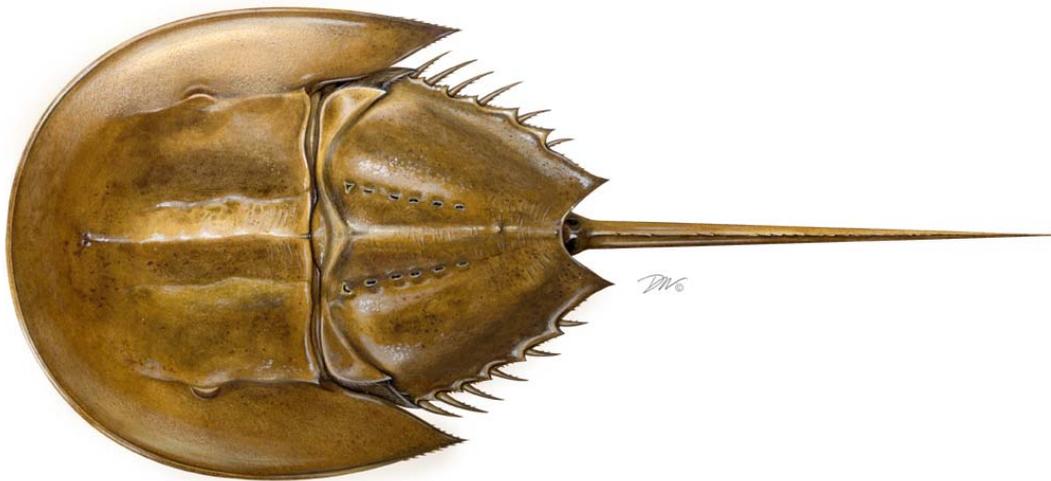


**Stock Assessment Report No. 09-02 (Supplement B)
of the**

Atlantic States Marine Fisheries Commission

*A Framework for Adaptive Management of Horseshoe Crab
Harvest in the Delaware Bay Constrained
by Red Knot Conservation*



November 2009



*Healthy, self-sustaining populations for all Atlantic coast fish species or
successful restoration well in progress by 2015*

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Harvest in the Delaware Bay Constrained
by Red Knot Conservation*

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Executive Summary

- We present a framework for the adaptive management of horseshoe crab harvest in the Delaware Bay constrained by Red knot conservation. The framework has been developed in conjunction and in communication with the Horseshoe Crab and Shorebird Technical Committees.
- The framework is comprised of objectives with utilities, alternative harvest policies, predictive models, optimization algorithms, monitoring programs, and procedures to update the predictive models. Uncertainty is incorporated throughout the framework.
- The objective statement and utility functions, which were developed through lengthy discussion with the Technical Committees, are the first step to identifying optimal horseshoe crab harvest policy. The utility functions specify the value placed on harvest as a function of the population sizes of both species. To achieve multi-species objectives, harvest of female horseshoe crabs is devalued when red knot and female horseshoe crab abundance are low, and male harvest is devalued when horseshoe crab population sex ratio limits population growth rate.
- The utility functions reflect the stakeholders risk tolerance to the possibility of red knot extinction and can be revised and update to reflect shifting society values or new data in future iterations of the adaptive management paradigm.
- The five alternative harvest policies range from full moratorium to a maximum harvest of 420,000 males and 210,000 females, including two male only harvest options.
- The linked population models for horseshoe crabs (*Limulus polyphemus*) and red knots (*Calidris canutus*) in the Delaware Bay predict the consequences of the alternative harvest levels on both horseshoe crabs and red knots.
- Computational constraints limit the set of competing models and uncertainties that can be evaluated simultaneously. Thus, with input from the Technical Committees priorities were established for which model set and sources of variation would be incorporated in the optimization.
- To obtain the most accurate estimates of parameters possible for the predictive models, we developed a new multistate robust-design model for Red knot mark-recapture-resighting data. We modeled mass transition probabilities of red knots during the Delaware Bay stopover period as a function of horseshoe crab population covariates. We also modeled Red knot survival as a function of mass at departure from Delaware Bay and environmental conditions in the Arctic. We found evidence supporting the link between these two species, with horseshoe crab numbers appearing to be associated with mass gain and annual survival of red knots dependent on mass at departure.

- Application of the framework results in an optimization table that recommends harvest policy for all possible combinations of population levels. The optimization table is too large to present in its entirety, however we present harvest recommendation from recent years population estimates and use simulation tools to project possible harvest rates into the future. The policy recommendations take into account ecological and environmental uncertainty.
- Lastly, an efficient monitoring program is necessary to monitor the populations and reduce uncertainty in the predictive models. Directed monitoring is an important part of any successful adaptive management program, and the development of this work has resulted in recommendations for improving current monitoring efforts.

Introduction

Since 1998, the horseshoe crab fishery has been managed cooperatively by Atlantic coast states through the Atlantic States Marine Fisheries Commission (ASMFC 1998). The onset of a regulated fishery led to a series of efforts to improve data collection needed for a formal coast-wide assessment (see Smith et al. 2009a for a review of assessments). Because much of the concern about a reduced horseshoe crab population centered on the ecosystem services provided by high abundance of horseshoe crabs within Delaware Bay, a traditional single-species assessment was not sufficient for managing harvest of the Delaware Bay population of horseshoe crabs. To correct this deficiency, an effort began in 2007 (Breese et al. 2007) to develop a multi-species approach to managing horseshoe crabs by employing the tools of structured decision making and adaptive management.

Structured decision making (SDM) is a formal and transparent approach to decision making (Hammond et al. 2002) that incorporates views of all stakeholders and utilizes predictive modeling to assess the potential consequences of alternative actions (Gregory and Keeney 2002). The key to successful decision making is to break a complex decision down into its component parts and address each part sequentially (Hammond et al. 2002, Gregory and Keeney 2002). The decision analysis follows a sequence in which the problem is defined, the management objectives are identified, potential alternative actions are determined, and models are developed for the purpose of projecting the consequences of the actions. For management of natural resource systems, estimates of system state (e.g., population size) are obtained and then used with the above components to make the decision, often with the help of an optimization algorithm.

SDM is an emerging tool in the field of natural resource management (Gregory and Long 2009, Martin et al. 2009). Adaptive management, which can be viewed as structured decision making for sequential decision processes, is becoming increasingly important and has been endorsed by federal management agencies (Williams et al. 2007). The approach entails making predictions about how a system will respond to management actions, followed by implementation and monitoring of the system to evaluate the accuracy of the a priori predictions. The SDM approach builds on existing approaches in several important ways. First, there is a great emphasis on complete elicitation of objectives and management actions from a full range of stakeholders. Second, competing models of how the system works (i.e., how species respond to management actions; how species interact with other species and their environment) can be incorporated into the decision process. Third, optimization tools, which allow for uncertainty, are used to find the management action that best meets the, sometimes conflicting, objectives. Fourth, monitoring data are used to assess the relative predictive abilities of competing models, and those predictive abilities can be used to update how much weight each model is given in the decision process. This last point illustrates that in an iterative setting where decisions are made repeatedly over time, the system models can be improved based on the accuracy of their predictions, and future decisions can be improved (Williams et al. 2007). Optimization algorithms, such as stochastic dynamic programming, enable managers to maximize gain or minimize risk in the face of uncertainty about the managed system (Williams et al. 2002). Four types of uncertainty characterize natural resources management: 1) ecological or structural uncertainty, 2) environmental uncertainty, 3) partial controllability, and 4) partial observability. In the face of

these sources of uncertainty, stochastic dynamic programming is used to find an optimal management policy given the objectives and available actions, the understanding of the system as reflected by the system models, and the estimated state of the system.

In 2007, the Horseshoe Crab and Shorebird Technical Committees met and endorsed the development of an SDM and adaptive management approach to harvest management. The committees nominated members of an adaptive resource management (ARM) working group and tasked the group with developing an adaptive management framework. The working group has met regularly and has met periodically with the technical committees to receive advice and consent.

In this report we present the progress of the ARM working group for the Delaware Bay in working through the SDM process as applied to horseshoe crab harvest. The report focuses on the details of structure and parameterization of population models with competing formulations of functional relationships and state dynamics for horseshoe crabs and red knots in the Delaware Bay. The models were coded into the software program ASPD (Lubow 1995, 2001) and will be used in an optimization setting to evaluate the consequences of the predetermined alternative actions and determine optimal harvest levels of horseshoe crabs in the Delaware Bay. These recommended harvests are optimal with respect to objectives that involve maintaining the crab fishery and providing sufficient resources to maintain viable populations of red knots. We have focused much of our effort on incorporating ecological uncertainty (competing models of system response to management) and environmental stochasticity into the decision analysis.

Management Objectives

Objective Statement

We are operating under the following general objective statement that describes management goals using qualitative language:

Manage harvest of horseshoe crabs in the Delaware Bay to maximize harvest but also to maintain ecosystem integrity and provide adequate stopover habitat for migrating shorebirds.

Translating the qualitative statement into a quantitative objective statement framed in terms of the measurable state variables of interest is a fundamental challenge (Keeney and Gregory 2005). We developed a set of utility functions that define under what conditions horseshoe crab harvest is valued. The utility functions (described below) reflect the stakeholders' risk tolerance/aversion to the possibility of red knot extinction due to horseshoe crab harvest regulations. The Technical Committees often preferred to invoke caution when determining management objective and set management thresholds with the intent of being conservative to account for our scientific uncertainty. The utility functions (as is partly demonstrated below) can be adapted, as the adaptive management effort moves forward, to reflect changes in societal values or new data and information about the system.

At the National Conservation Training Center structured decision making workshop in July 2007 (Breese et al. 2007) and at subsequent joint meetings of the Horseshoe Crab and Shorebird Technical Committees of the ASMFC, committee members developed the initial statement of management objectives:

Maximize allowable harvest of horseshoe crabs with the constraint that 90% of early arriving red knots reach 180 g by May 28th. [Comment: The objective statement links horseshoe crab and red knot populations by isolating the influence of horseshoe crabs, through their eggs on red knot weight gain during stopover.]

That statement has been scrutinized and revised repeatedly since that time because it did not adequately link management to the state variables of horseshoe crab and red knot abundance. The Joint Technical Committees has discussed objectives at length and made numerous revisions. This report reflects the most up to date objective statement devised by the ARM working group in conjunction with the Joint Technical committees. The current objective statement is:

Maximize harvest of horseshoe crabs in the Delaware Bay with constraints that 1) harvest of female crabs is valued only when red knots exceed an abundance threshold or female horseshoe crabs exceed an abundance threshold. 2) Harvest of males is valued only when males do not limit horseshoe crab reproduction (conversely, horseshoe crab population growth rate will not increase with additional males in the population). Figure 1 graphically depicts the utility functions.

This updated version of the objective statement changes the constraints on horseshoe crab harvest from the proximate objective of red knot weight gain in the Bay to the ultimate objective framed in terms of overall red knot abundance. In fact, all constraints on harvest relate to abundance of one species or the other. We made these changes because several of the metrics delineated in the early version of the objective statement were either hard to define in reality (i.e., “early arriving red knots”) or very difficult to empirically measure (i.e., the fraction of red knots that reach 180 grams by May 28th). Additionally, this objective statement places the metrics of the objective and utility functions in terms of the state variables of interest in the Delaware Bay system. This shift in focus is believed to be reasonable, because managers are fundamentally concerned with maintaining sufficiently large red knot population sizes and having a high percentage of fat red knots (as described by Breese et al. (2007)) is a means to achieving that fundamental objective.

The Objective and Utility Functions

The harvest objective and utility functions are quantitative translations of the objective statement, and these functions are used in the dynamic programming environment to find the set of harvest policies that maximize the utility or reward. Using management thresholds (Martin et al. 2009), the utility functions define under what conditions horseshoe crab harvest is rewarded. The utility functions assign no value to female horseshoe crab harvest when red knot abundance

is below 45,000 individuals, unless horseshoe crab numbers are sufficiently high that they are not likely to be limiting red knot numbers. The ARM committee initially chose 30,000 red knots as the abundance threshold because it was a number that was achievable, and also sufficiently large to greatly reduce the probability of extinction. After meeting with the joint Technical Committees on March 30th and 31st, 2009, the red knot abundance threshold was increased to 45,000 to more closely reflect historic abundances observed in the Delaware Bay. The committees believe that red knots are linked to horseshoe crabs through female crab abundance and egg deposition on the beaches. Horseshoe crab harvest management should ensure that there are sufficient female horseshoe crabs in the population to provide eggs for a red knot population of at least 45,000 (Figure 1A).

Secondarily, the utility function will assign value to female horseshoe crab harvest if abundance of female horseshoe crabs reaches 11.2 million individuals, regardless of red knot status. Above 11.2 million female crab harvest is awarded full value and below 11.2 female crab harvest has no value (Figure 1B). This second constraint is intended to allow harvest if horseshoe crabs are sufficiently abundant that they are not likely to limit red knot populations. To determine the horseshoe crab abundance constraints, the joint Technical Committees agreed to set the threshold at 80% of the predicted carrying capacity of 14 million female crabs. The specific values of these thresholds are the result of the collective judgment and extensive discussion of the Joint Technical Committees, the professional opinions of shorebird and horseshoe crab biologists, and the modeling expertise of the members of the ARM working group. The constraint on female harvest in the utility function is as follows:

$$u_f = \left\{ \begin{array}{l|l} 1, & \text{if } N_{RK} \geq 45,000 \\ 0, & \text{if } N_{RK} < 45,000 \end{array} \right. \left| \begin{array}{l} 1, & \text{if } N_{HSCAF} \geq 11.2 \times 10^6 \\ 0, & \text{if } N_{HSCAF} < 11.2 \times 10^6 \end{array} \right.$$

u_f is a utility multiplier that specifies the value of harvested females in the objective function, N_{RK} is the number of red knots in the population and N_{HSCAF} is the number of adult female horseshoe crabs. The vertical line between the two sets of conditional equations indicates that the first set of conditions is evaluated then the second. This is a mathematical representation of an “or” statement.

