

Considering economic efficiency in ecosystem-based management: the case of horseshoe crabs in Delaware Bay

Yue Tan*

Sunny L. Jardine[†]

Abstract The welfare gains from incorporating ecosystem considerations into fisheries management are unclear and can vary widely between systems. Additionally, welfare gains depend on how ecosystem considerations are adopted. This paper uses an empirically parameterized bioeconomic model to explore the welfare implications of two definitions of ecosystem-based fisheries management (EBFM). We first define EBFM as a fishery management plan that maximizes the net present value of ecosystem services. We then explore an alternative definition that adds ecosystem considerations to a fishery managed with regulated open access. Our biological model reflects horseshoe crabs in Delaware Bay, which are harvested in a commercial fishery and are ecologically linked to migrating shorebirds populations, e.g. the endangered red knot. We find that introducing ecosystem considerations to a regulated open access fishery generates welfare gains on par with gains from addressing the commons problem even when fishery rents are completely dissipated. Additionally, solving the commons problem within an EBFM approach can provide substantial welfare gains above those from solving the commons problem in a single-species management framework.

Keywords bioeconomics, delayed optimal control, ecosystem-based fisheries management, horseshoe crab (*Limulus polyphemus*), non-fishing values, open access, red knot (*Calidris canutus rufa*)

JEL Classification Q22, Q57

*Department of Economics, University of Delaware, Newark, Delaware 19716, U.S.A.

[†]✉ School of Marine and Environmental Affairs, University of Washington, 3707 Brooklyn Ave NE, Seattle, Washington 98105, U.S.A. E-mail: Jardine@uw.edu.

1 Introduction

Ecosystem-based fisheries management (EBFM) is a holistic approach to management that recognizes the vast array of ecosystem services derived from marine systems as well as the multitude of human impacts on these systems. There is a general scientific consensus on the merit of EBFM (Pikitch et al. 2004, Link 2002, Botsford et al. 1997) and the framework has been adopted in U.S. domestic ocean policy (Executive Order No. 13,547¹, Lubchenco and Sutley 2010). There is less agreement on how to implement EBFM. For example, some scientists argue that addressing the commons problem is critical to reaching the goals of EBFM (Hilborn 2004, Botsford et al. 1997). In contrast, many envision EBFM as an extension of the current regulatory framework that includes ecosystem considerations (e.g. Pikitch et al. 2004), either by applying the precautionary principal to current management (e.g. Essington 2001, Gerrodette et al. 2002) or expanding the stakeholders and metrics used to define management goals (e.g. Brodziak and Link 2002, Levin et al. 2009).

Economists, on the other hand, have adopted a consistent definition of EBFM founded in an efficiency criterion, i.e. EBFM should be designed to obtain the efficient use of fisheries resources. The economics literature has explored EBFM as optimal management that considers either explicit trophic linkages between species in an ecosystem (e.g. Kellner et al. 2011, Singh and Weninger 2009, Hannesson 1983), a wider array of ecosystem services beyond fishery harvest (e.g. Falk-Petersen and Armstrong 2013, Kellner et al. 2011, Bertram and Quaas 2016), or a broader set of human impacts on the system (e.g. Smith 2007b, Holland and Schnier 2006, Guttormsen et al. 2008, Jardine and Sanchirico 2015).

While the literature on the economics of EBFM is broad and growing, there have

¹3 C.F.R. 227 (2010), *reprinted in* 33 U.S.C. §857–19 (2015).

been relatively few assessments illustrating the potential gains from implementing EBFM using an efficiency framework. Two exceptions are [Smith \(2007b\)](#) and [Kellner et al. \(2011\)](#). [Smith \(2007b\)](#) examined the impact of water quality improvements on fishing rents in the North Carolina blue crab fishery finding that rent gains from transitioning from open access to optimal management outweighed rent gains from water quality improvements.² [Kellner et al. \(2011\)](#) explored efficient EBFM for a Caribbean reef community finding that, in most cases, moving from open access to optimal single-species management resulted in larger impacts on effort and standing stock levels than moving from optimal single-species management to optimal multi-species management (i.e. EBFM). Only when there were non-fishing values in the system did the move from optimal single-species management to EBFM lead to significant differences in effort and standing stock levels. Because many of the world's fisheries still lack well-defined property rights, together the results imply that, without the presence of non-fishing values, there are larger gains to be had from improving efficiency of single-species management rather than regulating a larger set of human activities impacting commercial fish species or adopting more complicated EBFM-derived target catch levels.

In this article we explore EBFM of the Delaware Bay horseshoe crab fishery. Horseshoe crabs are harvested in a commercial fishery and their eggs feed migrating shorebird populations, which provide non-market values to recreational birders. We examine two different approaches to EBFM. In the first approach managers seek to maximize the net present value (NPV) of ecosystem services from the system, explicitly considering trophic linkages between the target species and ecologically linked species. The second approach reflects current EBFM of horseshoe crabs

²As a point of clarification [Smith \(2007b\)](#) considered a “quasi-optimized” system rather than a fully optimized system where fishing effort was fixed at a constant level over time to maximize the net present value of the system rather than allowed to vary over time.

where managers simply add ecosystem considerations to an existing regulated open access fishery.

Our article makes several contributions to the literature. First, we add to the economics literature on the welfare gains from EBFM. In contrast to the past literature (i.e. [Kellner et al. 2011](#), [Smith 2007b](#)), we consider gains from adopting ecosystem considerations in a regulated open access fishery. Current U.S. domestic ocean policy advocates EBFM independently of any policies meant to address rent dissipation in fisheries (Executive Order No. 13,547¹, [Lubchenco and Sutley 2010](#)). Therefore, it is very likely that ecosystem considerations will simply be incorporated into the status quo regulatory framework, which has not solved the commons problem.

Second, we use a simple model to explore a range of welfare outcomes from a regulated open access fishery. This is in contrast to the current literature on regulated open access, which merges relatively complex models of industry and regulator behavior ([Homans and Wilen 1997, 2005](#), [Deacon et al. 2011](#)). Because our focus is to compare welfare outcomes between efficient EBFM and EBFM otherwise defined, the dynamics of the regulatory and rent dissipating processes are of less interest to us. Our approach can be useful in other settings, allowing researchers to avoid model complexity in analyzing outcomes from regulated open access modified to reflect ecosystem concerns (or not). Regulated open access is the status quo in most of the world's fisheries and therefore is an important benchmark.

Third, because multiple factors determine the optimal EBFM policy, key drivers of the optimal policy can be obscured. Therefore, to understand key drivers of the optimal horseshoe crab harvest we apply a method from time-series econometrics to decompose the shadow price of horseshoe crabs, identifying the most important determinants of the optimal policy. To our knowledge, we are the first to apply the method to an application in resource economics.

