in the early 2000s, by 2010 the population had evidently stabilized and possibly begun to increase (Dey et al. 2011). The results of the Baker et al. (2004) model have been used to support efforts to curb and, in some locales, eliminate horseshoe crab harvest (Niles et al. 2009).

As part of a larger adaptive management effort, McGowan et al. (2011b) developed a simulation model to predict Red Knot and horseshoe crab abundance. Their model co-simulated both populations and incorporated horseshoe crab-dependent mass gain dynamics for Red Knots in the Delaware Bay region to evaluate the effects of horseshoe crab harvest actions/strategies on population viability for the birds (McGowan et al. 2011b). The horseshoe crab components of the model built upon the Sweka et al. (2007) population model and added dual sex components to allow for sex specific harvest evaluations. The males and females were linked via a sex ratio fertility function (based on Caswell 2001) in which fertilization rates declined if horseshoe crab operational sex ratio fell below the critical 2:1 male to female ratio. McGowan et al. (2011b) established the critical threshold for the sex ratio linked fertility function relying on behavioral ecology studies (Brockmann 2003), and data from un-harvested populations in Taunton Bay, ME and Seahorse Key, FL (McGowan et al. 2009, 2011b).

The McGowan et al. (2011b) model linked Red Knot populations to horseshoe crab populations through a mass gain function where female spawning crab abundance determined what proportion of the migrating Red Knot population reached the 180 g mass threshold (based on the results from McGowan et al. 2011a). In the simulation model differential survival could be applied to those that reached the mass threshold and those that did not (McGowan et al. 2011b). McGowan et al. (2011b) ran a set of simulations that included vast differences in survival of heavy and light birds (the “Baker type model,” following Baker et al. 2004) and slight differences between the groups (the “weak survival effect” model, reflecting the results of McGowan et al. 2011a). McGowan et al. (2011b) reported that even with model uncertainty, a threshold based restriction on harvest, whereby crabs could only be harvested if Red Knot abundance exceeded a pre-specified threshold, allowed both populations to rebound and increase after several years. Further, McGowan et al. (2011b) assessed that the Baker type model, with significant survival consequences for light mass birds, was consistent with the observed population count data for Red Knots in Delaware Bay between 1998 and 2008. They also concluded that the observed population counts were within the 95 % confidence interval of the abundance predictions under the weak survival effect model and that model comparisons to the observed data were inconclusive (McGowan et al. 2011b).

24.3.3 Alternative Theories for Declines

The population decline in Red Knots was quickly attributed to the horseshoe crab harvest and a decline in horseshoe crab egg availability on Delaware Bay beaches without consideration of alternative hypotheses (Niles et al. 2009). Some available data support this hypothesis (Niles et al. 2009), but other data are inconclusive or even contradictory (e.g., McGowan et al. 2011a; Karpanty et al. 2011; Schwarzer et al. 2012). In light of these data, alternative causal mechanisms for the decline have been proposed with varying degrees of formality and analytical support. For example, Robinson et al. (2003) reported that birds arriving late in Delaware Bay were particularly susceptible to mass gain stress during stopover, and they suggested that birds may be arriving in the bay later in the season due to problems in the wintering grounds or at previous stop in the migration flyway. Robinson et al. offered explanations as to why birds' arrival might be delayed but found no conclusive evidence to support the explanations.

Fraser et al. (2012) proposed that Red Knot population collapse may be explained by a cessation or alteration of lemming cycles in the Arctic breeding grounds. Lemming cycles are driven by snow fall cycles whereby, in years of heavy snow in the Arctic, lemming overwinter survival is higher, and the populations exhibit spring and summer booms following years of heavy winter snows. Fraser et al. proposed that in years with lemming population booms, Arctic predators (e.g., Arctic fox, snowy owl) meet all of their energetic needs consuming super-abundant lemmings, and therefore predation pressures on Red Knot nests and fledglings are greatly reduced. Snow fall fluctuates cyclically in a 3–4 year pattern, and alterations in those patterns have been associated with shorebird population decline in Norway and other sites in the Arctic. Fraser et al. (2012) presented limited evidence of historic Red Knot population cycles at approximately 4 year intervals and showed evidence that the cycles ended in the late 1990s, coinciding with Knot population collapse in the early 2000s. The evidence was inconclusive because Fraser et al. (2012) did not have enough successive years of population monitoring data to detect a cyclical pattern with statistical significance, but the limited data do support the hypothesis. It is also noteworthy that the results of the McGowan et al. (2011a) multistate survival analysis show that Red Knot survival was positively correlated with snow depth in early June; this result is consistent with the lemming hypothesis.