A separate utility function assigns a value to male harvest. Based on published experiments on horseshoe crab fertility (cf Brockmann 1990 and 2003), comparisons of adult sex ratios during spawning surveys and offshore trawl surveys of the Delaware Bay population, equilibrium sex ratios in population models, and sex ratios in unharvested populations (Tauton Bay, ME and Seahorse Key, FL), we believe that maintaining the operational sex ratio (OSR, spawning beach sex ratio) at or above 2 males to 1 female will ensure that the population growth is not limited by sex ratio. The mechanisms for sex ratio limitations on population growth are 1) amplexus of breeding females, 2) fertilization of eggs, and 3) genetic diversity. Brockmann’s behavioral research (1990, 2003) indicates that a fecund female tends to spawn only if she achieves amplexus before coming ashore and that approximately 30% of males are not capable of amplexus. Thus, there needs to be excess males on the spawning beach so that available females can pair with a male capable of amplexus, otherwise reproduction will be limited. Also, fertilization of the eggs must be maximized. Brockmann (1990 and person. commun.) has found

that satellite males (i.e., those males not in amplexus) are not needed to fertilize the eggs, even though satellite males compete to fertilize eggs when present. Lastly, genetic diversity must be conserved. Based on effective population size (N_e) for the Delaware Bay horseshoe crab population, genetic diversity would not be affected by reducing population sex ratio to 1:1 (E. Hallerman, VT, person. commun.). Given these considerations and given the uncertainty in the sex ratio limitations on fertilization and population growth, the joint Technical Committees agreed that constraining harvest as a function of operational sex ratio is appropriate but should be applied cautiously. Utility of male harvest is equal to zero if males fall below a 2:1 OSR, equal to 1 if males exceed a 3:1 OSR, and will be determined by an increasing linear function if OSR falls between 2:1 and 3:1. This complex utility function is modeled as follows:

$$u_m = \begin{cases} 0, & \text{if } \frac{N_{HSCAM} \times C}{N_{HSCAF}} \leq 2 \\ \frac{N_{HSCAM} \times C}{N_{HSCAF}} - 2, & \text{if } 2 < \frac{N_{HSCAM} \times C}{N_{HSCAF}} \leq 3 \\ 1, & \text{if } \frac{N_{HSCAM} \times C}{N_{HSCAF}} \geq 3 \end{cases}$$

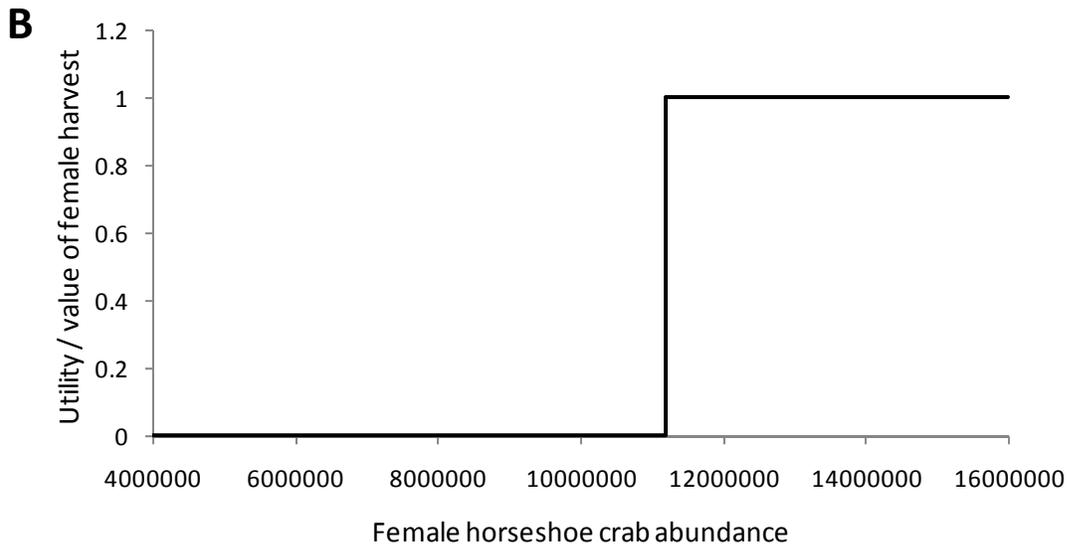
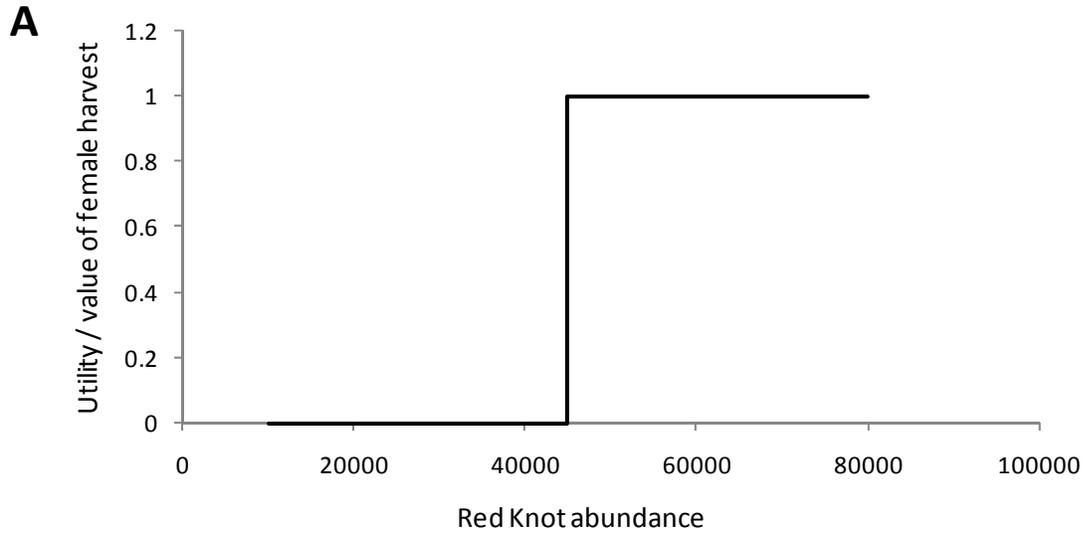
u_m is a utility multiplier on the number of males harvested in the objective function used by ASDP to maximize reward from HSC harvests over an infinite time horizon. N_{HSCAM} is the number of adult male horseshoe crabs in the population, C is the conversion factor for males from population sex ratio to OSR on spawning beaches, N_{HSCAF} is the number of adult females in the population. The operational and population sex ratios will be monitored and the underlying assumption that reproductive capacity will not be limited for OSR >2 will be evaluated periodically. Also, fertilization rate of deposited eggs should be monitored.

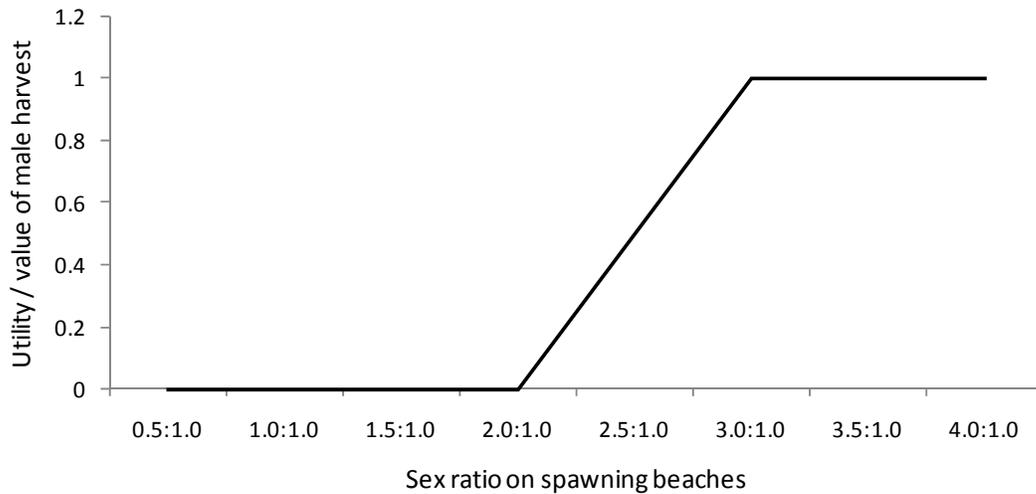
The objective or ‘reward’ function for the optimization analysis is:

$$Reward = \left(\sum_{t=1}^{\infty} (2 \times H_{HSCAF,t} \times u_{f,t} + H_{HSCAM,t} \times u_{m,t}) \right)$$

where *Reward* is the value extracted from the system, H_{HSCAF} is the number of adult females harvested, H_{HSCAM} is the number of adult males harvested. If either u_f or u_m equals zero, the value or reward from that harvest will be zero. In the reward calculation, we give harvested females twice the value of harvested males to reflect the higher market value of females horseshoe crab in the fishery (Figure 1). The optimization program is used to identify an optimal policy that maximizes the reward over an infinite time horizon. Use of an infinite time horizon implies value of horseshoe crab harvest into the indefinite future and thus imposes a conservation ethic on the objective (i.e., it is never optimal to harvest horseshoe crabs to extinction for current gain).

Figure 1: Graphical depiction of the utility function that constrains horseshoe crab harvests in the Delaware Bay. A) red knot abundance constraint, B) female HSC abundance constraint C) operational sex ratio constraint on male harvest



C

Alternative Actions

At the October, 2009 joint meeting of the Horseshoe Crab and Shorebird Technical Committees a set of alternative management actions was defined and finalized to reflect the recommendations of the managers, stakeholders, and researchers. The committees settled on 5 alternative horseshoe crab harvest packages. 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 October the Technical Committees agree to eliminate what was formerly option 6 (495,000 males, 330,000 females) from the management alternatives because this option appeared to be a politically infeasible option. Implementing this option at the current time would likely lead to political resistance to our management efforts and so the harvest option was set aside for possible reintroduction at a later date. Harvest option 4 approximately reflects current harvest allowance in the region. Our modeling and optimization does not address allocation of the harvest among states. Based on tagging (Swan 2005) and genetic analysis (Pierce et al. 2000), there is limited exchange between Chesapeake Bay and Delaware Bay populations. However, there is exchange between coastal embayments and Delaware Bay. The proportion of Maryland and Virginia landings that come from Delaware Bay is currently unresolved, but the stock assessment subcommittee has taken a conservative approach to estimating that proportion.

Models

Overview

Population models were developed to 1) predict the consequences of horseshoe crab harvest on abundance of horseshoe crabs and red knots, 2) represent competing hypotheses about the linkages between red knot and horseshoe crab populations, and 3) incorporate uncertainty in model predictions. We developed 6 alternative models to represent the hypothetical linkages

between horseshoe crab and red knot population dynamics. Two formulations of the horseshoe crab populations (a matrix based population model, and a logistic growth model), matched with three models of the relationship between horseshoe crab abundance and red knot population dynamics, and a single basic red knot matrix population model.

ASDP can only handle first order Markovian processes, meaning that the current state of the system can only be dependent on the state of the system at one time step prior. The Sweka et. al (2007) age structured population model for horseshoe crabs was essentially a non-Markovian system because current recruitment in that model was dependent on female population size 10 to 12 years in the past and on juvenile survival rates in the intervening years. It is possible to turn this population structure into a first order Markov process by keeping track of each age class as a separate state variable; however that approach far exceeds ASDP's computational capacity.

We created two alternative population structures for Delaware Bay horseshoe crabs. The first was a modified Sweka et. al (2007) model that converted the age structure into a stage structure, where all 10 juvenile age classes were transformed into one juvenile stage. We added an intermediate pre-breeding stage, and we included a breeding adult stage for both males and females. The stage structured model incorporates a sex ratio feedback whereby if the population becomes too skewed towards females, fecundity and population growth rates of both sexes will decline. It should be noted that the model does not entirely account for the time lag created by the long juvenile period. The second was a logistic growth model based on the Davis et. al (2006) surplus production model of horseshoe crabs in the Delaware Bay. This model required an intrinsic population growth rate and a maximum carrying capacity. At the March 30th – 31st joint meeting of the Horseshoe Crab Technical Committee and the Shorebird Technical Committee, it was agreed to set the logistic model aside, at least for the initial iteration of the SDM and ARM process. Because of optimization software limitations it was important to limit the candidate model set at this time, and the ARM working group recommended that the logistic model be excluded from the decision analysis, because the stage-structured model is predicts a slower growth rate for horseshoe crabs and is therefore more conservative. We intend to re-evaluate the logistic growth model as monitoring and data collection efforts continue.

Construction of the red knot population model was more straightforward, and we used a modified version of the Baker et al. (2004) three-stage population model. Within the adult stage, birds are in one of two weight states, above or below a threshold weight of 180g. Our model tracks arrival time and weight, weight gain and departure probabilities in the Delaware Bay. The weight gain probabilities are tied to horseshoe crab abundance and the proportion of the crab population that spawns during the stopover period. At the end of the stopover season, the two weight states of adult red knots survive and reproduce at different rates. This model structure reflects the discussions we have had within the ARM work group and follows the efforts of the ongoing multi-state survival estimation. The models use a pre-spawning/stop-over census to keep track of population size.

In summary, we developed an ASDP model with a total of six state variables (including one juvenile stage, a pre-recruit stage, adult males, and adult females for horseshoe crabs and juveniles and adult red knots). The high dimensionality of the resulting models limits our ability to incorporate sources of uncertainty (e.g., environmental stochasticity) into ASDP. For

inclusion in the model, priority was given to sources of uncertainties that were identified as important through sensitivity analysis, and expert elicitation. The three models in our set are representative of the primary hypotheses about the functional relationships between horseshoe crabs and red knots. We parameterized these models using the best available data, published demographic rates and our professional judgment.

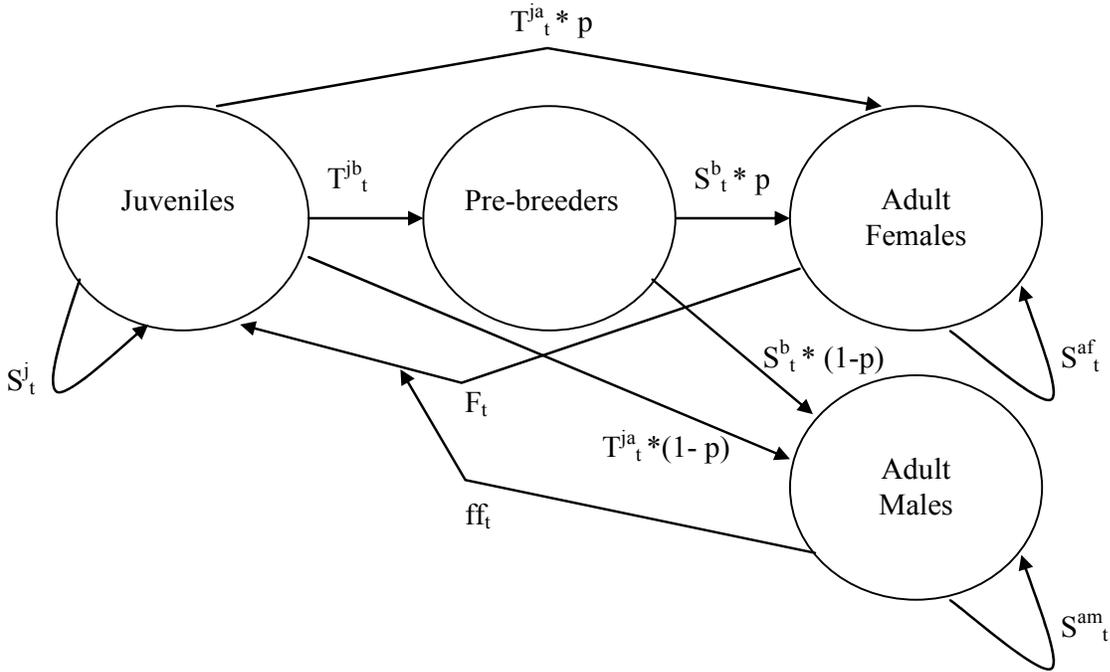
The Stage Structured Horseshoe Crab Model

This model structure and parameters were based on the Sweka et al. (2007) age structured population model. We condensed the many years of the juvenile period into one single stage with a constant probability of transition out of that stage and into either the pre-breeding stage or the breeding adult stage (Fig. 2). Juveniles may transition to any of three states: the probability of surviving the year and staying a juvenile is $S_j \sim 0.88$, the probability of surviving the year and transitioning to a pre-recruit is $T_{jp} \sim 0.093$, and the probability of surviving the year and transitioning directly to the breeding adult stage is $T_{ja} \sim 0.00074$. The animals are partitioned into different sexes as they enter the breeding adult stage, and there is an assumed sex ratio in the non-breeding stages, determined by p (probability of being female). The annual survival of pre-recruits is $S_p = 0.97$, and all surviving prebreeders transition to the breeding adult stage. Adult males and females have different survival rates associated with non-harvesting mortality sources ($S_{am} = 0.64$, $S_{af} = 0.63$), largely due to differential mortality caused by spawning. The system of equations for the stage structured model was as follows:

$$\begin{aligned}
 N_{HSCJ,t+1} &= N_{HSCJ,t} \cdot S_j + N_{HSCAF} \cdot F \cdot ff \\
 N_{HSCP,t+1} &= N_{HSCJ,t} \cdot T_{jp} \\
 N_{HSCAF,t+1} &= (N_{HSCJ,t} \cdot T_{ja} + N_{HSCP,t} \cdot S_p)p + (N_{HSCAF,t} - H_{HSCAF,t})S_{af} \\
 N_{HSCAM,t+1} &= (N_{HSCJ,t} \cdot T_{ja} + N_{HSCP,t} \cdot S_p)(1 - p) + (N_{HSCAM,t} - H_{HSCAM,t})S_{am}
 \end{aligned}$$

where N_{HSCJ} is the number of juveniles in the population, N_{HSCP} is the number of pre-recruits, N_{HSCAF} is the number of adult females, N_{HSCAM} is the number of adult males, F is the fecundity (see below), ff is a fertility factor that reduces fecundity when the male to female sex ratio of the adult population falls below 1:1 (2:1 operational sex ration, see below), S and T parameters are the survival and transition probabilities described above and p is the proportion of females in the non-breeding stages, which we set at 0.5 assuming a 1:1 sex ratio of eggs (Smith et al 2009). H_{HSCAF} and H_{HSCAM} are the number of adult females and males harvested from the population. These equations currently define a deterministic model for use with ASDP, but they can be modified to include stochastic variation in survival, transition, and fecundity rates, and in sex ratio.