Our findings show that introducing ecosystem consideration to a regulated open access fishery generates welfare gains roughly equal to gains from addressing the commons problems in the fishery even if fishery rents are completely dissipated. Additionally, solving the commons problem within an EBFM approach can provide substantial welfare gains above those associated with optimal single-species management. The results are consistent with [Kellner et al. \(2011\)](#) who demonstrated that EBFM can significantly impact optimal harvest policies when there are non-fishing values in the system. In our case horseshoe crabs provide non-fishing values through their ecological link to migrating shorebird populations, which are valuable to the recreational birding industry.

In what follows we first describe our research setting. We then present the biological and economic models respectively and describe the model calibration process. We explore both analytical and numerical solutions to the model including decomposing the shadow price of horseshoe crabs. We then analyze the sensitivity of our results to our empirically derived estimate of the red knot value function. We then discuss our findings and conclude.

2 Background

Horseshoe crabs (*Limulus polyphemus*), in Delaware Bay, provide a wide array of ecosystem services including value from harvest in a commercial bait fishery and value from supporting migratory shorebird populations, e.g. the red knot (*Calidris canutus rufa*), which provide recreational use values and potential non-use existence values. Horseshoe crabs can be harvested by hand, trawl, dredge, or other methods with most of the harvest over the Atlantic coast attributed to hand harvest ([ASMFC 2009b](#)), making it a low-cost fishery.

The *rufa* red knot, listed as threatened in 2015 under the Endangered Species Act

of 1973,³ has drawn considerable public support for horseshoe crab conservation.⁴ Each May, while migrating from South America to their Arctic breeding grounds, red knots stop over in Delaware Bay to feed on horseshoe crab eggs. This spring congregation of red knots and horseshoe crabs is a valuable tourist attraction (Eubanks et al. 2000, Myers et al. 2010, Edwards et al. 2011).

In the 1980s biologists identified Delaware Bay as a critical stopover for the red knot (Myers et al. 1987). At the same time horseshoe crab harvest was increasing in the Delaware Bay region (Fig. 1), peaking in the late 1990s, and biologists were observing declines in the abundance of horseshoe crabs in Delaware Bay (Niles et al. 2009, Smith et al. 2009; Fig. 2a) as well as the number of red knots visiting Delaware Bay (Niles et al. 2009, 2008; Fig. 2b).

Fig. 1 & Fig. 2

In 1998 the Atlantic States Marine Fisheries Commission (ASMFC) adopted a fishery management plan for the horseshoe crab.⁵ The management plan was motivated, in part, by the concern that declining horseshoe crab populations were detrimental to migratory bird populations that feed on horseshoe crab eggs. Managers were also motivated by a desire to protect resource stocks for sustained use by the commercial fishery. Since the adoption of fishery regulations, EBFM for the Delaware Bay horseshoe crab stock has continued to progress. Currently, harvest quotas in the limited-entry fishery (i.e. regulated open access) are derived from an adaptive, stochastic multi-species model of horseshoe crabs and red knots. Specifically, fishery managers define a set of harvest policies and select the policy that maximizes the long-run harvest of horseshoe crabs subject to a minimum popu-

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³79 Fed. Reg. 73,705 (11 Dec 2014).

⁴For example, in 2008 the Public Broadcasting System (PBS) released a documentary “Crash: a Tale of Two Species” detailing the importance of horseshoe crabs for the survival of the red knot.

⁵There were limited existing restrictions in New Jersey, Delaware, and Maryland (see ASMFC 1998 for more detail).

lation threshold of 11.2 million female horseshoe crabs or 81,900 red knots⁶ (see [ASMFC 2009a](#) for more detail).⁷

While the current EBFM of horseshoe crabs in Delaware Bay is relatively advanced it raises several important questions including: How do biological outcomes from the current policy compare to an economically efficient EBFM policy? What are the welfare gains from efficient EBFM? What information is needed to implement an efficient EBFM policy for horseshoe crabs in Delaware Bay? The remainder of this article addresses these research questions.

3 The Bioeconomic Model

We consider the fishery manager's problem of operationalizing EBFM to optimally rebuild the horseshoe crab population after a period of overfishing. To explore this problem, we develop a continuous-time, deterministic bioeconomic model. Our multi-species model includes two populations—the Delaware Bay horseshoe crab population and the red knots that use Delaware Bay as their last stopover site before migrating to the Arctic for breeding.⁸ Denote the number of adult horseshoe crabs and adult red knots at time t by C_t and R_t , respectively. The fishery begins in an

⁶The red knot threshold was originally 45,000 birds and was then adjusted to 81,900 birds in 2013 to reflect the change in the method of monitoring the red knot population. See [ASMFC \(2013b\)](#) for the detail on the adjustment.

⁷In the ASMFC's model the fishery manager weighs harvest of female and male horseshoe crabs differently and takes into account the operational sex ratio.

⁸Empirical evidence supports assuming well-defined populations. First, tagging and genetic evidence shows limited exchange between the Delaware Bay horseshoe crab population and the Chesapeake Bay horseshoe crab population or the Raritan Bay horseshoe crab population ([Swan 2005](#), [Pierce et al. 2000](#)). Second, the red knot population that winters along the Argentinian coast from Tierra del Fuego to Río Negro comprises the majority of red knots that stopover at Delaware Bay ([Niles et al. 2008](#)) although there are at least two other smaller populations identified feeding on horseshoe crab eggs in Delaware Bay ([Atkinson et al. 2005](#)).

unexploited state with both the horseshoe crab and the red knot populations at their respective full carrying capacities, i.e. $C_t = K_c$ and $R_t = K_r \forall t \leq -T_1$, and is then harvested in an open access setting for a period of T_1 years. During the open access period, harvest of horseshoe crabs is unregulated and effort responds myopically to current rents. Then, at $t = 0$, open access ceases and a period of T years of optimal fishery management begins.

Here we are interested in fishery management that targets efficient EBFM (hereafter ECON-EBFM). Under ECON-EBFM horseshoe crab harvest is optimally chosen to maximize the NPV of ecosystem services including rents in the horseshoe crab fishery and values from the red knot population. For comparison, we consider outcomes from a continued regulatory state of open access. We also consider two alternative fishery management plans for comparison: (i) single-species fisheries management (SSFm), which ignores ecosystem linkages or red knot values (or both) and simply selects horseshoe crab harvest to maximize fishery rents; and (ii) biological EBFM (hereafter BIO-EBFM), which acknowledges ecosystem linkages, but ignores the economic value of the system, by maximizing sustainable horseshoe crab harvest subject to a target red knot population level. Our BIO-EBFM scenario most closely represents the current management regime in the Delaware Bay horseshoe crab fishery.

In what follows we first describe the multi-species biological model, and then turn to the economic models of open access, ECON-EBFM, SSFM, and BIO-EBFM. More detail of our selection of the model parameters can be found in the online supplementary material.