24.3.4 Ongoing Monitoring and Research

Significant uncertainty remains regarding Red Knot population dynamics and the effect of horseshoe crab abundance on Red Knot population viability. Extensive monitoring efforts persist in Delaware Bay as part of ongoing management decision making and scientific research. Annually, the states of Delaware and New Jersey run banding and resighting programs to enhance the extensive database. Those data are used to update survival analyses, study spatial ecology within the Bay, estimate

stopover duration, and estimate stopover arrival/departure timing. Perhaps most importantly, the mark-recapture and resight data are being used to estimate annual abundance with significantly more precision and less error and detection bias than aerial surveys (Lyons et al. in review). The estimation methods use mark-recapture data and marked to unmarked ratio data in a hierarchical model that combines the traditional Jolly-Seber model, with a binomial detection model (Lyons et al. in review). The method estimates the “super population size” accounting for the flow through nature of a fly-way population that temporarily stops at a staging site in temporal disunity (i.e., they don’t all arrive and depart in unison). Preliminary results estimated super population abundance at approximately 45,000 Red Knots in 2011–2013 (J.E. Lyons, USFWS, personal communication).

24.4 The Adaptive Management Framework for Red Knots and Horseshoe Crabs

Adaptive management is increasingly used for difficult natural resource decisions characterized by recurrent decisions and reducible ecological uncertainty (Walters 1986; McCarthy and Possingham 2007; Martin et al. 2009; Runge 2011; Williams and Brown 2012). Adaptive management draws on principles of structured decision making (Conroy and Peterson 2013) and proceeds by the following steps during a set-up phase: development of the framework proceeded by articulating the management objectives, identifying the feasible alternative management actions, building models to predict the multiple species’ population status given the alternative actions, and using mathematical routines to identify the optimal actions—in the sense of best meeting the management objectives. After the set-up phase, adaptive management is implemented iteratively until revision of the set-up is triggered by periodic review or onset of substantial new knowledge. Fully incorporating uncertainty in the predictive models and a well-designed monitoring program are keys to reducing uncertainty and improving future decisions.

24.4.1 Problem Definition and Management Objectives

The ASMFC is the decision maker in this context, and the decision problem was how best to set harvest regulations. Stakeholder meetings were held to discuss and develop the framework (McGowan et al. 2009). The management objective was to sustainably harvest horseshoe crabs, which could include moratoria, given objectives to provide adequate stopover habitat for migrating shorebirds. The objective was reframed into a quantitative format to support predictive modelling and optimization. After deliberation, the consensus objective or ‘reward’ function was

$$R_t = v_{Ft} 2H_{Ft} + v_{Mt} H_{Mt} \quad (24.1)$$

where R_t is the reward in year t , H_F and H_M are number of female and male horseshoe crabs harvested in year t , and v_{Ft} and v_{Mt} are value functions determined by the level of female and male horseshoe crab harvest. The value function for females takes the value of 1 if Red Knot abundance exceeds 45,000 (i.e. 22,500 female Red Knot) or female horseshoe crab abundance exceeds 80 % of carrying capacity (i.e. 11 million, based on an age structured population model developed by Sweka et al. (2007)), and takes the value of zero otherwise. The Red Knot threshold of 45,000 was chosen to reflect historic abundances from aerial counts observed in Delaware Bay and is thought to be consistent with a recovering population (McGowan et al. 2009). The horseshoe crab threshold of 80 % carrying capacity is thought to be consistent with adequate egg availability (Smith 2007; Sweka et al. 2007). The value function for males is related to sex ratio, so that the function takes the value of zero when operational sex ratio (sex ratio on the spawning beach, expressed as males:females) is below 2:1, takes the value of 1 when operational sex ratio exceeds 3:1, and changes linearly in between those thresholds. The purpose of the value function for males is to value full fertilization and genetic diversity. The female value is multiplied by 2 because mature females are larger and considered better bait in the eel and conch fisheries; therefore females have at least twice the market value. These value functions and thresholds were developed through consultations and public meetings with managers and stakeholders with additional input from experts on horseshoe crab population ecology, specifically with respect to sex ratio and carrying capacity.