Figure 2: Schematic of the stage structure horseshoe crab population model

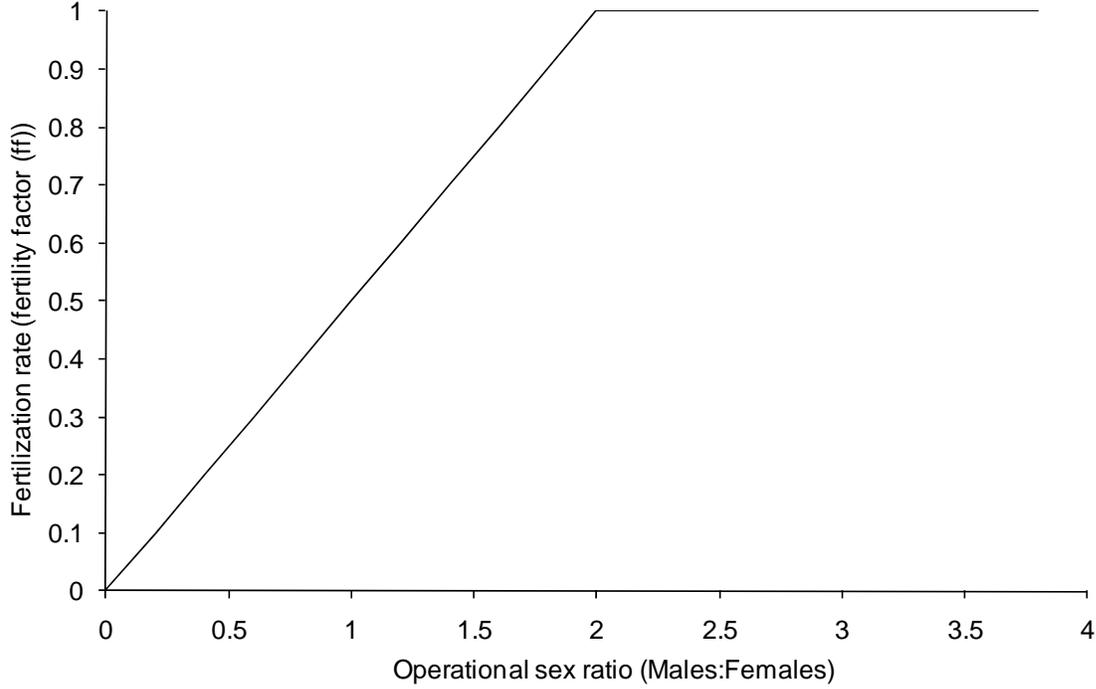


The fertility factor (ff) reduces reproduction when the operational sex ratio of the adult stages falls below a target, OSR^* . We used a simplified version of one of the fertility functions provided by Caswell (2001) to limit reproduction. We borrow Caswell's term 'fertility function' but recognize that the mechanism for sex ratio limitations of reproduction is the availability of sufficient males for amplexus. Our calculations were as follows:

$$ff = \begin{cases} 1, & \text{if } \frac{N_{HSCAM} \cdot C}{N_{HSCAF}} \geq 2 \\ 1 - \left(\frac{N_{HSCAF} - N_{HSCAM}}{N_{HSCAF} + N_{HSCAM}} \right), & \text{if } \frac{N_{HSCAM} \cdot C}{N_{HSCAF} + N_{HSCAM}} < 2 \end{cases}$$

where C is the conversion between population and operational sex ratio. C was estimated from the Delaware Bay spawning survey and the offshore trawl survey to be 1.88. The target OSR (i.e., OSR^*) is set equal to 2 based on reasoning presented earlier in the report. Both C and OSR^* will be periodically evaluated. .

Figure 3: Relationship between operational sex ratio (OSR) and population level fertility rates (ff). Derived from the above expression (also see Caswell 2001).



Finally, we imposed the same density dependent egg mortality function that Sweka et al. (2007) incorporated into their age structured model.

$$S_{e,t} = 1 - B \cdot \ln(N_{HSCAF}) - a$$

where $S_{e,t}$ is the survival of eggs to hatching, B and a are regression parameters, and N_{HSCAF} is abundance of mature females (Sweka et al. 2007). The density-dependent relationships were based on a simulation study linking egg exhumation and mortality to female spawning density based on spatial competition on spawning beaches (Smith 2007). Sweka et al. (2007) modeled 3 different density-dependent relationships, and we used the lowest level of density dependence. We chose the lowest level because Sweka et al. (2007) reported that highest level resulted in non-viable horseshoe crab populations and the intermediate level predicted a carrying capacity that was lower than the current population size (Hata and Hallerman 2009).

The number of eggs laid per female ($E = 80,300$), egg survival (S_e) and age zero survival ($S_{0,t} \approx 0.00003$) was incorporated as a multiplier on fecundity in the state dynamics equations for the horseshoe crab populations as follows:

$$F_t = E \cdot S_{e,t} \cdot S_{0,t}$$

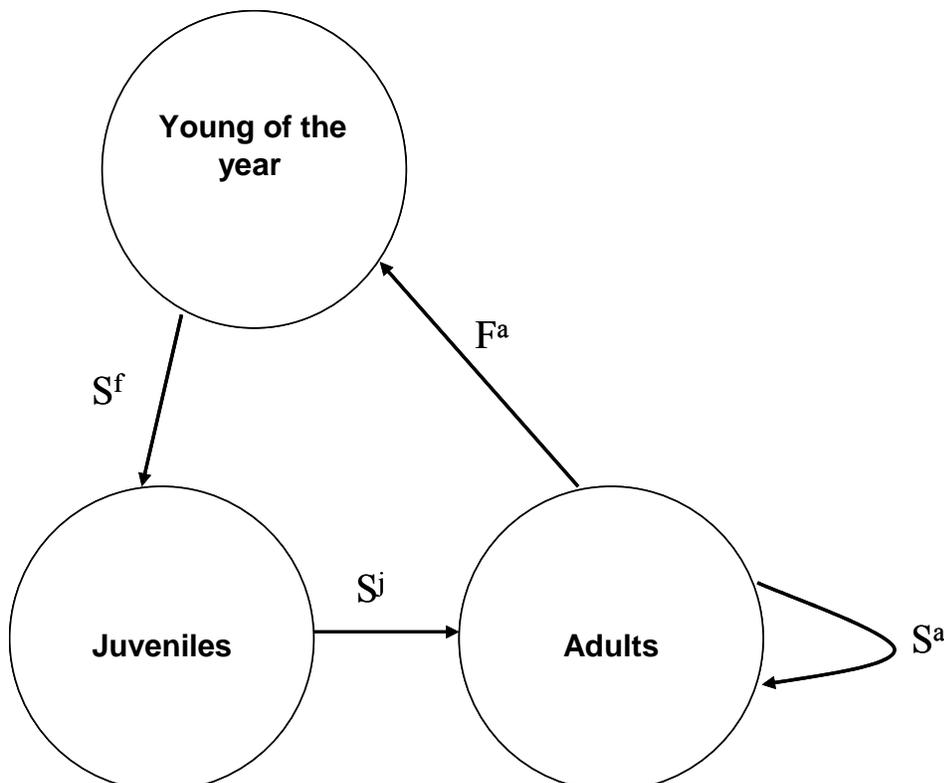
where F_t is the number of female offspring produced per breeding female. In the model, $S_{0,t}$ was modeled as a stochastic variable and ff_t varied annually with population sex ratio.

The Red Knot Population Model

The red knot population model was based on the Baker et al. (2004) formulation of the population. We created a female-only, three stage population model because young red knots do not fully mature and become breeders until after their second year (Baker et al. 2004, Niles et al. 2008). We assume an equal sex ratio in the red knot population and multiply all abundance values output by the model by two to calculate total red knot abundance (for the purposes of the utility function threshold). The ASDP program keeps track of juveniles and adults at each time step and creates two state variables in the model. For the purposes of this initial analysis the model was deterministic, and we input parameter values that were based on published literature, surrogate species or reasonable assumptions. We imposed a density dependent ceiling on the red knot population whereby if the red knot population exceeded the ceiling, fecundity was set to zero for that year. From this basic matrix model structure we created three alternative ways that horseshoe crab abundance can affect red knot population dynamics: 1) a “no interaction” model, where the two species operate independently of each other (Figure 4), 2) a fecundity only effect model, where horseshoe crabs affect only the fecundity or productivity of the red knot population (Figure 5), and 3) a full effect model where horseshoe crab abundance affects both fecundity and annual survival of adult red knots (Figure 6).

The no interaction model is a simple stage structured model with an adult stage, a young of the year stage, and an immature stage. Red knots do not typically breed until they are at least 2 years old, thus requiring a separate “immature” life stage in the population matrix. Adults breed and produce young of the year, those young of the year survive their first winter-spring at some rate and become immatures, and those immatures survive their second year and become adults.

Figure 4: Schematic of the simple stage structured population model for red knots, with no effects of horseshoe crabs on red knot population dynamics.



The equations for this model were as follows:

$$\begin{aligned} N_{j,t+1} &= N_{a,t} \cdot F_{a,t} \cdot S_f \\ N_{a,t+1} &= (N_{a,t} \cdot S_a) + (N_{j,t} \cdot S_j) \end{aligned}$$

where N_a is the number of adult females in the population, N_j is the number of juvenile females, S_a (0.92) is the adult survival rate, F_a (~ 0.3) is the fecundity rate of adults, S_f ($0.6 \cdot S_a$) is the survival rate of young of the year, and S_j ($0.85 \cdot S_a$) is the survival rate of immature (juvenile) birds. Our fecundity parameters inputs are based on published productivity data for red knots in Greenland (Moltofte et al. 2007, 2008, *islandica* sub-species). But given uncertainty in using data from a different subspecies in a different geographic location we made this parameter stochastic in our models. Some members of the Shorebird Technical Committee expressed concern that this fecundity value was too high for the *rufa* red knots, but without further data sources or published fecundity information we used the Moltofte (2007, 2008) estimates at this time. Justification for the S_a input value is given below in discussion of the alternative models and in the subsequent section on multistate survival analysis. Modeling young of the year survival and juvenile survival as 60% and 85% of adult survival follows conventions for modeling avian populations when direct estimates of these parameters are not available. Ornithology text books report that young of the year survival is typically 50-70% of adult survival rates (Gill 1995). Evans and Pienkowski (1984) showed that in some long distance migratory shorebirds first year survival was 80 - 90% of same year adult survival and second year survival did not differ from adults. To be conservative, we used fairly low rates of 60% and 85% of adult survival because we are very uncertain about these values. Other published shorebird population models have used the same approach as ours (e.g. Ryan et al. 1993).

An important current hypothesis is that red knot survival and reproduction are highly dependent on mass at the end of the stopover period in the Delaware Bay and that mass gain during the stopover period is dependent on horseshoe crab female abundance and egg densities on Delaware Bay beaches (Baker et al. 2004, Niles et al. 2009). We envision two alternatives for how horseshoe crabs affect red knots, and these models are detailed below. Both formulations of the model partition the population annually into the proportion of birds that do (P180) and do not (1-P180) reach or exceed a 180 g mass threshold in the Delaware Bay. The weight threshold is derived from metabolic studies and calculations of the minimum fuel required to fly the distance from the Delaware Bay to the breeding grounds, based on mean lean mass of the species (Kvist et al. 2001, Piersma 2002 (as cited by Baker et al. 2004)).

P180 was calculated each year in the simulation model by multiplying the proportion of birds that arrive in the bay below the threshold by the probability of transitioning from below to above threshold. The program then added the proportion of birds that arrive already above the threshold multiplied by the probability of staying above the threshold and subtracted the proportion of birds that arrive above the threshold times the probability of transitioning to below the threshold. The parameterization for this approach uses existing trapping, weight, and resighting data to estimate state-specific (where state is mass class) survival and transition probabilities. For results presented here, we partitioned the spring stopover season into three periods, early, middle and late. Birds arrive in the Bay either in the first, second or third time

period as heavy or lightweight birds and then either transition to the other weight class or remain in the same class based on some probability. The equation for calculating P180 was as follows: $P_{180} = \beta^{L,1} \cdot \psi^{LH,1} + \beta^{L,2} \cdot \psi^{LH,2} + \beta^{L,1}(1 - \psi^{LH,1})\psi^{LH,2} + \beta^{H,1} \cdot \psi^{HH,1} \cdot \psi^{LH,2} + \beta^{H,2} \cdot \psi^{HH,2}$ where $\beta^{L,i}$ is the probability of arriving in the Bay during period one or two as a lightweight bird, $\psi^{LH,i}$ is the probability that a bird arriving under the weight threshold will transition to a heavyweight bird, $\beta^{H,i}$ is the probability that a bird arrives in period one, two or three as a heavy bird, $\psi^{HH,i}$ is the probability that a bird arriving over the weight threshold will remain over the. The above equation assumes that birds arriving in the third period do not have the opportunity to transition and that once a bird has arrived in the bay and success fully transitioned to above 180 g they will not lose weight and transition back. The probability of departing the bay under the 180 g threshold was simply $1 - P_{180}$. ψ^{HH} was set to 0.95 assuming that most animals do not transition to lower weight classes once they reach the Bay. The parameter ψ^{LH} was modeled as a function of the number of female crabs that were spawning during the spring migration period as follows:

$$\psi^{LH} = \frac{\exp(B_0 + B_1(N_{HSCAF} \cdot P_{sp}))}{1 + \exp(B_0 + B_1(N_{HSCAF} \cdot P_{sp}))}$$

N_{HSCAF} is the number of adult female horseshoe crabs, and P_{sp} is the proportion of the crab population that spawns during the migration. The slope (B_1) and intercept (B_0) of the relationship relating ψ^{LH} to the horseshoe crab population under 1 model were estimated in the multistate robust-design analysis described in this report.

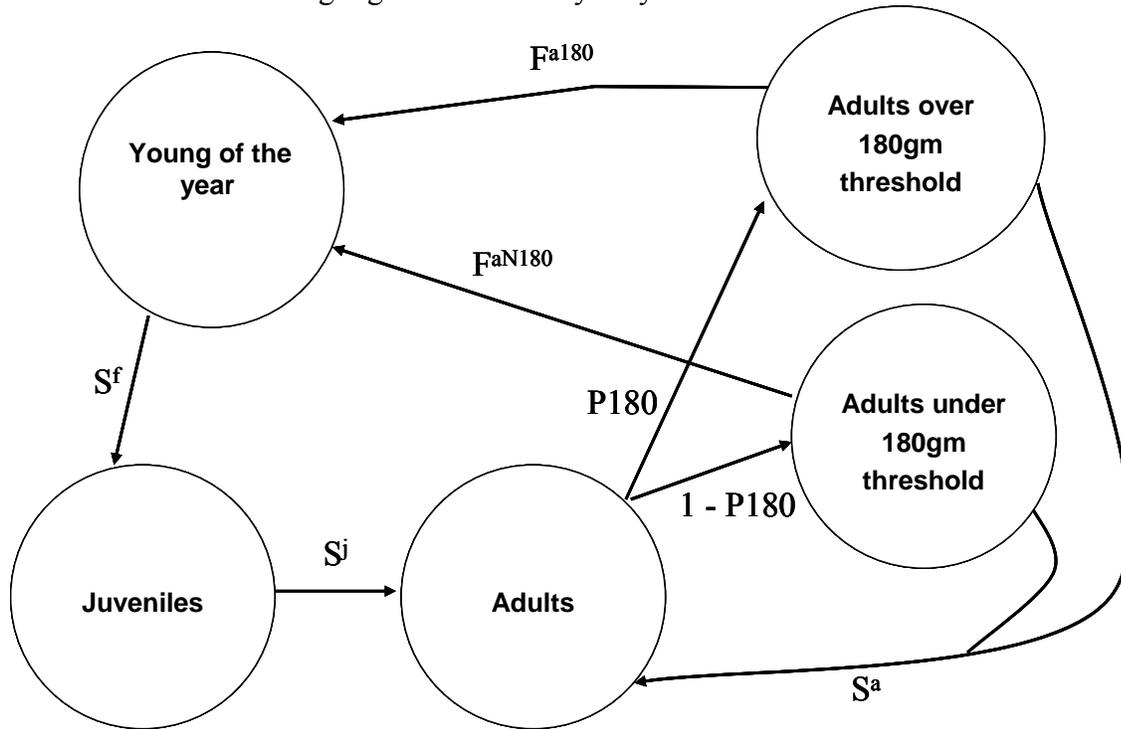
The fecundity-only effect model has similar survival rates for birds above and below the 180 g mass threshold at the end of the stopover period (see the multistate survival analysis section in this report, Figure 5). However, the model does incorporate differential fecundity for birds that achieve the mass threshold and those that do not (Figure 5). Fecundity for birds that reach 180 g (F_{180}) was set at 0.4 females produced per breeding female, and fecundity for birds not reaching the 180 g threshold was set at 0.05. Heavy bird fecundity was based on data presented in Meltofte et al. (2008) for red knots in Greenland, where they reported that 2.5 chicks fledged per successful brood and that approximately 20% of all birds successfully bred. Because the F^{a180} parameter only applies to the proportion of the population that reaches 180 g, we assumed that the success rate was higher than Meltofte (2008) reported rates and set F^{a180} at 0.4. Adult survival was estimated in the multistate survival analysis, young of the years was set at 60% of adult survival and juvenile survival was set as 85% of adult survival. This model accounts for the possibility that most birds that do not achieve the necessary weight during stopover, forego migrating to the Arctic to breed, thus minimizing or erasing the effects of mass on survival but retaining the effects of mass gain on fecundity. The model equations were as follows:

$$N_{j,t+1} = N_{a,t} \cdot P_{180,t} \cdot F_{180,t} \cdot S_f + N_{a,t}(1 - P_{180})F_{N180,t} \cdot S_f$$

$$N_{a,t+1} = N_{a,t} \cdot S_a + N_{j,t} \cdot S_j$$

where N_a is the number of adult females in the population, N_j is the number of juvenile females, S_a is the adult survival rate, P_{180} is the proportion of the population that reaches 180 g during the stop over period, F_{180} is the fecundity rate of birds that reach 180 g, S_f is the survival rate of young of the year, S_j is the survival rate of immature (Juvenile) birds, and F_{N180} is the fecundity rate of birds that do not reach 180 g.