3.1 The biological model

We track sexually mature adults in the horseshoe crab and the red knot populations.⁹ Because horseshoe crabs take approximately $\tau = 10$ years to reach sexual maturity (Shuster and Sekiguchi 2003), we adopt a delay-differential model of horseshoe crab population dynamics. We model the red knot population dynamics with a modified logistic equation.¹⁰

Denoting differentiation with respect to time with a dot over a variable, e.g. $\dot{C}_t = dC_t/dt$, the horseshoe crab population dynamics are governed by

$$\dot{C}_t = g_c C_{t-\tau} \exp(-C_{t-\tau}/K_c^*) - \eta_c C_t - h_t, \quad (1)$$

where g_c is the maximum per capita egg production rate of horseshoe crabs adjusted for egg-to-adult survival, η_c is the per capita death rate of horseshoe crabs, $K_c^* = K_c/\ln(g_c/\eta_c)$ is the population size at which horseshoe crab recruitment is maximized, and h_t is the instantaneous harvest rate. The growth equation (1) is based on Nicholson's blowflies equation (Gurney et al. 1980). Horseshoe crab eggs are buried in the sand and become unearthed due to spawning activities or wave action (Botton and Loveland 2003, Smith 2007a). Because the unearthed eggs are either consumed, e.g. by red knots, or desiccate and die (Niles et al. 2009), the horseshoe crab population dynamics are not a function of the red knot population.

Red knot population dynamics are governed by

$$\dot{R}_t = g_r R_t \left(1 - \frac{R_t}{K_{r,t}^*(C_t)} \right), \quad (2)$$

⁹We ignore the sex composition and assume 1:1 sex ratios for both populations.

¹⁰Because red knots are believed to breed in their second year (Harrington and Morrison 1980), their recruitment delay is relatively short compared to that of horseshoe crabs. Therefore, to simplify the model we assume instantaneous recruitment for red knots.

where g_r is the intrinsic growth rate of red knots and $K_{r,t}^*(C_t)$ is the time- t carrying capacity of red knots, which is a function of the time- t population size of horseshoe crabs to be specified below.

We introduce a density-dependent carrying capacity for red knots, which is a function of the population size of horseshoe crabs, in an attempt to capture real-world dependence of red knots on horseshoe crabs. During their stopover at Delaware Bay the red knots primarily feed on the eggs of horseshoe crabs and the resulting weight gain is crucial to the success of their subsequent flight to and breeding in the Arctic (see e.g. Baker et al. 2004, McGowan et al. 2011a, Haramis et al. 2007).¹¹ Therefore, a large population of red knots needs high density of horseshoe crab eggs to support it, which in turn requires a large population of horseshoe crabs.

We assume a logistic functional form for the density-dependent carrying capacity of red knots:¹²

$$K_r^*(C) = \frac{a}{1 + \exp(b_0 + b_1 C)} K_r, \quad (3)$$

where a , b_0 , and b_1 are parameters. The sigmoidal relationship has two attractive features. First, while abundant horseshoe crabs do not impede growth of the red knot population, a reduced horseshoe crab stock can severely limit the population size of red knots. Second, (3) introduces a convexity shift in the relationship between the number of horseshoe crabs and their importance to red knots. Since the primary process that makes horseshoe crab eggs available to red knots is spawning female horseshoe crabs unearthing eggs previously deposited in the sand (Smith 2007a), it

¹¹See also USFWS (2014, pp. 28–33) for a review of the literature on this matter.

¹²This is motivated by McGowan et al. (2011b), who modeled the probability of red knots transitioning from light-weight (departure weight, i.e. weight upon departing Delaware Bay, < 180 g) to heavy-weight (departure weight \geq 180 g) during the stopover as a logistic function of the abundance of spawning female horseshoe crabs.

seems reasonable to assume that the unearthing process increases with the density of eggs previously deposited in the sand. Thus the *marginal* increase in the density of horseshoe crab eggs available to red knots should become higher as the egg density rises from very low levels.¹³ On the other hand, as red knots are gradually saturated with horseshoe crab eggs, additional eggs are less important.¹⁴

3.2 The economic models

3.2.1 *Open access baseline*

We adopt a model of open access to describe the unregulated period in the horseshoe crab fishery. We assume open access starts at $t = -T_1$ and lasts for T_1 years.

Fishermen obtain profit solely from harvesting and selling horseshoe crabs and fishery harvest is of the [Schaefer \(1954\)](#) form:

$$h_t = qC_tE_t. \quad (4)$$

Therefore, instantaneous industry rents are given by

$$\Pi_t(C_t, E_t) = pqC_tE_t - \delta E_t^2, \quad (5)$$

¹³[Smith \(2007a\)](#) found a slightly sigmoidal relationship between the number of eggs disturbed by subsequent spawning and density of spawning female horseshoe crabs through simulation. [Sweka et al. \(2007\)](#) modeled the number of horseshoe crab eggs available to shorebirds as a convex function of the number of spawning females. Both studies modeled after horseshoe crabs in the Delaware Bay area.

¹⁴Several studies have revealed that increased egg density has diminishing returns on red knots' egg-intake rate. See [Niles et al. \(2008, pp. 36–39\)](#).

where p is the ex-vessel price of horseshoe crabs,¹⁵ q is a “catchability” coefficient, E_t is the instantaneous fishery effort, and δE_t^2 is the instantaneous cost.

To model fleet dynamics under open access we use the [Smith \(1968\)](#) model of dynamic open access with [Clark’s \(1990\)](#) specification of industry sluggishness:

$$\dot{E}_t = \gamma E_t (\Pi_t / E_t) = \gamma E_t (pqC_t - \delta E_t), \quad t \in [-T_1, 0], \quad (6)$$

where γ is the speed of effort adjustment or the “sluggishness” parameter.

In summary, the baseline model of open access consists of three differential equations: the population dynamics of horseshoe crabs (1) with the initial condition $C_t = K_c, t \in [-T_1 - \tau, -T_1]$, the population dynamics of red knots (2) with the initial condition $R_{-T_1} = K_r$, and the effort dynamics (6) with the initial condition E_{-T_1} .

3.2.2 *Efficient ecosystem-based fishery management (ECON-EBFM)*

After a period of open access the manager begins efficient EBFM for horseshoe crabs at $t = 0$. The manager seeks to maximize rents in the horseshoe crab fishery and conservation values associated with the red knot population.¹⁶ For the purposes of comparison we assume that the revenue and cost structures from the open access period remain unchanged and utilize estimates of non-market recreational use value from [Eubanks et al. \(2000\)](#), [Myers et al. \(2010\)](#), and [Edwards et al.](#)

¹⁵Our calculation with landings data shows that the inflation-adjusted ex-vessel price of horseshoe crabs was relatively low and stable from the late 1970s through the early 1990s. Although the price has risen considerably since the late 1990s, it exhibited much less variation than landings did in some years when landings fluctuated dramatically. See the online supplementary material.

¹⁶We note that optimal management may conflict with limits to incidental take defined by the Endangered Species Act. As ours is a conceptual analysis conducted for the purposes of exploring the welfare gains from various frameworks for ecosystem-based management, we do not incorporate any constraints imposed by the Endangered Species Act.