24.4.2 Alternative Management Actions

Because the decision problem addressed how to sustainably harvest horseshoe crabs, the management alternatives were expressed in terms of harvest packages (McGowan et al. 2009). Harvest packages included sex-specific harvest quotas due to male and female crabs having different market value and different contributions to population dynamics. The packages included (1) full moratorium on both sexes, (2) 250,000 males and 0 females, (3) 500,000 males and 0 females, (4) 280,000 males and 140,000 females, (5) 420,000 males and 210,000 females. In addition to the harvest quotas set through adaptive management, there are harvest controls that are constant among packages, such as season closures, trip limits, and a marine refuge off the mouth of Delaware Bay.

24.4.3 Predictive Models

To compare and select among the alternative harvest packages to implement at any given time, predictive models were necessary to express the likely outcome of implementing a package on each species' populations. Stochastic population

models were developed for horseshoe crabs (Sweka et al. 2007) and Red Knots (McGowan et al. 2011b), and these models were linked to predict the outcome of implementing harvest packages on horseshoe crabs and Red Knots (McGowan et al. 2009). Uncertainty was incorporated in model parameters and by using a set of three models to represent different levels of functional dependency between horseshoe crabs and Red Knots. Once integrated, the suite of models linked horseshoe crab spawning to Red Knot weight gain and vital rates, i.e., adult survival and fecundity (McGowan et al. 2011b).

24.4.3.1 The Horseshoe Crab Population Model

The model to predict horseshoe crab abundance included age-specific survival, a sex-specific partial recruitment schedule starting at age 9, sex-specific harvest, sex-ratio specific fertilization/fecundity, and density-dependent egg mortality (Sweka et al. 2007; McGowan et al. 2009, 2011b). The horseshoe crab population model was (Sweka et al. 2007):

$$N_{i,j+1,t+1} = (N_{i,j,t} - H_{i,j,t})S_{i,j,t}, \quad (24.2)$$

where $N_{i,j,t}$ was pre-harvest abundance, $H_{i,j,t}$ was harvest, and $S_{i,j,t}$ was survival of the i^{th} sex, j^{th} age, and t^{th} time. Harvest quota was distributed proportionately by age among adults (i.e., $H_{i,j,t} = 0$ for subadults). Age-specific probability of recruitment to sexual maturity starting at age 9 was 0.2, 0.45, 0.99, and 1 for females and 0.36 and 1 for males (Smith et al. 2009a). Based on a maximum age for horseshoe crabs of 20 years, starting at age 18 survival rates were 0.08 to simulate senescence (Sweka et al. 2007). The number of age 1 offspring was a product of the number of fertilized eggs per female, egg to hatch survival (i.e., 1- egg mortality), and first year survival. Egg mortality was a non-decreasing function of spawning female abundance due to density-dependent nest disturbance (Smith 2007; Sweka et al. 2007). The number of fertilized eggs was modeled as a product of eggs per female and fertilization rate (McGowan et al. 2009). Fertilization rate declined linearly from one to zero as the population sex ratio (males:females) declined below 1.06. Note that for a population sex ratio of 1.06, the sex ratio during spawning, i.e., the operational sex ratio, is expected to be two males per female (McGowan et al. 2009). Other vital rates and variances were taken from Sweka et al. (2007).

24.4.3.2 The Red Knot Population Models

The set of models to predict Red Knot abundance was based on an age-structured Red Knot population model with differently parameterized relationships between horseshoe crab egg availability and Red Knot weight gain, survival, and fecundity (Sweka et al. 2007; McGowan et al. 2011b). Horseshoe crab eggs that are available for shorebird consumption result from density-dependent exhumation of nests and

transportation by waves and swash. These exhumed eggs will not develop due to desiccation or low oxygen (Penn and Brockmann 1994; Nordstrom et al. 2006; Smith 2007; Jackson et al. 2008; Weber and Carter 2009), and shorebird consumption of these non-viable eggs is not thought to limit horseshoe crab population growth. Multi-state mark-recapture modeling was used to parameterize the relationship between Red Knot weight and horseshoe crab spawning abundance during the shorebird stopover period and to estimate the probability of gaining a threshold weight (McGowan et al. 2011a). We used a threshold weight of >180 g to categorize Red Knots into two weight classes (*heavy* and *light*) characterized by different survival and/or reproductive rates (McGowan et al. 2011b). The Red Knot population model was (McGowan et al. 2011b):