Figure 5: Schematic of the red knot population dynamics model with effects of horseshoe crab abundance and knot weight gain on fecundity only.



Baker et. al (2004) estimated that survival of birds that do not reach the mass threshold by the time of departure was much lower than that of birds that did attain the weight threshold. This inference corresponds to the third formulation of the red knot model in which the proportion of birds reaching 180 g survive and reproduce at one rate and the proportion not reaching 180 g survive and reproduce at lower rates. Fecundity for birds that reach 180 g (F_{180}) was set at 0.24 females produced per breeding female, and fecundity for birds not reaching the 180 g threshold was set at 0.05. Adult survival was set at 0.92 for birds reaching 180 g, young of the years was set at 60% and juvenile survival was set at 85% of heavy adult survival. Adult survival for birds not reaching 180 g was set at 0.60. The model equations were as follows:

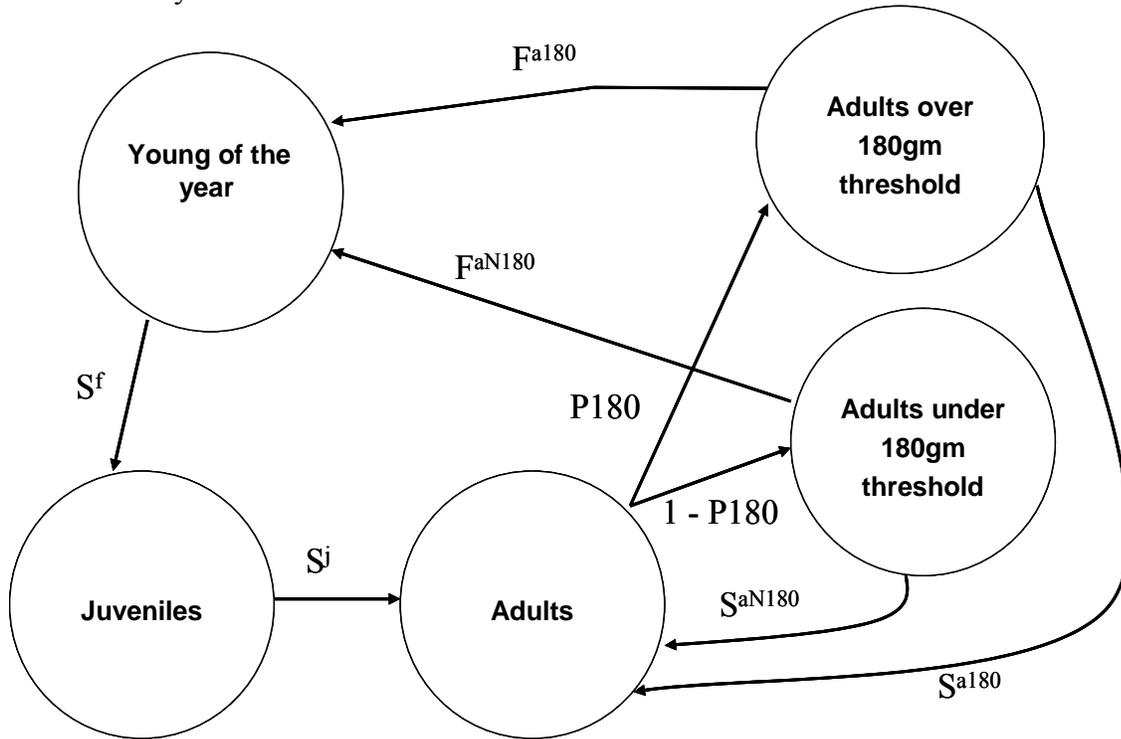
$$N_{j,t+1} = N_{a,t} \cdot P_{180,t} \cdot F_{180,t} \cdot S_f + N_{a,t}(1 - P_{180,t})F_{N180,t} \cdot S_f$$

$$N_{a,t+1} = N_{a,t} \cdot P_{180,t} \cdot S_{a180} + N_{a,t}(1 - P_{180,t})S_{aN180} + N_{j,t} \cdot S_j$$

where N_a is the number of adults in the population, P_{180} is the proportion of the population that reaches 180 g during the stop over period, S_{a180} is the survival rate of adult birds that reach 180 g,

S_{aN180} is the survival rate of birds that do not reach 180 g, F_{180} is the fecundity rate of birds that reach 180 g, S_f is the survival rate of young of the year, S_j is the survival rate of immature (Juvenile) birds, and F_{N180} is the fecundity rate of birds that do not reach 180 g.

Figure 6: Schematic of the red knot population model where horseshoe crab abundance affects both fecundity and adult survival.



Weight-based Multistate Survival Analysis

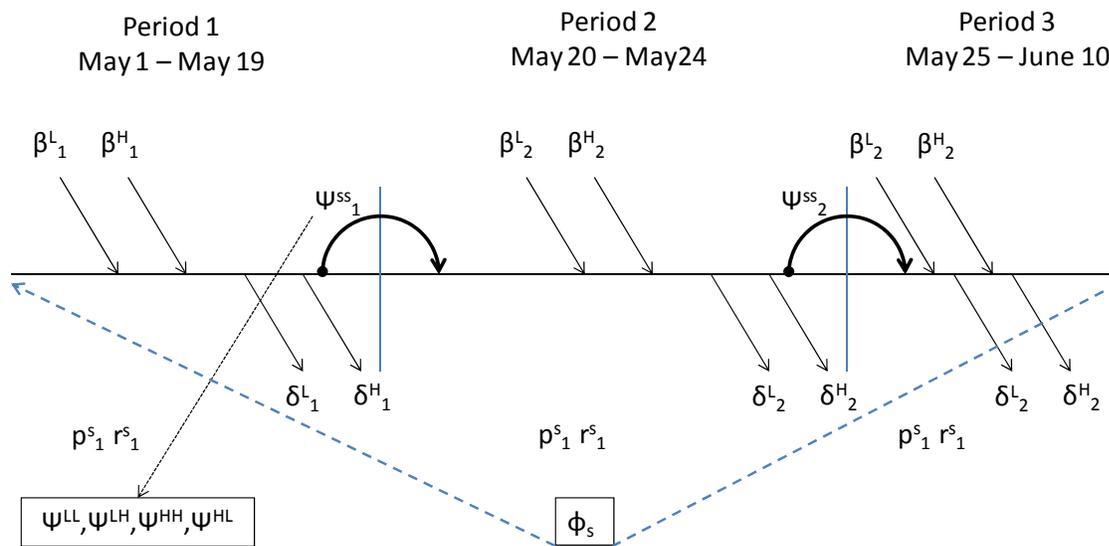
Introduction and Methods

We developed mark-recapture models to estimate annual survival of Delaware Bay red knots based on mass at the end of the migratory stopover. Because of the hypothesized relationship between female horseshoe crab abundance and mass gain of red knots (Niles et al. 2009), the survival modeling provides a direct link between red knot population dynamics and female horseshoe crab abundance. Our approach expanded on existing methods of open robust design (Kendall et al. 1997, Kendal and Bjorkland 2001) and multistate survival analyses (Nichols and Kendall 1995), and incorporated both mark-recapture data and mark-resighting data to estimate mass-specific survival probabilities and transition probabilities among mass states. The resighting data do not have any information on an individual’s weight state at the time of observation; however, we developed models to take advantage of the substantial resighting dataset, which greatly improves survival estimate precision but would have otherwise been unusable for our purposes. This analysis represents an effort to directly and quantitatively link

red knot demographics (annual survival) to horseshoe crab abundance through weight gain in the Delaware Bay.

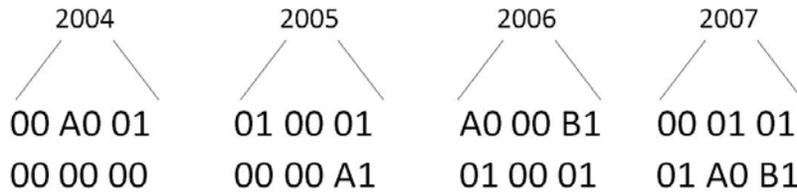
We established two weight classes (states) for Knots in the Bay, < 180 g and ≥ 180 g. We also split the stopover season into three periods, 1 May – 19 May, 20 May – 25 May, and 26 May – 5 June. Most of the information required by the state transition analysis is provided by individuals that were caught and weighed. Birds that were weighed in two different sampling periods within a single season were especially useful in informing the models of state transition dynamics. We created the sampling periods to try and maximize the number of within season recaptures to improve estimation precision. Approximately one third of all captures between 1997 and 2008 occurred in each of the three sampling periods.

Figure 8: Depiction of the division of the stop-over period into three sub-periods to estimate survival and weight gain probabilities in a multistate open-robust-design analysis



In the analysis, birds could enter the Bay during any of the 3 periods and depart the Bay during any period in either weight state. Once in the Bay, the birds could transition from either weight state to another weight state or stay in the same weight state between periods. In the data, birds could be physically captured, weighed and assigned to a weight state, or they could be observed in the field without state information. For each observation period we had two pieces of data in the individual capture histories, captured or not (with weight state for captures) and observed or not for each capture period in the stopover season:

Figure 9: Presentation of example capture histories for the multistate, open-robust-design analysis.



The above figure displays example capture histories for four years of data collection. The data are grouped into three doublets in each year to represent the three capture periods. In the figure, “A” indicates that a bird was captured below the 180 g threshold (L), “B” indicates that a bird was captured above the 180g threshold (H), and “1” indicates that a bird was observed. A “0” in the first column of a sampling period doublet indicates the bird was not captured, and a “0” in the second column indicates that a bird was not seen or observed.

With these data and our multistate, open robust design analysis we can estimate a number of parameters associated with the ecological and sampling processes that generated the data: arrival probability (β), departure probability (δ), capture probability (p), resight probability (r), transition probability (ψ) and annual survival probability (s). Survival probability was assumed to approach 1 during the stopover period, but otherwise we had the potential to evaluate possible state-dependence, period-dependence, and/or year-dependence for all other parameters. We can also assess whether time-specific environmental covariates can be used to model any of the parameters as a means of examining relationships between the environment and red knot demography. The data are excellent in some respects (large number of resightings) but marginal in other respects. Data on body mass are not abundant and data on mass transitions are very sparse. In our data set, we have only 188 total within-season recaptures between 1997 and 2008, and some years had no within-season recaptures.

We developed and compared a set of candidate models (Brunham and Anderson 2002) describing the potential relationships between horseshoe crab populations, red knot weight gain and red knot annual survival. The models focused on evaluating three research hypotheses: 1) heavy birds have a higher probability of annual survival than light birds, 2) arctic weather conditions upon arrival influence red knot annual survival, with lower survival rates predicted for years of high snow cover, 3) horseshoe crab spawning abundance positively affects red knot weight transition probabilities during the Delaware Bay stopover. Initially, we determined the best model structure for parameters associated with the sampling process (capture probabilities, resighting probabilities) and ecological parameters not under direct investigation (arrival probabilities, departure probabilities). We compared the various combinations of state-, time-, and period-dependency of capture and resighting probabilities while keeping other parameters as general as possible (year-specific survival probabilities, period-specific mass transition probabilities constant across years, state- and period-specific entry and departure probabilities). We settled on capture probabilities that were state plus year dependent (i.e., capture probabilities varied across years but in a parallel manner for the 2 mass classes) and resight probabilities with state, period and year interactions. Adding period dependency (interaction or additive) to the capture probabilities produced models that appeared to fit the data well, but that produced

unrealistic parameter estimates. We set resighting probabilities before to 2003 to zero since field readable bands were not used prior to that season.

To examine our research hypotheses regarding state transition probabilities, we modeled these transitions as a function of female horseshoe crab abundance, as period dependent, and as horseshoe crab and period dependent (additive and interaction terms), as well as with null models (no covariates or temporal structure). As an index of horseshoe crab spawning abundance we combined data from the annual Virginia Tech offshore trawl survey (Hata and Hallerman 2008), with the beach based spawning survey (Smith et. al 2002, Smith and Michels 2006). We multiplied the proportion of spawning that occurred during the month of May (from the spawning survey data) by the estimated female abundance from the trawl survey following fall. We used trawl survey data from the same calendar year as the modeled stopover period, because we believe that the trawl survey samples the post spawning population as they exit the bay and return to the Atlantic Ocean for the winter months. We also compared models that restricted the covariate structure on transitions from heavy to light. In looking at the data set, we only observe four within-season transitions from a heavy state to a light weight and an additional seven transitions from heavy to heavy. Because of this paucity of data, we included in the candidate model set models that removed horseshoe crab covariate relationships from the heavy to light transitions.

To examine our research hypotheses regarding adult annual survival we included models with no structure on survival (null models), state dependent survival models, snow dependent survival models, and snow and state dependent survival models (additive and interactions terms). Morrison (2006) and Morrison et al. (2007) reported that the arrival condition in the arctic was a key predictor of survival for European red knots (subspecies *icelandica*) breeding on Ellesmere Island, Canada. They concluded that birds leaving the stopover sites in Iceland at low weights had high mortality when arriving on the breeding grounds if there was extensive snow cover on the ground. Those same effects may hold true for *rufa* red knots of the Delaware Bay. We hypothesized that the effects of poor departure condition would be exacerbated by deep snow on the breeding grounds and expected to see low survival of low weight birds in years of high snow. We also expected to find no relationship between heavy birds and Arctic snow depth. We used data from the Canadian National Climate Data and Information Archive (available online) from four weather stations distributed throughout the red knot breeding range (Resolute, Cambridge Bay, Taloyoak, and Coral Harbour). We chose these stations because they were within the red knot breeding range and had data spanning all years of our mark recapture study. We used the average snow depth and number of days below zero from all four sites as covariates in our “arctic conditions” survival models. We used an AIC information theoretic approach to compare the fit of candidate model to the data (Burnham and Anderson 2002).

Results

We had a total of 188 within season recaptures in the data set after partition captures into the three sampling periods (Table 1). One hundred thirty three within season recaptures were of individuals that did not transition between weight states, but remained light or heavy weight. Fifty five within season recaptures document transitions between weight states, four of those

were transitions from heavy to light. Despite this sparse data, we still estimated the hypothesized relationship and the model selection procedure supported all three of our research hypotheses.