(2011) to characterize the red knot conservation value.¹⁷ Additionally we conduct a sensitivity analysis over the conservation value function (see Sect. 5.2.7). Our baseline conservation value function $V_t(\cdot)$ is described in what follows.

We assume that the demand for birding trips, from which consumer surplus is ultimately generated, depends positively on the number of red knots, which implies that $V_t(\cdot)$ is a function of the number of red knots R_t :

$$V_t(R_t) = \begin{cases} w(R_t - R_m)^\alpha, & R_t \geq R_m, \\ 0, & R_t < R_m, \end{cases} \quad (7)$$

where w is the value per thousand red knots, R_m is a threshold population level below which red knots are no longer valued, and α is a shape parameter.¹⁸ The valuation function features a minimal number of red knots valued, which was identified by Eubanks et al.'s (2000) survey of New Jersey birders.¹⁹

The fishery manager's objective is to regulate the trajectory of harvest effort E_t over the horizon $[0, T]$ to maximize the NPV of the sum of rents in horseshoe crab fishery and the economic value of red knots subject to biological feasibility, i.e. the population dynamics of horseshoe crabs and red knots ((1) and (2), respectively). Essentially, the manager solves a delayed optimal control problem:

$$\max_{E_t, t \in [0, T]} \int_0^T e^{-\rho t} (\Pi_t(C_t, E_t) + V_t(R_t)) dt \quad (8)$$

¹⁷While the total economic value of horseshoe crabs should also include any non-use values for both horseshoe crabs and red knots, these values have not been estimated in the literature.

¹⁸This valuation function is motivated by Kellner et al. (2011), who modeled the non-fishing value proportional to the square root of fish density.

¹⁹Additionally, we check that applying our valuation function to the lowest population count data on red knot does not yield an infinite marginal value of red knots. In fact, the highest marginal value of red knots observed was \$118.5 (2009 dollars).

$$\text{subject to } \dot{C}_t = g_c C_{t-\tau} \exp(-C_{t-\tau}/K_c^*) - \eta_c C_t - q C_t E_t, \quad t \in [0, T], \quad (9)$$

$$\dot{R}_t = g_r R_t \left(1 - \frac{R_t}{K_{r,t}^*(C_t)}\right), \quad t \in [0, T], \quad (10)$$

$$E_t, C_t, R_t \geq 0, \quad t \in [0, T], \quad (11)$$

$$C_t = \phi_t, \quad t \in [-\tau, 0], \quad \text{and} \quad R_0 = \psi_0, \quad (12)$$

where ρ is the discount factor, $\Pi_t(\cdot, \cdot)$, $V_t(\cdot)$, and $K_{r,t}^*(\cdot)$ are defined respectively in (5), (7), and (3), and the initial conditions ϕ_t and ψ_t , respectively, are the solutions of C_t and R_t on $[-T_1, 0]$ from the open access model.²⁰

3.2.3 *Alternative management plans (SSFm and BIO-EBFM)*

In addition to the ECON-EBFM plan, we consider two alternative management plans. First, we consider SSFM under which the fishery manager ignores the impact of horseshoe crab harvest on red knots in managing the horseshoe crab fishery. Specifically, under SSFM the manager solves a delayed optimal control problem similar to the one under ECON-EBFM but sets $w = 0$.

Second, we consider a biological approach to EBFM, BIO-EBFM, where the manager considers ecosystem linkages and sets a red knot population target equal to Θ_r . BIO-EBFM is most similar to current horseshoe crab harvest policy in Delaware Bay (described in [ASMFC 2009a](#)). Under this plan, the manager's interest is to maximize sustainable harvest while maintaining ecosystem integrity, i.e. eliminating the possibility of collapse of either the horseshoe crab or the red knot. To accomplish this goal, harvest is restricted whenever the red knot target is not met.

Additionally, consistent with National Standard 1 of the Magnuson–Stevens

²⁰We implicitly assume that the manager assigns equal weights to the rents from horseshoe crabs and the economic value from red knots. We conduct a sensitivity analysis on our red knot value function later by varying w , which is equivalent to varying the relative weights.

Fishery Conservation and Management Act²¹, the manager implementing BIO-EBFM restricts fishery mortality to be less than or equal to the fishing mortality that produces a harvest equal to maximum sustainable yield (MSY) when the stock is at the level that can continuously deliver MSY, denoted by F_{MSY} .²²

Current horseshoe crab quotas, based on ecosystem considerations, are imposed on a regulated open access fishery.²³ However, to avoid model complexity and examine a range of outcomes we assume that managers can perfectly control fishing effort. In contrast, [Homans and Wilen \(1997\)](#) modeled a regulated open access fishery where effort was unrestricted, but harvest was indirectly controlled by managers through adjusting season length. In [Homans and Wilen \(1997\)](#) effort was drawn to the regulated open access fishery until fishery rents were completely dissipated. [Deacon et al. \(2011\)](#), on the other hand, considered a regulated open access fishery where effort was restricted along some margins, but not others. Therefore, rents were only partially dissipated.²⁴ This implies our results provide an upper bound on fishery rents that can be generated under current policy and the lower bound is zero. The simplification allows us to analyze harvest policies and resource stocks that emerge from the current policy and bound plausible welfare changes without specifying a more complex model of the horseshoe crab production function and the intricacies of real-world horseshoe crab management and harvester behavior.

²¹16 U.S.C. §1851(a)(1) (2015); see also 50 C.F.R. §600.310 (2015).

²²To determine F_{MSY} in our model, we first solve (1) for sustainable harvest, which gives $h = g_c C \exp(-C/K_c^*) - \eta_c C$. Maximizing the preceding equation with respect to C gives the MSY harvest rate, h_{MSY} , and the stock level that delivers it, C_{MSY} . Then the upper bound on fishery mortality is $F_{MSY} = h_{MSY}/C_{MSY}$.

²³State-level fisheries are managed with gear-specific permit restrictions and quotas.

²⁴Rents earned depended on the elasticity of substitution between restricted and unrestricted inputs.