$$N_{t+1} = N_t \left[P_t S_{a,t}^H + (1 - P_t) S_{a,t}^L \right] + N_{t-1} \left[P_{t-1} F_{t-1}^H + (1 - P_{t-1}) F_{t-1}^L \right] S_{f,t-1} S_{j,t}, \quad (24.3)$$

where N_t was abundance of adults, P_t was the probability of gaining the threshold weight, $S_{a,t}^H$ and $S_{a,t}^L$ were adult survival rates for heavy and light birds, F_{t-1}^H and F_{t-1}^L were fecundity rates for heavy and light birds, and $S_{j,t}$ and $S_{f,t}$ were survival rates for juvenile (first and second-year birds). Unlike the adult birds, juvenile birds do not migrate through Delaware Bay during the horseshoe crab spawning period, and thus mass state of juveniles was not modeled.

Three Red Knot population models were parameterized to represent the range of hypothesized effects of weight gain on Red Knot survival and fecundity. The No Effects Model hypothesized equal survival and fecundity for heavy and light birds. The Moderate Effects model hypothesized weight-class specific survival with estimates taken from McGowan et al. (2011b). The Strong Effects model hypothesized weight-class specific survival with estimates taken from Baker et al. (2004). Fecundity was weight-specific in the Moderate and Strong Effects Models with parameter estimates taken from McGowan et al. (2011b). Variances in the vital rates were from McGowan et al. (2011b) and McGowan et al. (2011a). Model weights reflect the relative degrees of faith in each of the three models (e.g. Williams et al. 2002). The initial model weights were set based on a consensus process of members of the ASMFC technical working group to 0.2, 0.4, and 0.4 for the No Effects, Moderate Effects, and Strong Effects Models, respectively (McGowan et al. 2009).

24.4.4 Model Optimization

Adaptive stochastic dynamic programming, implemented within the software ASDP (Lubow 2001; Williams et al. 2002; Martin et al. 2009), was used to develop optimal harvest recommendations from the predetermined set of possible harvest policy options based on the reward function (Eq. 24.1) that included both harvest value for horseshoe crabs and Red Knot abundance. The optimization results in a decision matrix used to identify the optimal harvest package for the following year given the most recent estimates of horseshoe crab and Red Knot abundance.

The technical aspects of optimization start with the algorithm within ASDP, derived from Bellman's equation (Miranda and Fackler 2002; Williams et al. 2002), as given by:

$$V_t(\underline{N}_t, \underline{w}_t) = \max_{A_t} \left\{ R(\underline{N}_t, \underline{w}_t, A_t) + \delta \cdot E \left[V_{t+1}(\underline{N}_{t+1}, \underline{w}_t + 1 | \underline{N}_t, \underline{w}_t, A_t) \right] \right\}, \quad (24.4)$$

where V_t was the maximized utility that depends on the state variables (i.e., the vectors of abundances, \underline{N}_t and model weights, \underline{w}_t), the reward function (R) was maximized over all harvest policy options (A_t), δ is a discount factor, and the expectation operator, $E[\cdot]$, is an average utility taken across the uncertainty in the predictive models. The recursive algorithm works by starting at a terminal time T , finding V_T , and then working backward to the current time. The discount factor (δ) was set to one in our application. The algorithm was implemented within ASDP with an arbitrarily large time horizon ($T=1,000$ years), as recommended by Lubow (2001), to effectively approximate an infinite time horizon. The model weights at $t + 1$ are updated using Bayes' Theorem based on the previous time weights (\underline{w}_t), model predictions of abundances at $t + 1$, and monitoring observations of abundances at $t + 1$.

24.4.5 Monitoring

Several requirements are met by the targeted monitoring programs that estimate horseshoe crab and Red Knot abundance each year. First, the most recent estimates are compared to the ASDP decision matrix to look up the optimal harvest package for the following year. Second, the estimates are compared to model predictions to update model weights using Bayes' Theorem; the updated weights reduce model uncertainty and are incorporated into the optimization analysis (Eq. 24.4). Third, the estimates are used to improve the predictive models directly and reduce parametric uncertainty.

Currently, horseshoe crab abundance is estimated by a trawl survey and Red Knot abundance by mark-recapture sampling. The sampling designs and the monitoring program, in general, are under review to ensure that the required information is available to support the adaptive management framework.