Table 1: Summary of red knot within season recaptures and observed transitions between 1997 and 2008

Year	Total L->H	Total H->L	Total L->L	Total H->H	total
1997	0	0	0	0	0
1998	2	1	2	2	7
1999	11	2	18	4	35
2000	2	0	7	0	9
2001	7	0	8	0	15
2002	6	0	7	0	13
2003	4	0	30	0	34
2004	1	0	2	1	4
2005	1	0	5	0	6
2006	2	0	5	0	7
2007	2	1	7	0	10
2008	13	0	35	0	48
	51	4	126	7	188

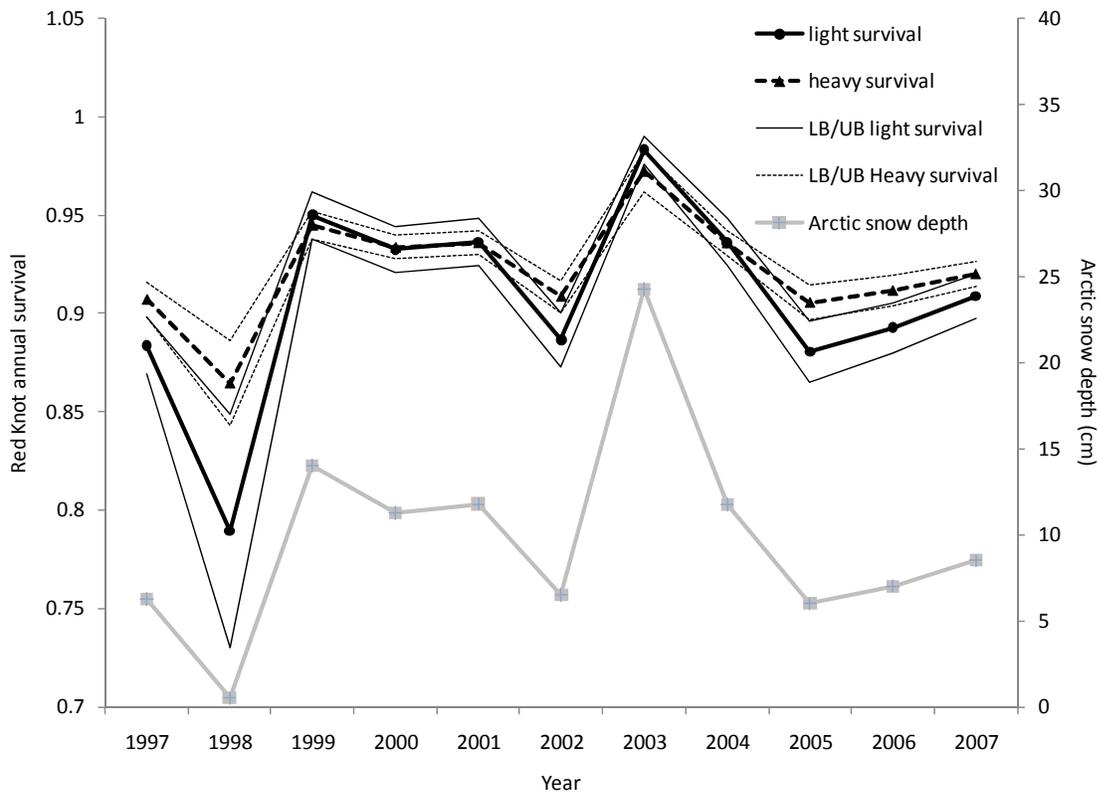
The most supported model based on AIC modeled annual survival as dependent on state and snow covariates (with interaction terms), light to heavy transition probabilities as dependent on horseshoe crab abundance and period (with interaction terms) heavy to light transition rates as a function only of period (Table 1). The second most supported model had arctic snow conditions as the only covariate on annual survival and the third model had a state plus snow structure on the survival parameters. The second and third models were within 1.5 AIC units of the best model, which indicates substantial uncertainty among the top three models (Burnham and Anderson 2002). The top three models together comprised over 98% of the AIC weight. The uncertainty amongst the top three models might require model averaging of parameter estimates across those three models. Models with no state structure or snow covariates on survival rates (e.g., null survival models) received no support in the AIC analysis.

The coefficients of the state covariates on annual survival rates were in the expected direction (positive), indicating that heavy birds have a higher survival probability than light birds. The model averaged mean annual survival rate of heavy birds was approximately 0.92 and light birds was approximately 0.91. The largest differences in survival between these groups seem to occur in specific years. For instance, the 1998-1999 survival rate was 0.86 for heavy birds and only 0.79 for light birds. During most other years the survival rates were similar and high (Figure 10), though light bird survival was estimated to be lower than that for heavy birds in 6 of the 11 years of data we analyzed.

Table 2. Model descriptions and statistics resulting from multi-state analysis of red knot mark-recapture and mark-resighting data for the top three most supported models of survival and transition. Covariates were weight state (s) horseshoe crab spawning (hsc), Arctic snow cover (snow), year (t), and within-year period (per).

Model	delta AICc	AICc	-2LogLik	k	w _i
$\phi(s \times \text{snow})\Psi(1-2(\text{hsc} \times \text{per}), 2-1(\text{per}))p(s+t)\delta(s \times p)r(s \times t \times \text{per})\beta(s \times \text{per})$	0	20644	-10256.9	65	0.433564
$\phi(\text{snow})\Psi(1-2(\text{hsc} \times \text{per}), 2-1(\text{per}))p(s+t)\delta(s \times p)r(s \times t \times \text{per})\beta(s \times \text{per})$	0.523997	20644.5	-10259.2	63	0.333633
$\phi(s + \text{snow})\Psi(1-2(\text{hsc} \times \text{per}), 2-1(\text{per}))p(s+t)\delta(s \times p)r(s \times t \times \text{per})\beta(s \times \text{per})$	1.42184	20645.4	-10258.6	64	0.212963

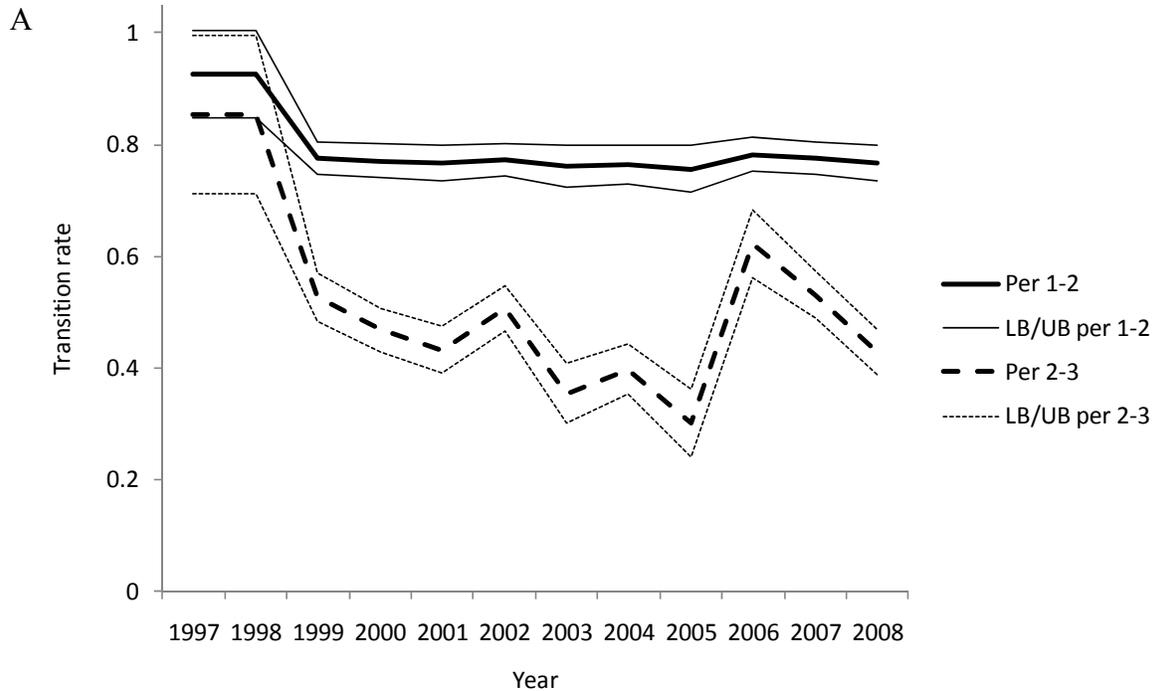
Figure 10: Model averaged annual survival rate estimates of heavy (above 180 g) and light (below 180 g) birds and annual average snow depth in the Arctic breeding range.

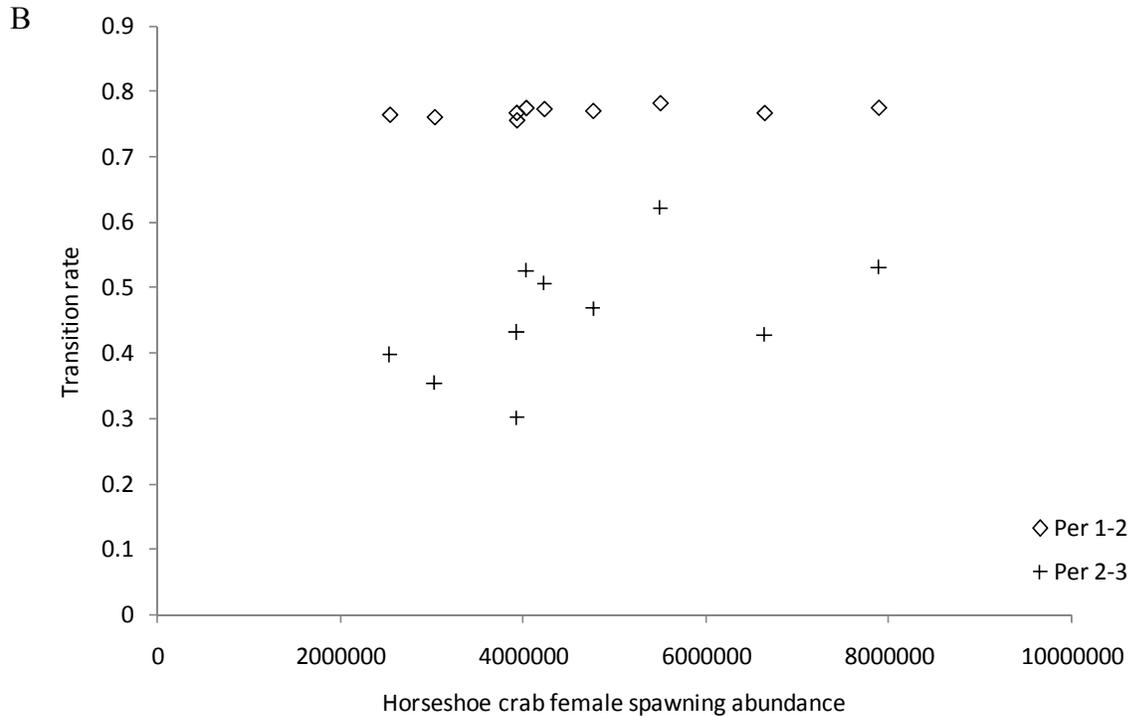


The model averaged coefficients on the transition probabilities indicated that from period two to three the probability of transition from light to heavy is positively correlated with female horseshoe crab spawning abundance ($\hat{\beta}_1 = 1.14$, $\hat{SE}(\hat{\beta}_1) = 0.20$). The coefficients for the light to heavy between the first and second periods were also positive, although the evidence for this relationship was weaker ($\hat{\beta}_1 = 0.13$, $\hat{SE}(\hat{\beta}_1) = 0.09$). Removing the horseshoe crab relationship

from the heavy to light transition probabilities improved the model. The transition probabilities were not modeled as a function of female horseshoe crab abundance for 1997 and 1998 because we do not have spawning or trawl survey data from those years. Assessing temporal trends in these estimates should not include the first two years.

Figure 11: A) Model averaged annual transition probabilities (\pm 95% CI) from light (below 180 g) to heavy (above 180 g) for periods 1 to 2 (solid lines) and periods 2-3 (dashed lines). B) Plot of the model averaged early (\diamond markers) and late season (+ markers) estimated light to heavy transition probabilities vs estimated female spawning abundance.





Discussion

Our results show evidence of two key relationships that provide a direct link between red knot demography and spawning abundance of female horseshoe crabs in the Delaware Bay. The probability of transition from the light mass state to the heavy state was positively related to estimated female crab abundance on spawning beaches in the Delaware Bay. Subsequent annual survival was dependent on weight state and arctic snow conditions upon arrival in the breeding grounds. The effect of weight state on survival was not as strong as we anticipated in most years (1998-1999 was an exception), nor as strong as predicted by previous analyses (Baker et al. 2004). Furthermore, our results did not account for weight loss following capture (Atkinson et al. 2007) or weight loss during capture and handling (H. Sitters, British Trust for Ornithology, personal communication). Not accounting for these sources of weight loss might diminish the relationship between knot weight state transitions and crabs in the Bay and might affect the state based annual survival estimates. However, our results indicate that weight state may have a large impact on survival in some years and that Arctic snow conditions may also play a role, interacting with weight state as a determinant of annual survival.

An additional reason for our results not showing the expected large differences in survival between heavy and light birds could be due to the categorical nature of the multi-state analysis. It is possible that a 180 g threshold is too rigid. In some years 170 g may be sufficient (an annually variable threshold) to insure adequate survival. It is also possible (and likely) that heterogeneity exists such that the relationship differs among birds. Some birds may do just fine with 165 g, while others may require 190 g to survive the transition to the Arctic (individual variation). Future analyses might consider using more weight states (e.g. below 140 g, between

140 and 180 g, and over 180 g). However, it should be emphasized that the primary reason for our weak inferences about relationships involving body mass is inadequate data. Although the resighting data are outstanding, the information about mass state of individual birds is very sparse. The key to learning more about relationships involving body mass is to change survey methods to place a premium on capture and recapture data, recognizing that a balance must be struck between data needs and we chose to limit our analyses to two weight state with a rigid 180 g threshold because of data limitations and because previously published analyses identified 180 g as the required mass to survive the transition to the Arctic (Baker et al. 2004).

Incorporating these Results into the ARM Models

We do not think that these results require a major reparameterization of the alternative models in the structured decision making analysis. Instead, we can incorporate these results into our current models relatively easily. We will use the transition rate parameters estimated by this multi-state analysis in the model where horseshoe crab abundance affects red knot fecundity, and in the model where horseshoe crab abundance affects red knot fecundity and survival. Furthermore, we can use the mean survival estimates for heavy (0.92) and light (0.90) birds from these multi-state analyses in the model where horseshoe crabs originally affected red knot fecundity only. This model was conceived as an intermediate model between the two more extreme models (not limiting and the fecundity and survival model), and we think that incorporating a small survival differential between heavy and skinny birds is highly appropriate given the results of our analyses. Lastly the mean annual survival estimates ($S_a = 0.91$) from the second most supported model in our multi-state survival (survival was dependent on snow only) analysis will be used as the annual red knot survival estimate for the model where horseshoe crabs do not limit red knot demographics.

Model Weighting

We can assign initial model weights or confidence values to each model. The weights are used in the optimization analyses to weight the influence of each model on the analyses (Williams 1996a, 1996b). Model weights can be updated annually reflecting accuracy of model prediction compared to observed data (Williams 1996a, 1996b). We will use Bayes theorem to update the prior probability of a given model based on the likelihood that the observed data would have arisen had that model been a good approximation to truth (Williams 1996a, 1996b). Over time the best predictive model should accrue more and more weight and thus gain greater influence over management decisions.

There are a number of ways to set initial model weights, with the only constraint that they must sum to one. Under conditions of complete ecological uncertainty we could simply apply equal weights to each model. If we have historic data, we could use patterns and trends in those data to put more weight on one model than the others. It is also possible to take a more democratic approach and use elicitation to generate prior model weights. Each member of the ARM modeling team set his/her own model weights, and we calculated the average of those weights. The average weights were 0.2 for the not limiting model, 0.4 for the fecundity only model, and 0.4 for the fecundity and survival model.

Optimization Methods

We have implemented the three competing models of the system with the parameterizations described above into the program ASDP to execute the optimization analysis and conduct simulations. This program uses the population models we have described here to generate a policy matrix that maximizes horseshoe crab harvest given the constraints of our agreed upon utility functions. In this section of the report we describe some specifics of the optimization analysis specific to ASDP. The optimization analysis uses a backwards iteration process, starting at the “end of time” and working towards the present (e.g., see Williams et al. 2002). The approach requires substantial computing power, and this imposes restrictions on the dimensionality of the analysis. Some of the limitations were discussed in the model description section above, with respect to number of state variables and efforts to simplify the population models.