Specifically, we assume the manager solves a delayed optimal control problem with additional constraints on E_t under BIO-EBFM:

$$\begin{aligned}
& \max_{E_t, t \in [0, T]} \int_0^T q C_t E_t \, dt \\
\text{subject to } & \dot{C}_t = g_c C_{t-\tau} \exp(-C_{t-\tau}/K_c^*) - \eta_c C_t - q C_t E_t, \quad t \in [0, T], \\
& \dot{R}_t = g_r R_t \left(1 - \frac{R_t}{K_{r,t}^*(C_t)} \right), \quad t \in [0, T], \\
& q E_t \leq F_{\text{MSY}}, \quad t \in [0, T], \\
& E_t \leq 0 \quad \text{if } R_t < \Theta_r, \quad t \in [0, T], \\
& E_t, C_t, R_t \geq 0, \quad t \in [0, T], \\
& C_t = \phi_t, \quad t \in [-\tau, 0], \quad \text{and} \quad R_0 = \psi_0.
\end{aligned}$$

4 Methods

We take several steps to calibrate our bioeconomic model, which are described in detail in the online supplementary material and summarized here. For the majority of parameters of population dynamics we either take their values directly from the literature or calculate their values from literature estimates of related life history parameter. We compute the per capita ex-vessel price of horseshoe crabs from data on the value of reported annual landings from [ACCSP \(2016\)](#) and the reported annual counts of horseshoe crabs landed from [ASMFC \(2013a, Table 2; 2004, Table 1\)](#). We estimate the red knot value function from literature estimates of willingness to pay for birding trips to the Delaware Bay area and the number of birders visiting birding sites. We estimate or select values for the cost parameter, the parameters of dependence of red knots on horseshoe crabs, the speed of effort adjustment under open access, and the initial effort level under open access with a data-fitting exercise (see the online supplementary material for more detail). The red knot target under BIO-EBFM is taken from [ASMFC \(2009a\)](#). The rest parameter values are assumed.

Table 1 summarizes the model parameters, their values, and empirical support. Table 1 about

We first explore the analytical solution to the efficient horseshoe crab management plan (ECON-EBFM) and the various drivers of the optimal harvest policy. We then solve the open access model and the ECON-EBFM model numerically, analyzing optimal effort, harvest, and stock levels as well as each component of the shadow price of the horseshoe crab stock. Alternative management plans (SSFM and BIO-EBFM) are also solved numerically for comparison.

We adopt the numerical method by Göllmann et al. (2009) to solve the delayed optimal control problems associated with various fishery management plans. We use a grid size of 400,000 and error tolerances of 10^{-10} or smaller for our main results. All numerical solutions are computed with MATLAB R2015b.

Finally, we conduct a sensitivity analysis to explore the robustness of the results to assumptions on the red knot value function (7).

5 Results

Our analysis highlights the key drivers of optimal horseshoe crab management in Delaware Bay and the potential gains implementing EBFM either through modifying status quo fishery regulations or through an efficiency-based approach.

5.1 Analytical results

The current-valued Hamiltonian for the fishery manager's delayed optimal control problem under ECON-EBFM, (8–12), temporarily ignoring the non-negativity

constraints (11),²⁵ is

$$\begin{aligned}
& \mathcal{H}(t, C_t, C_{t-\tau}, R_t, E_t, \lambda_t, \xi_t) \\
&= pqC_tE_t - \delta E_t^2 + w(R_t - R_m)^\alpha \\
&\quad + \lambda_t [g_c C_{t-\tau} \exp(-C_{t-\tau}/K_c^*) - \eta_c C_t - qC_tE_t] \\
&\quad + \xi_t g_r R_t \{1 - R_t/K_r/a \cdot [1 + \exp(b_0 + b_1 C_t)]\} ,
\end{aligned}$$

where λ_t and ξ_t are the two costate variables associated with (9) and (10), respectively. Necessary optimality conditions include²⁶

$$0 = \frac{\partial \mathcal{H}}{\partial E_t} = pqC_t - 2\delta E_t - \lambda_t qC_t, \quad 0 \leq t \leq T, \quad (13)$$

$$\begin{aligned}
-\dot{\lambda}_t + \rho \lambda_t &= \frac{\partial \mathcal{H}}{\partial C_t} + e^{-\rho\tau} \frac{\partial \mathcal{H}}{\partial C_{t-\tau}} \\
&= pqE_t - \lambda_t(\eta_c + qE_t) - \xi_t g_r R_t^2 / K_r / a \cdot b_1 \exp(b_0 + b_1 C_t) \\
&\quad + e^{-\rho\tau} \lambda_{t+\tau} g_c (1 - C_t / K_c^*) \exp(-C_t / K_c^*), \quad 0 \leq t < T - \tau,
\end{aligned} \quad (14)$$

$$\begin{aligned}
-\dot{\lambda}_t + \rho \lambda_t &= \frac{\partial \mathcal{H}}{\partial C_t} = pqE_t - \lambda_t(\eta_c + qE_t) \\
&\quad - \xi_t g_r R_t^2 / K_r / a \cdot b_1 \exp(b_0 + b_1 C_t), \quad T - \tau \leq t \leq T,
\end{aligned} \quad (15)$$

and $\lambda_T = 0$ (see [Kamien and Schwartz 1991](#), Part II, Sect. 19). From (13) we obtain

$$E_t = \frac{q}{2\delta} C_t (p - \lambda_t), \quad 0 \leq t \leq T. \quad (16)$$

²⁵The non-negativity constraint on effort level E_t binds when $\lambda_t > p$, at which point effort level is no longer determined by (16) but constrained to zero. On the other hand, the non-negativity constraints on C_t and R_t turn out to be non-binding in our numerical solutions. Proper treatment of these non-negativity constraints is included in the appendix.

²⁶Full set of necessary optimality conditions is included in the appendix.

Since the costate variable λ_t can be interpreted as the current-value shadow price (the marginal shadow value) of horseshoe crabs, (16) clearly shows that a positive harvest rate is optimal only when the market price of horseshoe crabs exceeds the current-value shadow price of horseshoe crabs.

Horseshoe crabs provide multiple ecosystem services. Therefore, multiple factors drive the shadow price of the horseshoe crab stock and the optimal ECON-EBFM harvest policy. We decompose λ_t into various components: $\lambda_{1,t}$, $\lambda_{2,t}$, $\lambda_{3,t}$, and $\lambda_{4,t}$, which are defined as follows:

$$-\dot{\lambda}_{1,t} + \rho\lambda_{1,t} = pqE_t, \quad 0 \leq t \leq T, \quad (17)$$

$$-\dot{\lambda}_{2,t} + \rho\lambda_{2,t} = -\lambda_t(\eta_c + qE_t), \quad 0 \leq t \leq T, \quad (18)$$

$$-\dot{\lambda}_{3,t} + \rho\lambda_{3,t} = e^{-\rho\tau}\lambda_{t+\tau}g_c(1 - C_t/K_c^*)\exp(-C_t/K_c^*), \quad 0 \leq t \leq T - \tau, \quad (19)$$

$$-\dot{\lambda}_{4,t} + \rho\lambda_{4,t} = -\xi_t g_r R_t^2 / K_r / a \cdot b_1 \exp(b_0 + b_1 C_t), \quad 0 \leq t \leq T, \quad (20)$$

and

$$\lambda_{1,T} = \lambda_{2,T} = \lambda_{4,T} = 0, \quad \lambda_{3,t} = 0, \quad T - \tau \leq t \leq T, \quad (21)$$

such that

$$\lambda_t = \lambda_{1,t} + \lambda_{2,t} + \lambda_{3,t} + \lambda_{4,t}, \quad 0 \leq t \leq T. \quad (22)$$

The right-hand-side terms in (17–20) are found on the right-hand sides of (14) and (15).