24.4.6 Operational Adaptive Management

The ASMFC sets harvest regulations for horseshoe crabs annually. The adaptive management framework allows harvest policy to be responsive to abundance of horseshoe crabs and Red Knots. If the abundances remain low, then harvest will remain low or decrease. Conversely, if abundances increase and management objectives are being achieved, harvest can increase. To ensure that the framework is

servicing its intended purpose, the ASMFC will periodically review all components of the adaptive management framework, typically on a 3–5 year cycle.

24.5 The Horseshoe Crab-Red Knot Alliance: Progress with an Uncertain Future

As prefaced by Smith et al. (2009b), the North American horseshoe crab population in the Delaware Bay region is now being managed with an explicit link to the status of a migratory shorebird population. The implementation of this multispecies management framework is a credit to both the State and Federal fishery managers within the ASMFC, as well as the scientists who developed the protocol. If left in place, the utility of the adaptive management framework process should continue to increase over time, as both quantitative parameters and value-based thresholds points are refined. This collaborative resolution to a 15-year-long, often controversial process of managing harvest of horseshoe crabs with shorebird needs in mind can serve as a useful model for other multispecies management scenarios where the link between the species can be quantitatively characterized.

While the adaptive framework represents a significant advancement in managing the fishery in the mid-Atlantic, many variables remain that could alter the nature of both the exploitation of horseshoe crabs and the ecology of their interaction with the Red Knot. The use of bait bags can decrease the demand for horseshoe crabs, whereas advances in the development of alternative baits could potentially eliminate the bait harvest altogether (Ferrari and Targett 2003; Fisher and Fisher 2006; Gauvry 2009). We discussed the increasing trend in horseshoe crabs collected in the biomedical industry. A greater awareness of best management practices in handling and processing animals in the biomedical industry may ameliorate the concomitant trend in mortality. Moreover, adoption of a pyrogen test which employs synthetic coagulation enzymes (Ding and Ho 2001) and other alternative endotoxin assays (Novitsky 2009) would significantly decrease the dependence of the pharmaceutical industry and medical community on horseshoe crabs. On the other hand, anecdotal evidence suggests that the *Limulus* amebocyte lysate industry in Asia may be experiencing a period of rapid growth. Societal and technological pressures for prosecuting the North American *Limulus* fishery are likely to evolve in the foreseeable future.

Despite implementation of the adaptive management process, attaining the value-based population benchmarks inherent in the framework, particularly for Red Knot, is not guaranteed. As can be expected for any global migrant, the Red Knot population faces many threats outside of Delaware Bay (Niles et al. 2008). While the adaptive management framework represents the best available science for predicting the effects of horseshoe crab harvest on the population dynamics of the *rufa* Red Knot, the nature of their intertwined ecology while in Delaware Bay is likely not static. Geologically speaking, the relationship between horseshoe crabs and Red Knots in Delaware Bay is a relatively recent phenomenon, evolving during

the glacial retreat and sea level rise which conspired 7,000 years ago to form the current approximate physiognomy of Delaware Bay (Delaware DNREC 2005). Phenological synchrony is an essential element of the ecological interplay between the two species, where the timing of arrival of Red Knots in Delaware Bay has generally overlapped with the bulk of the spawning of horseshoe crabs, thereby maximizing the availability of horseshoe crab eggs for meeting the energetic demands of migration. Emerging stressors, primarily climate change, are known to impact the phenology in many taxa including migratory birds (Cotton 2003; Visser and Both 2005; Both et al. 2006). The accelerated effects of climate change observed in Arctic regions present particularly acute challenges for Arctic breeding species (Liebezeit et al. 2014), with some evidence that long-distance migrants lack the flexibility to adapt adequately (Both and Visser 2001). The effect of climate change on the breeding phenology of the *rufa* Red Knot, which breeds in the Canadian Arctic, remains unknown. Given the highly disparate nature of the two species and their life histories and the environmental pressures on the respective phenologies of Red Knots and horseshoe crabs, their individual responses to such pressures are likely not consistent in direction or magnitude. Gradually increasing phenologic asynchrony remains a possible factor in the future utility of the adaptive framework as well as perhaps the success of *rufa* Red Knot population as a whole. The environmental generalist strategy of the horseshoe crab (Sekiguchi and Shuster 2009) gives hope that, even in the face of accelerating climate change, they will remain an important component of the Atlantic coast biota.

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