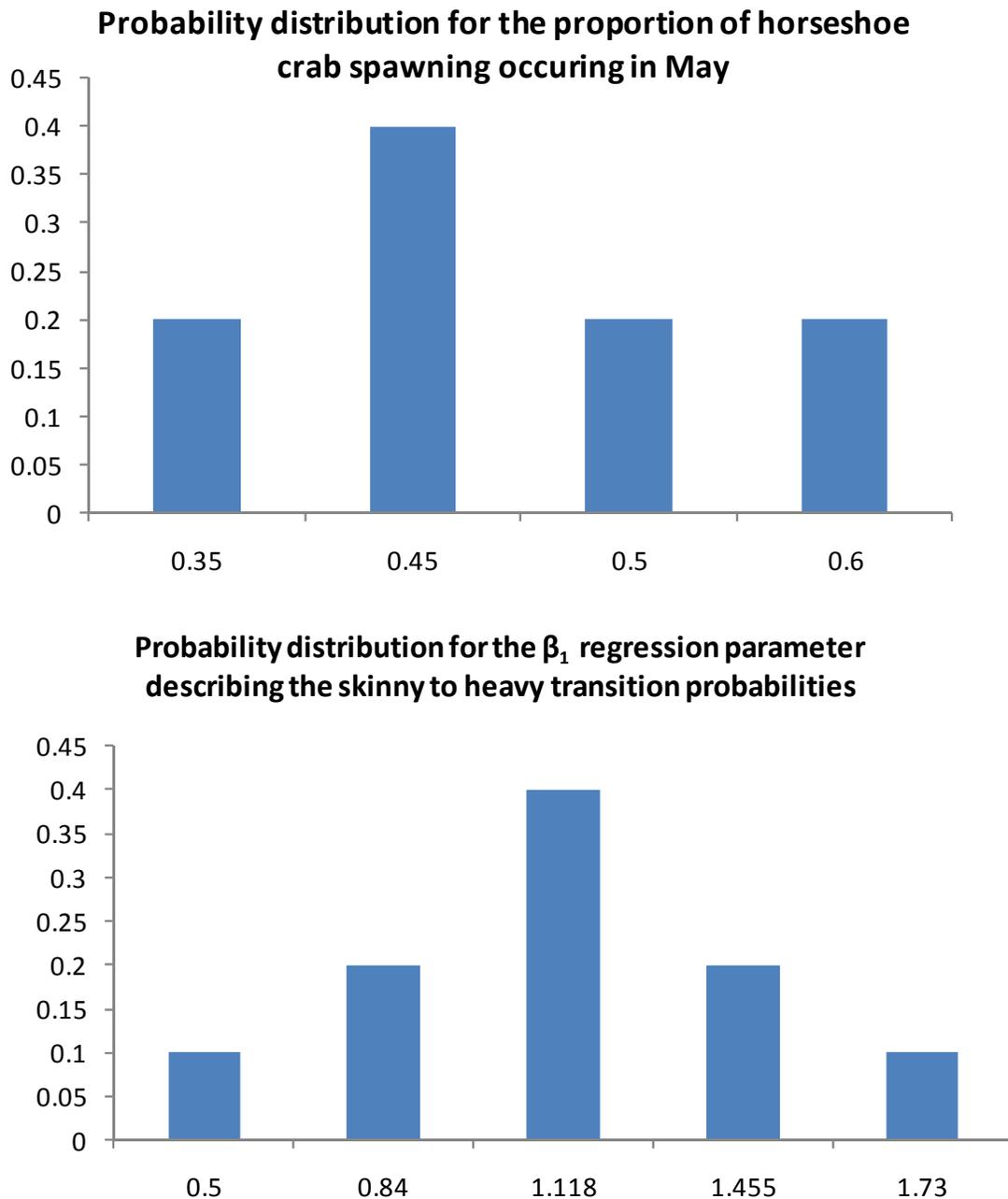
To accomplish this optimization the program requires that the user describe specific state variable size bins and specific probability distributions on the random variables. Continuous metrics are discretized under this approach. For state variables, the user defines the maximum value, the minimum value, and the increment that defines the classes between the minimum and the maximum. For example, in the model, the adult red knot abundance variable can range from 0 to 90,000 (females only) with a 9,000 individual increment. This instructs the optimization program to determine what the best management action is with red knot adult abundances of 0, 9,000, 18,000, 27,000...90,000 females, when combined with all possible combinations of the values of the other state variables in the model. The fewer bins created for each of these state variables, the smaller the dimensionality of the optimization. To save on computing capacity, we chose to create large size bins for the state variables that are empirically difficult to measure and state variables for which no estimates are currently available. We do not have ways to estimate juvenile horseshoe crab abundance and immature red knots abundance, and we will thus use model-based predictions for these values (see the section on monitoring). The table below presents the minimum, the maximum and the increment for each state variable in the model.

Table 3: Range of values and discretized increment of the model state variables for the ASDP optimization procedure.

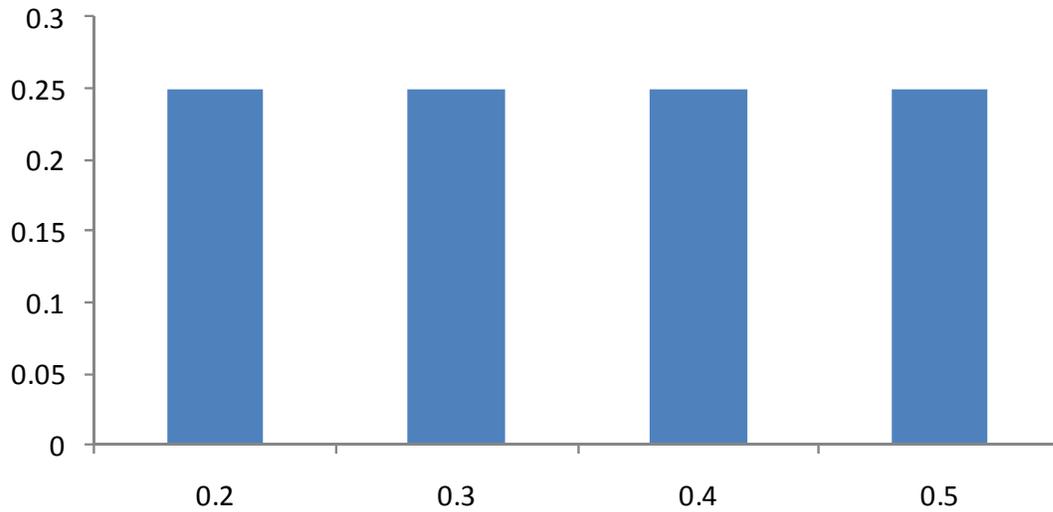
Variable	Minimum	Maximum	Increment
Juvenile HSC	0	2.0×10^8	4×10^7
Pre-Breeding HSC	0	1.8×10^7	3.0×10^6
Adult Male HSC	0	1.6×10^7	1.6×10^6
Adult Female HSC	0	1.6×10^7	1.6×10^6
Immature Red Knot	0	20,000	5,000
Adult Red Knot	0	90,000	9,000

The random variable distributions are created with a similar level of specificity. The user defines a set of possible values for a random variable, and the probability of occurrence for each value. Again, because of computing limitations we only incorporated three random variables into the analysis, and we limited the number of possible values for each variable to five. We included temporal stochasticity in the proportion of crabs spawning in May, the β_1 slope parameter of the transition probability from light to heavy relationship, red knot fecundity, and age zero survival of horseshoe crabs. The figures below describe probability distributions for each random variable in the model:

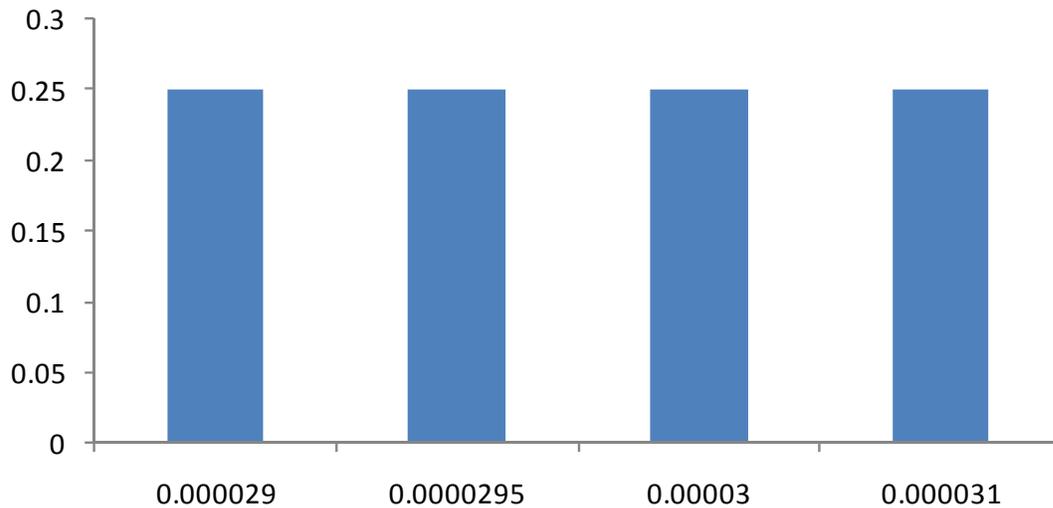
Figure 12: Discretized probability distribution of the three random variables in the state dynamics models for the ASDP optimization and simulation program.



Probability distribution for Red Knot fecundity ($F_{a180,t}$) parameters



Probability distribution for the age zero survival parameter in the horseshoe crab population model



These probability distributions are based on the best available data from published literature, recent unpublished data analyses, and expert opinion. The distribution for the proportion of crabs that spawn in May was based on the Delaware Bay spawning survey (Michels et al. 2009), the shape of this relationship may change resulting from new data analyses (D. Smith, USGS, Personal Communication) but those changes will not affect our decision framework. The distribution for the β_1 parameter is based on the mean and standard error of β_1 from the multistate analysis described in this report. The minimum and maximum of the modeled distribution are the lower and upper bound of the 95% confidence interval, assuming a normal distribution around the mean. The distributions on the red knot fecundity age zero survival for horseshoe

crabs were modeled as a uniform distribution. The red knot fecundity parameter was derived from published estimates for a different subspecies in a different geographic location. The stakeholders expressed strong preference for expressing our certainty in this parameter as a uniformly distributed random variable. The Botton et al. (2003) age zero survival was a point estimate with no reported associated variance, so we used a simple uniform distribution to introduce variability to this very important demographic parameter in the models.

The goal of the optimization procedure is to find an optimal policy (set of state-specific harvest regulations) over an infinite time horizon. In practice, select an arbitrarily large time horizon and look for convergence to a stationary policy. We ran the model for up to 1000 iterations (backward time steps), requiring a minimum of 20 and requiring that the model execute 20 successive iterations with zero changes in the recommended policies (practical approach to assessing stationarity). The optimization was passive and did not include information state and uncertainty reduction as part of the analysis (Williams 1996a, 1996b). We also used ASDP to run some simple simulations to demonstrate possible population trajectories and associated management actions.

Optimization Results

Because of the number of state variables and the complexity of our utility function, it is virtually impossible to neatly and concisely summarize the output files of the optimization analysis. The policy table is a 735 megabyte file that presents every possible state variable combination, and the corresponding optimal policy under different model weights. Because of the sex ratio linked horseshoe crab male harvest utility function, there are no simple patterns in the policy table. Even when focusing on the red knot state variable, in the vast majority of cases when the population is above the 45,000 abundance threshold, harvest package 5 (210,000 females, 420,000 males) is the optimal option. However, when horseshoe crab abundances are low, then more restrictive, harvest packages are optimal. In the table below, we present a portion of the harvest policy table to demonstrate the output from the analysis:

Table 4: Example output from the optimal policy table. The table lists each state variable, the model weight and the optimal policy under those conditions.

HSC J	HSC P	HSC F	HSC M	RK J	RK A	M1	M2	M3	Policy
...									
1E+8	1.8E+7	4E+6	4E+6	0	15000	0	0.4	0.6	4
1E+8	1.8E+7	4E+6	4E+6	0	15000	0.2	0	0.8	4
1E+8	1.8E+7	4E+6	4E+6	0	15000	0	0.2	0.8	4
1E+8	1.8E+7	4E+6	4E+6	0	15000	0	0	1	4
1E+8	1.8E+7	4E+6	4E+6	0	30000	1	0	0	5
1E+8	1.8E+7	4E+6	4E+6	0	30000	0.8	0.2	0	5
1E+8	1.8E+7	4E+6	4E+6	0	30000	0.6	0.4	0	5
1E+8	1.8E+7	4E+6	4E+6	0	30000	0.4	0.6	0	5
...									

In the table, “HSC J,” “HSC P,” “HSC F,” “HSC M,” “RK J,” “RK A,” are the state variables of the system models, “M1,” “M2,” “M3” indicate the model and present the model weights for

each of the system models (M1 = not limiting, M2 = Fecundity only, M3 = Fecundity and Survival). The “Policy” column displays the optimal harvest package (1-5) to select, given these conditions and the model set with the respective model weights.

The process for adaptive management is to annually assess the state of the system, search the optimal policy output table for the line that most closely matches the current system state and model weights, and select the policy recommended for that line in the output table. This process requires annually estimating the state variables in the model/output table through a carefully design monitoring program. We describe the monitoring plan in a later section of this report.

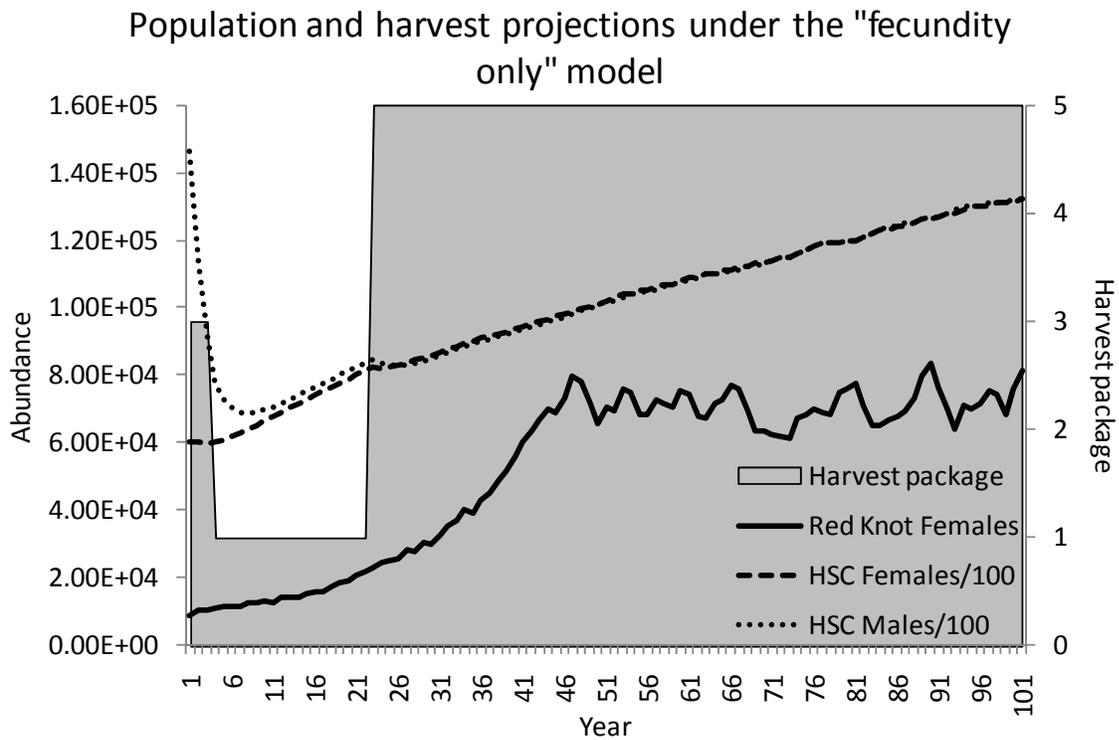
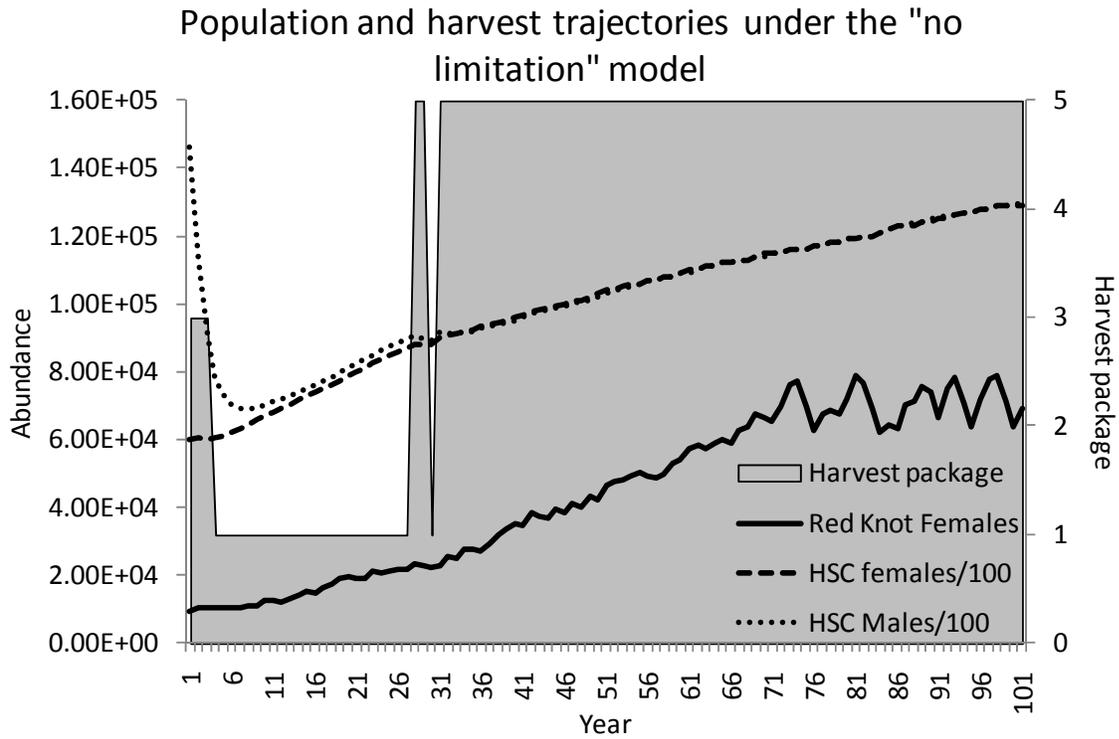
We can use the optimal policy table to look back at estimated abundances from recent years and find the corresponding harvest option. We used horseshoe crab abundances for adult females, adult males and pre-recruits from the annual Virginia Tech trawl survey (Hata and Hallerman 2008). We input horseshoe crab juvenile abundance as 40 million. We don’t have an estimate for this state variable and 40 million is approximately the expected value based on the estimates for the other state variable in the horseshoe crab population. Red knot abundances for 2006 - 2008 were based on population estimates in Niles et al. (2008). We do not have estimates for red knot juvenile abundance, so again we input a value that is approximately expected based on the other red knot abundance estimates.