Therefore λ_t is comprised of four components: (i) the marginal value of immediate harvest associated with a marginal increase in the horseshoe crab stock, $\lambda_{1,t}$; (ii) the marginal cost of increasing the horseshoe crab stock associated with a reduction in the instantaneous growth rate, $\lambda_{2,t}$; (iii) the marginal value of increasing horseshoe crab recruitment at time $t + \tau$ discounted to time t , $\lambda_{3,t}$; and (iv) the marginal value of increasing the density-dependent carrying capacity of

red knots and thus promoting growth in the red knot population (which is valued at a shadow price of ξ_t), $\lambda_{4,t}$. Among the four components, $\lambda_{2,t}$ and $\lambda_{3,t}$ reflect the intertemporal tradeoffs involved in single-species management of the horseshoe crab, which has a long delay in recruitment, while $\lambda_{4,t}$ provides the economic link between the horseshoe crab and the red knot. Note that $\lambda_{4,t}$ would be absent if the value of red knots is excluded from the manager's objective function, or if red knots were not dependent on horseshoe crabs for survival. Therefore, the presence of the $\lambda_{4,t}$ component distinguishes the ECON-EBFM plan from the SSFM plan, in which the two populations are not linked biologically nor economically (or the linkages are ignored), and the BIO-EBFM plan, in which the biological link is present but the economic link is missing.

Additionally, to aid intuition, we also explore various mutations of λ_t obtained through setting the cumulative historical impact of some components of the shadow price equal to zero. Specifically, for $t \in [0, T]$ and fixed $t_0 \in [0, T]$, we define

$$\lambda_t^{(i)} = \lambda_{t_0} + (\lambda_{i,t} - \lambda_{i,t_0}), \quad i = 1, 2, 3, 4,$$

and

$$\lambda_t^{(i,j)} = \lambda_{t_0} + (\lambda_{i,t} - \lambda_{i,t_0}) + (\lambda_{j,t} - \lambda_{j,t_0}), \quad i, j = 1, 2, 3, 4, i \neq j.$$

The purpose of the mutations is to examine what would have happened to λ_t if only certain components of λ_t , not all of them, had been driving λ_t , conditional on the optimal trajectories of effort, harvest and population sizes, and consequently to assess the relative importance of the various components in shaping λ_t . It is similar to the purpose of historical decomposition in vector autoregression models.²⁷

In what follows we examine the decomposition and its mutations numerically to

²⁷The technique of historical decomposition in vector autoregression models was pioneered by Sims (1980) and subsequently developed by Burbidge and Harrison (1985).

assess which components are driving the current-value shadow price of horseshoe crabs and thus the optimal decision of harvest.

5.2 Numerical results

We first consider the numerical solutions for effort, harvest, and horseshoe crab and red knot stocks. We then describe the numerical decomposition of the shadow price of horseshoe crabs. Fig. 3 and Fig. 4 show the trajectories of effort levels, harvest rates, and horseshoe crab and red knot populations in the open access period and the first 125 years under continued open access and the three fishery management plans we consider (ECON-EBFM, SSFM, and BIO-EBFM). Trajectories after $t = 125$ are not shown because the terminal periods are of less interest to us and we speculate that the trajectories towards $t = 125$ here approximate what the optimal trajectories would have been as $t \rightarrow \infty$ over an infinite horizon.²⁸

Fig. 3 & Fig. 4
about here

5.2.1 Trajectories under open access

The open access period is characterized by an immediate expansion of effort in the horseshoe crab fishery (Fig. 3a). At first harvest increases reaching more than one-hundred-and-sixty-five-fold from its initial level in about 15.2 years, then it plateaus before falling (Fig. 3b). The horseshoe crab population decreases faster than effort increases driving the eventual decline in harvest. The plateau is created by the ten-year lag period required for horseshoe crabs to reach sexual maturity. For example, recruitment of horseshoe crabs fifteen years into the open access period

²⁸To our best knowledge, the turnpike property for finite-horizon delayed optimal control problems with discount criterion has not yet been formally established in the literature, although we speculate that it is true. We observe that, within the management horizon, the effort level, the harvest rate, and the horseshoe crab and the red knot populations approach certain stationary levels. The levels that are sustained for the majority of the optimization horizon should be very close to the respective turnpikes.

depends on the population size five years into the open access period, when the population size is still high (Fig. 4a). Moreover, recruitment is maximized when $C = K_c^* \approx 22.5$ (in millions), which is a little below the carrying capacity of $K_c = 28$ (in millions). As a result, actual recruitment of horseshoe crabs continues to rise by a small amount for a short period of time after harvest peaks, slowing down the decline in horseshoe crab population and thus generating the plateau period of about four years with a relatively high harvest rate.

Harvest drives a decline in the horseshoe crab and the red knot populations (Fig. 4). However, the red knot population shows a delayed response to the decline in the horseshoe crab population. At high population levels of horseshoe crabs, the red knots are saturated with horseshoe crab eggs and a small decline in the number of horseshoe crabs only marginally affects the red knot population. In fact, based on our model parameters, a horseshoe crab population 80% of its carrying capacity supports a red knot population at roughly 99% of its full carrying capacity, and the horseshoe crab population does not fall below 80% of its carrying capacity until about 10.8 years into the open access period.

If open access were to continue beyond $t = 0$ (when fishery management takes over), the effort level would continue to rise and peak in about 2.5 years, at which time rents in the horseshoe crab fishery would be fully dissipated. Excessive fishing effort would drive both the horseshoe crab and the red knot populations to the verge of collapse. After thirty years of continued open access, the horseshoe crab population would be about 2% of its carrying capacity and the red knot population would be about 3% of its full carrying capacity.²⁹ The result is driven by the low

²⁹Such extremely low population sizes are no surprise and are direct consequences of matching the predictions of our model with real-world trends in populations. For instance, the Delaware 30-foot trawl survey found the lowest horseshoe crab abundance index in 2004, which was only 1.1% of the index in 1990. Refer to Fig. 2a.

harvest cost in a fishery where horseshoe crabs can be harvested directly from local beaches by hand (ASMFC 2009b).

5.2.2 Trajectories under SSFM

At $t = 0$, the fishery manager begins regulating harvest of horseshoe crabs. With SSFM, the manager allows harvest immediately after the end of open access and harvest rate increases to a local high of about 52% of MSY after about 3.8 years (Fig. 3). Despite being harvested, the horseshoe crab population recovers quickly, doubling in about 1.2 years (Fig. 4a). Such recovery from a depleted state is possible largely because of the ten-year delay in recruitment. Since the horseshoe crab population declines continuously over the open access period, recruitment exceeds deaths by a large margin at $t = 0$ and shortly after $t = 0$, enabling a quick recovery allowing immediate harvest under optimal SSFM.