Table 5: Abundance estimates for the model state variables and the corresponding optimal harvest policy for the Delaware Bay region between 2006 and 2008.

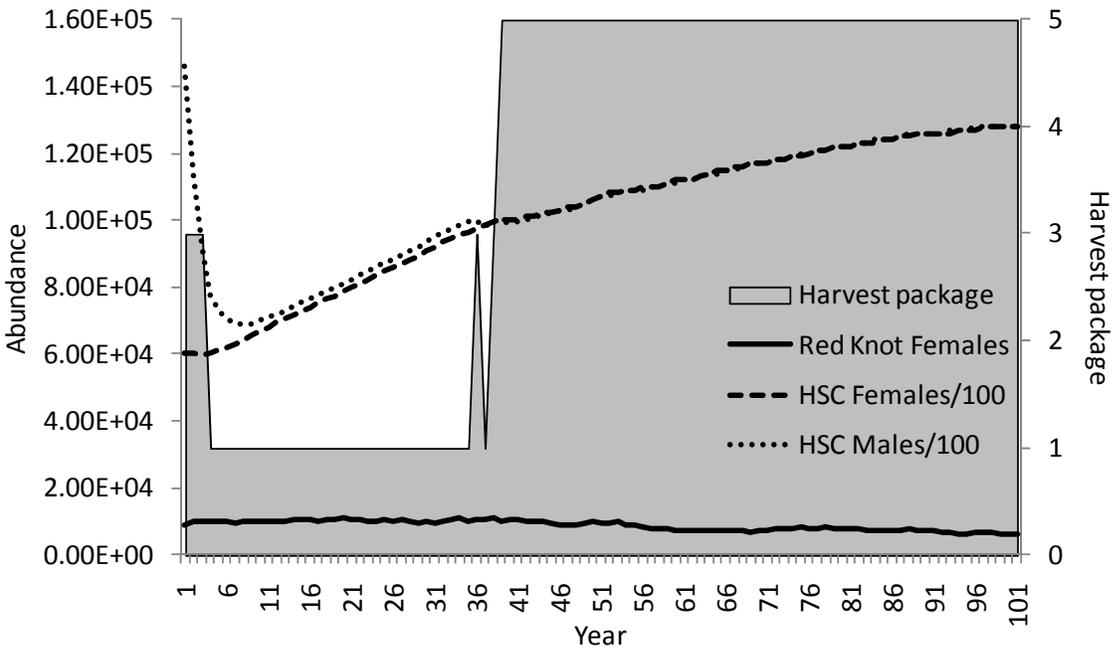
Year	HSCAM	HSCAF	HSCP	HSCJ	RKF-A	RKF-J	Harvest option
2006	14,300,000	5,500,000	5,200,000	40,000,000	9,000	1,500	3
2007	18,330,000	7,890,000	5,930,000	40,000,000	8,500	1,500	3
2008	14,350,000	6,640,000	3,670,000	40,000,000	10,000	1,500	3

To demonstrate how these policies might be implemented in the future, we conducted some simple simulations using the simulation function in ASDP. The program simulates the state dynamics into the future under the limited amounts of stochasticity that we have incorporated. Each year of the simulation the program consults the optimal policy file and implements the optimal harvest policy given the state of the system and the model weights. The program runs three simulations, one where each model represents truth, and it updates model weights using Bayes theorem to learn which model predicts “best” and thus to improve decision making as time progress. The figures below show these three simulations, the population trajectories and the optimal harvest policy each year. Initial horseshoe crab abundance was set at 4.76×10^7 juveniles, 4.6×10^6 pre-recruits, 6.1×10^6 adult females, 1.4×10^7 , and red knot abundance was set at 9000 adult females (18,000 total), and 2500 juvenile females. Initial model weights we set at the model weights elicited from the ARM working group team members (“No limitation” = 0.2, “Fecundity only”= 0.4 and “Fecundity and survival” = 0.4.

Figure 13: Simulation results demonstrating population trajectories and optimal harvest policy under specified starting conditions and optimal harvest strategies.



Population and harvest projections under the "fecundity and survival" model



The harvest policy is the optimal harvest policy, where 1 is no harvest, 3 corresponds to alternative 3 (500,000 male only harvest) and 5 corresponds to alternative 5 (420,000 males, 210,000 females). The projected harvest policies show similar patterns (an initial male only harvest followed by a period of moratorium, followed by a full male + female harvest) for the different underlying models of “truth” in the simulations. Initially, because of the currently observed highly skewed sex ratio, all three models recommend a male only 500,000 animal harvest. After 3 years, all three models switched to a full moratorium and each eventually shifts back to harvest package 5. The not limiting model makes the switch in year 27, the fecundity only model in year 22, and the fecundity and survival model in year 38. In the simulations there was some switching between policies at the end of the moratorium periods. This probably results from the environmental variation incorporated into the models creating some unlikely decline in red knot abundance for these unreplicated trajectories.

Again, the actual harvest policy over the next several decades may not follow any of these simulated patterns; there is no way to know what the harvest policy will be in any given year until the state variables are estimated from the monitoring data and the policy table is consulted. Furthermore, as we implement management actions in the coming years and we observe the system response through the monitoring program the model weights will be updated and the optimal policy will change based on the new weights.

Monitoring

Monitoring in Adaptive Management

We envision that monitoring will play four primary roles in the adaptive management process for the Delaware Bay horseshoe crab harvests (Williams et al. 2007, Lyons et al. 2009).

- 1) Monitoring will annually assess the state of the system by estimating abundance for the 6 state variables in the system models: Horseshoe crab abundance (juveniles, pre-recruits, adult males and adult females), and red knot abundance (immatures and adults). These abundance estimates will define the current state of the system and will be used to determine the optimal harvest policy for next year.
- 2) Monitoring will be used to compare observations to model predictions for update model weights. Each of the three system models makes predictions about what the state of the system should be if that model were “true” (a good approximation to reality). Empirical estimates of system state variables (horseshoe crab abundance, etc.) from monitoring data will be compared with predicted state variable values from each of the models, and we will evaluate model performance based on the likelihood of observing the estimated state variable value under each model. The approach uses Bayes’ theorem to compare model predictions with observed values. Initially each model of the system is given a prior “weight” (reflecting our confidence in that model, see “Model Weighting” section above), and Bayes’ theorem will be used to update the model weights given the comparison between predicted and observed values of state variable. The weights are used in the optimization analysis to create a sort of weighted average optimal harvest policy across the alternative models.
- 3) Monitoring will be used to assess whether management objectives are achieved. Evaluating abundance of each species in relation to our management thresholds will tell us whether the harvest policies we have instituted are pushing the system in the “right” direction.
- 4) Monitoring will be used to improve the models and model parameterization in the long term. This component of monitoring is part of the double loop learning process of adaptive management whereby, periodically, the models of the system can be re-evaluated, revised or reparameterized. We have examined the system models and pinpointed which parameters need improvement by determining which parameters the model is most sensitive to, and which parameters have the least amount of empirical or literature support.

In this section of the report we describe our recommendations for monitoring the system in the Delaware Bay to serve the four purposes we described above. We first examine the red knot population models and monitoring needs and then address the horseshoe crab. We make recommendations for annual state variable assessment, as well as needed research to improve parameter estimates for the models to support decision making. Models for both species entail significant knowledge gaps and uncertainties regarding structure and parameterization, and the monitoring recommendations herein are designed to reduce uncertainty.

Red Knot Monitoring

The red knot's annual cycle spans vast distances in the northern and southern hemispheres. There is a great deal of this species' annual cycle that is not well understood or studied. We have very limited data on the breeding season in the Arctic. We have an incomplete understanding of the annual cycle and wintering ecology (e.g. wintering locations). It is neither possible, nor prudent, for our management program to attempt to resolve all of this uncertainty, and we have focused our monitoring and research recommendations on the needs of the adaptive management process. Specifically, we focus on the response of the managed system to horseshoe crab harvest regulations. Below is a list of each of the parameters in the red knot model, a brief description of the current methods to estimate those parameters followed by our recommendations for moving forward.

Adult Abundance: Currently red knot abundance is estimated from aerial surveys in the Delaware Bay and in the wintering areas in Tierra del Fuego. Aerial surveys on Delaware Bay are conducted once weekly using a fixed wing aircraft. Surveys begin at Cape May, NJ approximately 1.5 hours after high tide and end at Cape Henlopen, DE. Delaware Bay surveys require two observers and one scribe. One observer estimates total flock size while the other observer estimates the species composition of the flock. In 2009, ground counts were used to supplement the aerial counts. Ground counts are conducted at each site immediately prior to resighting scans and are, therefore, conducted at each beach/study site every three to four days. Counts are made of each species observed on a beach, and flock sizes are estimated using direct counts for smaller flocks or extrapolated estimates for larger flocks.

Aerial surveys are subject to high sampling variance due to temporal fluctuations in bird presence in the Bay, due to observer capabilities, due to weather and visibility related factors, and numerous other factors. Our monitoring needs to assess the number of birds in the bay over the whole stop-over season and aerial count are insufficient for that purpose. We do not have high confidence that aerial surveys are accurate measures of red knot abundance in Delaware Bay. Instead we are recommending that adult red knot abundance monitoring using a mark recapture approach based on the number of marked to unmarked birds detected during observation surveys. Marked to unmarked ratio data can be incorporated into the open-robust-design analysis (used to estimate state-based survival), to estimate abundance for each sampling period, but more importantly, the total number of birds using Delaware Bay during the entire stopover period. The approach allows for departures and arrivals between sampling periods and can account for population changes over the season. To accomplish this we recommend continuing the cannon netting, banding and resighting efforts that have been in place in the Bay for a number of years. We also recommend modifying these methods to obtain marked-unmarked ratios of birds during observations (described below).

Capture methods: Capturing shorebirds in Delaware Bay is primarily completed using cannon nets. Researchers in DE Bay have agreed to a yearly target of 350 birds of each species in both DE and NJ. This is meant to provide enough samples to evaluate weight gain, while also maintaining a marked population of approximately 10% and limiting researcher disturbance to foraging and roosting birds. Each bird is banded with a USGS incoloy band as well as a lime-colored darvic flag inscribed with a unique 3-character code. Capture events are spread out

through the migratory period to try and evaluate weight gain of birds while in Delaware Bay. (We also recommend increased focus on capture-recapture data as a means of obtaining better estimates of state transitions and state-specific survival (see survival rate monitoring below).)

Resighting methods: Shorebird resighting efforts consist of scanning flocks of red knots to look for and record codes on leg flags. Resighting scans of coded leg flags have been conducted in Delaware Bay since 2003 with high resighting (capture) efficiency (~ 0.40 observation probability). All main beaches used by shorebirds are scanned at least every three days to ensure all areas that could be used by red knots are identified. In addition, a subset of beaches has been identified as having particularly high shorebird densities, and these are scanned every day using standard operating procedures to limit human disturbance. A goal is set to record a minimum of 50 marked individuals per day during scanning efforts, though often many more are observed.

Marked to un-marked ratio data collection: We can estimate a sighting probability from resighting data of individually marked birds using capture-recapture techniques. This will allow us to estimate the number of marked birds in the Bay population for a given sampling period (determined by full, Bay-wide coverage). By obtaining marked-to-unmarked ratios, we can then translate the number of marked birds in the Bay to the total stopover population for that sampling period. Further, utilizing the individual histories of each marked animal will provide immigration/emigration probabilities that can be combined with abundance estimates for each sampling period to derive an estimate of the total stopover population size.

The ARM committee recommends that the marked-to-unmarked ratio be obtained by integrating an additional sampling procedure into resighting methodology. This procedure was designed to be relatively quick, so as to limit double counting marked and unmarked birds and to limit time taken from scanning for flagged birds. It also had to be applicable to all situations and sites in the Bay. The procedure is described as follows:

- Upon arrival to a site, collect site and bird count information as usual.
- Complete a marked-to-unmarked bird scan:
 - Select a section of the flock that seems representative of the entire flock with regard to size and composition.
 - Start to count the number of unmarked birds until you get to a coded flagged bird and make a notation of that bird. All flag colors should be included as being marked.
 - Continue until 50 total birds have been scanned for flags. A simple datasheet has been developed to aid in keeping track of the number of birds counted.
 - Disregard individual codes during this phase of sampling, as the time it takes to record the codes may cause the observer to double count birds either marked or unmarked.
 - If there is a flock of fewer than 50 birds, attempt to get a ratio for the entire flock
 - If a flock flies, stop the count and note the total number scanned for marks.
- Once the ratio scan is complete, begin scanning for individual flag codes.

- Repeat a ratio scan approximately every ½ hour during resighting scans.

Immature abundance: Currently there is no way to estimate immature abundance in the red knot population. The annual cycle of immature birds is largely unknown. We do not know where they migrate, if they migrate at all, and we do not know where they spend their first or second winter before entering the breeding population, so using age ratios and count data does not seem plausible. None of the immature birds are marked, so a mark recapture based analysis to estimate abundance is not possible. It might be possible to estimate recruitment rates into the Delaware Bay breeding population, however, recent a report by Cohen et al. (2009) indicate that not all young red knots use the Bay every year which might confound recruitment rate estimates. In addition, the way our models are structured, a Delaware Bay recruitment rate estimate would be one year too late in the annual cycle for use in estimating the immature abundance state variable. With all that in mind we recommend using a model averaged prediction of immature abundance in the annual policy selection process. The three models of the system will output three differing immature abundance predictions, and we will simply use the weighted average (from the prior model weights) of the three predictions instead of some highly uncertain empirical estimate from counts on the wintering grounds, etc. If new methods for assessing juvenile abundance are devised, then this decision can be revisited.