After time, increasing deaths and harvest outnumber decreasing recruitment, resulting in a temporary decline in the horseshoe crab population. The temporary decline ends shortly after $t = 10$, when recruitment begins to improve. The horseshoe crab population continues to grow afterwards and gradually stabilizes around 27% of its carrying capacity after 36 years since the beginning of management. The harvest rate is sustained at about 90% of MSY after 47 years since the beginning of management. In general, changes in effort level are synchronized with changes in the population size of horseshoe crabs, i.e. effort rises as the population expands and drops as the population shrinks.³⁰

On the other hand, under SSFM the red knot population rebounds slowly and stabilizes around 29% of its full carrying capacity after 60 years since management begins (Fig. 4b). With SSFM (and all three management scenarios) there is an

³⁰Strictly speaking, effort level has a very small lead in time. We do not imply causality here, however.

ephemeral (less than one year) and small (less than 4%) decline in the red knot population at the beginning of the management period; see the enlarged detail in Fig. 4b and Fig. 5. This is caused by the red knot’s (density-dependent) carrying capacity being below the current population size at the end of the open access period. The decline represents a delayed adjustment to the carrying capacity. Then, as the horseshoe crab population quickly recovers, the red knot’s (density-dependent) carrying capacity soon surpasses its current population size, after which the red knot population begins to rebound.

To summarize, based on our parameterization, the optimal harvest policy under SSFM features an immediate start of harvesting, synchrony between the effort level and the population size of horseshoe crabs, and a long period of sustained harvest.

5.2.3 Trajectories under BIO-EBFM

Under BIO-EBFM, there is an immediate moratorium on harvest because the red knot population target of Θ_r is not met at the beginning of management (Fig. 3 and Fig. 4b). During the moratorium period the horseshoe crab population recovers quickly, quadrupling in about 5.6 years and continuing to grow to levels higher than the population size in any year under SSFM (Fig. 4a). Therefore, the red knot population rebounds faster than it does under SSFM.

The moratorium ends immediately when the population size of red knots reaches the target at $t = T'_M \approx 14.0$. Since the manager’s interest under BIO-EBFM is to maximize sustainable harvest, he or she would like to keep the horseshoe crab population size close to C_{MSY} , which delivers MSY. At the end of the moratorium, the horseshoe crab population stands about 18% above C_{MSY} .

Ideally, if there were no limit, legal or physical, on fishery mortality at all and there were no delay in recruitment of horseshoe crabs, the fishery manager would find it optimal to exert an “infinitely high” effort immediately following the

achievement of the red knot target to instantly bring the horseshoe crab population size to C_{MSY} and then harvest constantly at MSY thereafter.

However, in our case the manager is constrained by both a limit on fishery mortality and a long delay in recruitment of horseshoe crabs, which renders the optimal harvest policy no longer trivial. The manager starts by exhausting the overhead in horseshoe crabs by exerting the maximum allowed effort level. Then at $t \approx 16.8$ the overhead is exhausted, after which harvest is reduced due to the fact that recruitment of horseshoe crabs is declining because of a low stock history and the delayed population dynamics. The reduction in harvest dampens future fluctuations in the horseshoe crab population size created by the moratorium period. Therefore, the horseshoe crab population size can be better stabilized around the desired level of C_{MSY} .

Then, at $t \approx 21.3$ the manager resumes the maximum allowed effort. The horseshoe crab population finally stabilizes around C_{MSY} , which is about 42% of its carrying capacity, after 28 years since the beginning of management while the red knot population stabilizes around 65% of its full carrying capacity after 48 years since the beginning of management.

To summarize, based on our parameterization, the optimal harvest policy under BIO-EBFM features a moratorium period of 14.0 years in the beginning to meet the red knot population target and constant effort levels except a short period of reduced effort levels to help stabilize the horseshoe crab population size around the desired long-run level.

5.2.4 Trajectories under ECON-EBFM

Under ECON-EBFM, given the depleted state of both the horseshoe crab population and the red knot population, the fishery manager first enforces a moratorium on harvest of $T_M \approx 12.6$ years during which the horseshoe crab population experiences

a quick recovery while the red knot population experiences a milder one (Fig. 3 and Fig. 4). At the end of the moratorium, the horseshoe crab population has recovered to about 42% of its carrying capacity and the red knot population has rebounded to about 27% of its full carrying capacity.

Following termination of the moratorium, harvest rate rises quickly from zero to a local maximum of about 67% of MSY in about 4 years. After that harvest rate experiences a small and temporary decrease, and then increases again. In the meanwhile, the red knot population continues to grow steadily, doubling its size in about 10.3 years. The harvest rate stabilizes around 93% of MSY after 47 years since management begins. The horseshoe crab population stabilizes around 55% of its carrying capacity after 42 years since management begins. The red knot population stabilizes around about 88% of its full carrying capacity after 59 years since management begins. We note that the sustained effort level under ECON-EBFM is significantly (about 30%) lower than that under BIO-EBFM despite that the sustained harvest rate under ECON-EBFM is slightly (about 7%) lower than that under BIO-EBFM.

In addition to higher sustained levels of both the horseshoe crab population and the red knot population, two other features of the ECON-EBFM trajectories notably distinguish them from the corresponding ones under SSFM or BIO-EBFM. First, there is lack of synchrony between the effort level and the population size of horseshoe crabs in the first several decades of management. Under SSFM, changes in effort level are synchronized with changes in the population size of horseshoe crabs, as mentioned in Sect. 5.2.2. Under ECON-EBFM, both the horseshoe crab and the red knot populations grow continuously after the end of the moratorium, yet the effort level does not always increase.

Second, under ECON-EBFM the trajectory of the red knot population to recovery is less variable than under SSFM or BIO-EBFM. Fig. 5 shows the instantaneous

growth rates of the red knot population in the first six decades of the management horizon under the three management plans. Under ECON-EBFM, the value of the red knot population encourages the impatient manager to avoid exploiting the excess of recruitment of horseshoe crabs for an early harvest (as done under SSFM) and instead to utilize the excess for rebuilding both stocks. Because fluctuations in the horseshoe crab stock size are transmitted to the red knot stock, the fluctuations are suppressed to generate a steady flow of value from both stocks. In contrast, under SSFM the horseshoe crab population displays multiple fluctuations and thus the growth of red knots after the first year is more variable, and even negative in some periods. Under BIO-EBFM, the manager would like to maintain the horseshoe crab population size steady at C_{MSY} , but is constrained by limits on fishery mortality. Fig. 5 about

To summarize, based on our parameterization, the optimal harvest policy under here ECON-EBFM features a moratorium period of 12.6 years in the beginning, varying harvest rates following termination of the moratorium to deliver continued, steady recovery of both the horseshoe crab and the red knot populations, and a long period of sustained harvest.