Adult Annual Survival and mass state transition rates: As described earlier in this report we recommend continuing to use the multi-state open robust-design survival analysis. The approach estimates annual survival of heavy and light birds and the probability of transition from light to heavy and vice versa. Though the transition rate estimates resulting from these analyses are subject to high uncertainty due to limited information on body mass, the survival rate estimation is highly precise because of the tremendous resighting effort that annually occurs in the Bay. We do need to improve the transition rate parameter estimation and the estimation of state-specific survival. Thus, we recommend increasing capture efforts in the Bay during the stopover period to increase the number of birds caught twice within one season. Alternatively we think that devising ways to assess physiological condition (weight) of birds without physically capturing and handling the birds would be extremely beneficial because of reduced disturbance and stress to the birds. Analyses to examine space use of red knots could potentially improve within-season catching probability. We are exploring the use of a spatial multistate model to look at transition probabilities among study sites in the Bay to help guide cannon netting efforts and design. Weight state transition rate and state-specific survival are parameters for which increased precision of estimates is important, as they are central elements of the competing hypotheses about the influence of horseshoe crab abundance on red knot population dynamics (Baker et al. 2004, Niles et al. 2008). Understanding the factors that govern the probability of transition from a light to a heavy bird during the migratory stopover period is key to building accurate models of the system we are trying to manage.

Immature Survival: We currently have no method for empirically estimating immature (second year birds) survival. There are few or no efforts to mark and subsequently resight pre-breeding individuals for the *rufa* subspecies. To do this would require targeted banding efforts on Juvenile birds either during the southward fall migration, or banding efforts on the wintering grounds. However to be successful we first need more information of the annual cycle of immature birds: Where do they spend the winter, where do they spend the breeding season? This

parameter is likely not highly influential in our decision analysis, and we put a low priority on devising ways to estimate this parameter. Currently, we simply model immature survival as 85% of heavy adult survival. This method follows convention for modeling bird populations where immature bird survival is unknown (e.g., Ryan et al. 1993,). There is no hypothesized influence of horseshoe crab spawning abundance on immature survival, and so there are no differences across the three models with respect to immature survival. Developing more precise estimates of immature survival will not help to resolve the central ecological uncertainty incorporated into our decision analysis, and so we place low priority on estimating this parameter.

Juvenile Survival: The story for Juvenile (first year birds) survival in our model and decision analysis is very similar to that of immature survival. Resolving uncertainty in the parameter will not reduce the key ecological uncertainty in our analysis and will likely not affect the optimal policies since juvenile survival is modeled similarly in all three models of the system. Currently first year survival is set at 60% of heavy bird survival (again following bird population modeling convention), and we place low priority on improving estimates of this parameter.

Fecundity/productivity: Currently fecundity in our models is set at 0.48 female chicks fledged per female. This number is based on fecundity estimates for similar species (Meltote et al. 2007, Meltote et al. 2008) and the very few published data on red knot productivity from other subspecies in the Arctic. Estimating fecundity directly for the *rufa* population will be difficult because of the remoteness of their breeding grounds; efforts to locate and monitor nests in the arctic have returned few observations. It may be possible to monitor annual productivity by observing south bound migrant flocks to estimate juvenile to adult ratios, or to observe wintering flocks in South America for the same purpose. Unfortunately there is tremendous uncertainty as to the annual cycle of young of the year birds. They migrate at different times than the adults, and they might use different migratory routes. Furthermore it is thought that they do not winter in the same areas as adult birds, thus causing substantial issues for age ratio productivity estimators (Skalski et al. 2006).

Alternatively, we could attempt to estimate recruitment to the adult breeding population utilizing the available mark recapture dataset. In fact such estimates can be computed directly from the estimates obtained in our current estimation modeling efforts, given the addition of the marked-unmarked ratios that were discussed above. We do place a high priority on devising and developing methods to estimate fecundity or productivity for this species. This metric would be the primary way to distinguish the “fecundity only model” from the “not limiting model” in our set of three alternative ecological models. Though there are potentially other ways of differentiating between these models, estimation of annual fecundity would be the most direct way to reduce the uncertainty between these two models. At present we plan to estimate recruitment to the adult population in year t and then relate these estimates to horseshoe crab abundance in year $t-2$.

Horseshoe Crab Monitoring

The horseshoe crab model is more complex than the red knot model, has more parameters, substantial uncertainties and requires significant monitoring effort. It is neither possible, nor prudent, for our adaptive management program to attempt to resolve all of this uncertainty, and

we have focused our monitoring and research recommendations on the needs of the adaptive management process. Below is a list of parameters in the Horseshoe Crab model, a brief description of the current methods to estimate those parameters followed by our recommendations for moving forward.

Adult Male and Female abundance and Pre-recruit abundance: Current estimates of abundance for male and female adults and pre-recruits of both sexes come from catch per unit effort estimates from the Virginia Tech off shore trawl survey conducted in the fall of each year (Hata and Hallerman 2009). Full details on the methods used for this survey can be found in Hata and Berdson (2003) and Hata and Hallerman (2009). The survey follows a stratified random design and trawl transects to sample offshore habitats where horseshoe crabs are present in the fall and early winter. We believe this is the best available method for estimating abundance of breeding adults in the population. However, catchability is not estimated and thus the trawl survey results in estimates of minimum abundance. Gear susceptibility is thought to be size dependent, but that horseshoe crabs of adult size, which includes pre-recruits, are assumed to have equal susceptibility. Gear susceptibility could vary by substrate, temperature, and time of the day. Catch rates have been compared across some environmental and temporal gradients (cf Hata and Berkson 2004), and estimates correspond to those conditions that are known to maximize catch rates. For example, the survey is conducted at night because catch rates are higher than during the day. Recent application of the catch survey model (ASMFC 2009 stock assessment report) indicates that catchability of pre-recruits is lower than that of adults possibly because of different spatial distributions throughout estuarine, near shore and off shore habitats. Variation in catchability can reduce accuracy of model predictions and confound assessment of change over time. We recommend that evaluating catchability receive high priority. We suggest paired comparisons with a hydraulic dredge to evaluate gear susceptibility. Extending survey area to include near shore and estuarine habitats would help describe age-specific distributions

Juvenile abundance: Currently there is no method in place to estimate abundance of the Juvenile age classes. In the model we initially used a value based on a stable age distribution, but given the observed skewed sex ratios among adults (Smith et al. 2009), this value is likely underestimated. In the short-term, similarly to the red knot juvenile abundance estimation, we propose using the model averaged juvenile abundance prediction to inform the annual decision making process. In the longer term, we think a survey should be developed to estimate this parameter that can influence the annual decision process. It might be possible to modify the existing Delaware 16' trawl survey for this purpose, extending the survey in to New Jersey waters, applying a stratified random design – stratifying by habitat type, and executing gear efficiency and size and age based catchability studies. We think this research takes a lower priority than the catchability work needed on the adult and pre-recruit trawl survey.

Male and Female Adult Survival: Current estimates of annual survival for adult animals are based on published survival estimates from Botton and Lovelend (1989) and Carmichael et al. (2003). The parameter estimates we used are the same used in the synthesis of Sweka et al. (2007). These are based on a cohort analysis in a different geographic location (Carmichael et al. 2003). The estimates represent the best available peer reviewed estimates. There are a number of possible approaches to estimating these parameters for the Delaware Bay population. One approach with great potential might be to utilize the US Fish and Wildlife Service's growing,

long-term mark-recapture data base. There are likely to be significant statistical issues and limitations to these data, however we believe that using a local data source spanning multiple years has the potential to improve the predictive models. Expanding the mark-recapture efforts to include a well-designed tagging study specific for predictive modeling might be warranted.

Pre-recruit Survival: Estimates of pre-recruit survival, like those of adult survival, are derived from the Carmichael et al. (2003) cohort analysis. Again we believe that a locally based mark recapture analysis would be more appropriate and improve the model's predictive capabilities.

Juvenile Survival: The current estimate of juvenile survival is based on the Carmichael et al. (2003) cohort analysis. For our model, we converted the age based survival estimates to stage based survival and transition probabilities out of the juvenile stage to the pre-recruit or adult stages. The Carmichael et al. (2003) analysis was over one year in one location with no variance estimates. These factors limit the utility of these estimates for our modeling purposes; however, the estimates are again the best available peer reviewed and published estimates of survival for these age classes in this species. For future iterations of model development and improvement we suggest executing local studies in the Delaware Bay over multiple years to estimate annual survival. The State of Delaware's 16' trawl survey could be used to assess survival in the juvenile life stage if annual growth rates of juvenile horseshoe crabs could be estimated and catchability of different sized animals could be assessed and addressed. Using the 16' survey to estimate survival would face the same challenges discussed under estimating juvenile abundance.

Age Zero Survival: This is an extremely important parameter in the horseshoe crab models. Sweka et al. (2007) reported that the horseshoe crab age based matrix model output was most sensitive to changes in age zero survival. The current estimate in the model (0.00003) is based on a cohort analysis from Botton et al. (2003). The estimate was from one year of data from one site in the Delaware Bay. Because of the sensitivity of population growth to this parameter, we highly recommend continued study of age zero survival using multiple years of data from multiple sites in the Delaware Bay to account for potentially high variability in this parameter. Spatially and temporally repeating the Botton et al. (2003) study, and finding ways to verify assumptions about growth rates and growth curves on which the survival analysis depends would improve the predictive capabilities of our adaptive management models.

Egg Mortality: The density dependent egg mortality function currently in the model is derived from a simulation study examining the relationship between female spawning density and egg/nest exhumation (Smith 2007). Sweka et al. (2007) used their population model to simulate the population under three different density dependent relationships, and we used the relationship with the lowest levels of density dependent egg mortality in our adaptive management models, because it corresponded most closely with recent population growth and abundance estimates. The model and the decision analysis are sensitive to changes in the regression parameters of the density dependent egg mortality function, and a better understanding of this relationship could improve model predictions and management decision making. However, empirically evaluating these relationships will be extremely difficult. Estimating egg survival rates can be done but relating egg survival to female spawning density would be extremely difficult. Experimental manipulations could be designed and executed on Delaware Bay beaches to create treatment groups of high and low density spawning, but the challenges to empirically estimating the

functional form of the density dependence relationship might be insurmountable. Because of this difficulty, we place a lower priority on estimating the regression parameters in this relationship. We envision future model development that relies on a recruitment function to the juvenile stage and skipping over much of the detail need to parameterize the density dependent egg mortality function.

Fecundity: Current fecundity estimates (number of eggs produced per female per year) are based on results of Shuster and Botton (1985) as reported in Sweka et al. (2007). Changing fecundity does alter the carrying capacity estimates of the Delaware Bay spawning population. However, the model and decision analysis have relatively low sensitivity to this parameter, compared to egg mortality functions or year zero survival. We conclude that current fecundity estimates are sufficient, and we place a low priority on reevaluating and re-estimating this parameter.

Sex ratio linked fertility function: Our model restricts horseshoe crab fertility by sex ratio, with a declining fertility rate if males fall below a threshold population or operational sex ratio. The sex ratio fertilization rate link and the decline rate are based on published population modeling theory (Caswell 2001). Threshold population sex ratio value in the fertility function are based on limited published data from behavioral studies (Brockman, 1990 and 2002) and unpublished population genetics data (E. Hallerman, Virginia Tech University, personal communication). We acknowledge there are substantial uncertainties in the designations of the decline rate and the sex ratio threshold levels in the model and we recommend future empirical research on this subject. Observational studies could be conducted to examine patterns between operational sex ratio and fertilization rate of eggs in female nests. The spawning survey and benthic trawl survey can be used to monitor operational and population sex ratios.

Spawning Survey: The spawning survey plays a direct role in providing abundance estimates of horseshoe crab for making state-specific decisions. In addition, the spawning survey plays a very important role in parameterizing the relationship between red knot and horseshoe crab populations. The transition probability analysis of the multistate robust-design analysis (reviewed in this report), is dependent on the data from this survey. Continuing this survey will enhance precision to the multistate analysis by simply increasing the time series in the analysis. It may be possible to improve the survey by conducting surveys during the neap tide periods to reduce variability. We place very high priority on, at the very least, continuing the spawning survey to improve parameter estimates in the models.

Egg Survey: We are not currently using the egg survey data in our modeling or decision analysis. The egg survey has a shorter time series than the trawl and spawning surveys, and we chose to use the longer time series for linking red knots to horseshoe crabs. Given enough years of data, it might make sense to one day use egg density data as a covariate in the multistate survival analysis described in this report. However, the egg survey is further subject to high temporal and spatial uncertainty which could be due to sampling issues or real biological/ecological patterns. There is a tremendous amount of uncertainty that needs to be resolved in this data set before incorporating it into our decision analysis. For example, egg densities are an order of magnitude higher on Delaware beaches in comparison to New Jersey beaches and the difference is in part believed to be due to differences in sample processing (R. Weber, Delaware Coastal Program, person. commun.). Furthermore, we believe that it makes

most sense to link red knot population dynamics directly to horseshoe crab abundance rather than through eggs. Even though the eggs are the food source for the birds and are the actual link between these species, our decision analysis (model state variables, management actions, utility functions/objective statements) is focused on abundance of these two species. We view egg availability/density as a relevant quantity that is a direct function of spawning crab numbers. Incorporating egg density data and ecological links into our decision analysis would require a restructuring of the analysis. However, some members of the Shorebird Technical Committee and the ARM committee are in favor of continuing the egg survey as an independent assessment of the success or failure of our management efforts. This survey could contribute to the third purpose for monitoring in adaptive management, assessing whether we are achieving our objectives. We do not foresee using the egg survey data in our models or in our decision analysis in the foreseeable future, and we place low priority on continuing this survey and researching/improving survey methodologies.

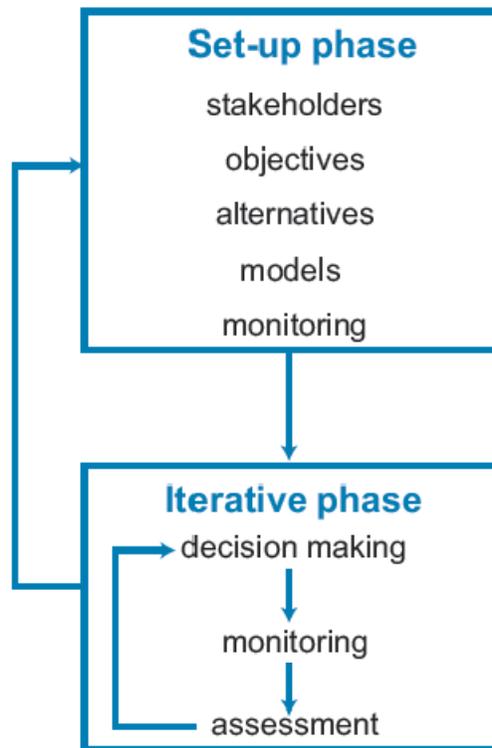
Conclusions

The introduction of structured decision making and the adaptive management paradigms have allowed us to progress towards a formal multi-species management policy for horseshoe crab harvest in the Delaware Bay that is acceptable to multiple stakeholder groups. Of course there are still challenges to overcome, especially those laid out in the monitoring section of this report, but regardless, structured decision making techniques have focused disagreements and led to productive discussions about such topics as desired system objectives and ecological and parametric uncertainty. An inherent part of the structured decision process is to identify and subsequently work towards reducing uncertainty regarding system response to management. We have incorporated three models representing widely different hypothesis about system response into the decision analysis. Although our treatment of uncertainty in the optimization process was limited by computing power, these models represent the full range of uncertainty about ecosystem function.

The multistate robust design survival analyses demonstrate the ability of structured decision making to direct research and monitoring towards the essential questions of the decision analysis and to help researchers focus on reducing uncertainty. We presented a state-of-the-art analysis explicitly linking the demographics of these two species. Our analysis incorporated both horseshoe crab metrics and Arctic snow cover as covariates and examined the critical crab-shorebird link while testing alternative hypotheses and addressing significant points of contention regarding management decisions.

The adaptive management work begins with this report. As stated and emphasized herein, successful adaptive management requires a sustained commitment to monitoring, model updating and model improvement. We envision the completion of this report as the initial setup phase of the adaptive management process discussed in the Department of the Interior's technical guide on adaptive management (Williams et al. 2007, pg 38). Double-loop learning encourages revision of the initial decision structure outlined in this report.

Figure 14: The double loop learning diagram of adaptive management, taken from Williams et al (2007, pg 38).



The next phase is to make and implement management decisions, monitor the system to see how the system responds, update the model weights and make a new set of decisions, improving the decisions as we move forward in time.

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