5.2.5 Determination of the optimal harvest policy under ECON-EBFM

Now we take a closer look at the drivers of the optimal harvest policy under ECON-EBFM. We examine the determination of λ_t by decomposing it into four components defined in (17–21). Fig. 6 about Fig. 6 shows the decompositions in the first three decades of management. Note that in this period the horseshoe crab population is generally increasing.

Fig. 6a about here Fig. 6a shows the trajectories of λ_t and its components in levels. The current-value shadow price λ_t starts above the market price p , causing the fishery manager to enforce a moratorium on harvest. The shadow price then fluctuates over time, and finally drops below p . When $\lambda_t = p$ the moratorium is terminated and harvest

begins (at $t = T_M$). For the components, $\lambda_{1,t}$ and $-\lambda_{2,t}$ have upward trends in general, $\lambda_{3,t}$ has a general downward trend, and $\lambda_{4,t}$ has mixed trends. While λ_t is the sum of all the components, it is difficult to assess which component dominates simply by examining component levels in Fig. 6a.

Fig. 6b, however, presents the cumulative historical impact of each component, clearly showing that during the moratorium period λ_t is dominated by $\lambda_{4,t}$ because the counterfactual trajectory of λ_t where all components other than $\lambda_{4,t}$ are muted is most similar to the actual trajectory of λ_t . Recall that $\lambda_{4,t}$ is the marginal value of horseshoe crabs for promoting growth in the red knot population. Therefore, the red knot recreational use value (relative to fishery rents) is the main driving force underlying the determination of the optimal length of moratorium given our parameterization of the bioeconomic model.

Once harvest starts, no individual component dominates λ_t , as it is clear from the historical decomposition on $[T_M, 30]$ in Fig. 6b. We consider the joint force of $\lambda_{1,t}$ and $\lambda_{2,t}$ and the joint force of $\lambda_{3,t}$ and $\lambda_{4,t}$. From Fig. 6b we see that the joint force of $\lambda_{3,t}$ and $\lambda_{4,t}$ appears to be the dominant driver of policy in the post-moratorium period, since the trajectory of the counterfactual $\lambda_t^{(3,4)}$ is closer to the trajectory of the actual λ_t than the trajectory of the counterfactual $\lambda_t^{(1,2)}$ is. Intuitively, this means, after the horseshoe crab stock is optimally rebuilt, the marginal value of the horseshoe crab stock for red knot conservation ($\lambda_{4,t}$) and future production of horseshoe crabs ($\lambda_{3,t}$), are key determinants of the optimal horseshoe crab harvest. Conversely, less important are the marginal values of the stock for current harvest ($\lambda_{1,t}$) and for impacting the current growth rate ($\lambda_{2,t}$).

5.2.6 Comparison of net present values (NPVs)

We turn to assess the welfare implications of the open access baseline and the three fishery management plans considered here. Table 2 lists the NPVs of the

horseshoe crab fishery rents and the red knot conservation value in various scenarios. Under continued open access, the stocks are so depleted that the horseshoe crab fishery is unprofitable most of the time and thus the combined NPV is negative. Among the three management plans considered, SSFM generates the highest NPV of horseshoe crab fishery rents, yet has the lowest NPV of red knot conservation value and one of the lowest combined NPV. The two EBFM plans, despite lower NPVs of horseshoe crab fishery rents, generate considerably higher NPVs of red knot conservation value than SSFM. Under either EBFM plan, the NPV of red knot conservation value consists of more than 75% of the combined NPV.

Table 2 about

Considering ecosystem linkages in establishing the total allowable catch in a regulated open access fishery can generate welfare gains on par with optimal SSFM even if fishery rents are completely dissipated. In our case, BIO-EBFM increases welfare from recreational use values from red knots that are 99.9% of the combined NPV of SSFM. Additionally, if fishery rents are being dissipated under the regulated open access, large gains can be had from transitioning to an efficiency approach to EBFM. Specifically, the combined NPV from ECON-EBFM is roughly 38% greater than the lower bound of the combined NPV with BIO-EBFM.

here

5.2.7 Sensitivity analysis on the red knot valuation function

Because the red knot use value plays such a dominant role and because there is limited information regarding the red knot value function (7),³¹ we explore the sensitivity of the results to the red knot value function by varying the w parameter and the α parameter. Denote the new parameter values of w and α by w' and α' , respectively. We vary w'/w from 0.2 to 2 and α' from 0 to 1. We note that increasing

³¹Our function is calibrated to fit through two data points based on the literature and our assumptions; see the online supplementary material for more detail.

w' or α' implies increasing the value of red knots in general.³² We track the NPVs as w' and α' vary. Fig. 7 presents the results of the sensitivity analysis at two extremes: one where fishery rents are not dissipated under BIO-EBFM (Fig. 7a) and one where fishery rents are completely dissipated (Fig. 7b).

Fig. 7 about

While our main results show only modest gains from moving from BIO-EBFM to here ECON-EBFM, the results are quite sensitive to the parameters in the red knot value function. Within the ranges of w' and α' that we explore, if fishery rents were to be preserved under BIO-EBFM the gains from transitioning to ECON-EBFM could potentially be as high as 24% (up from roughly 3.3% achieved with our baseline parameters). The results are most sensitive to the shape parameter α and fairly robust to w . We find even greater sensitivity in our results when we assume that fishery rents are completely dissipated under BIO-EBFM, with a maximum NPV gain of 2,327% (up from roughly 38% in the baseline). Additionally the results in this case are sensitive to both α and w .

6 Conclusion

While the concept of EBFM is gaining support, it is unclear how EBFM will be implemented. One possibility is that ecosystem considerations will be simply added to the status quo regulatory regime, which does not address the commons problem. In this paper we examine the potential welfare gains from various definitions of EBFM using an empirically calibrated bioeconomic model.

We find that, first of all, if fishery rent dissipation is minimal, the BIO-EBFM plan, which is close to the current management regime for the Delaware Bay horseshoe crab population, is only marginally outperformed by the ECON-EBFM plan in terms of the NPV of ecosystem services provided. Two factors are responsible for the result. First, the biologically efficient harvest rate (i.e. MSY) is very close to

³²This holds when the stock size is larger than $R_m + 1$, which is always true in our case.

the economically efficient harvest rate³³ due to the low harvest cost, so the optimal harvest policy under BIO-EBFM is able to generate large fishery rents.

Second, the biological link between the horseshoe crab and the red knot keeps the fishery manager's long-run interest in the horseshoe crab fishery (the target stock of C_{MSY}) consistent with conservation of the red knot. Given the strength of reliance of red knots on horseshoe crabs in our bioeconomic model, a horseshoe crab stock at C_{MSY} is able to support a fairly large red knot stock, so the manager, who is largely motivated by the sole interest in horseshoe crabs under BIO-EBFM once the red knot target is achieved, might unintentionally improve non-fishing values in the system.

Furthermore, we find that ECON-EBFM may or may not be justified based on achieving significant welfare improvements, although the result depends on the extent to which fishery rents are dissipated in the horseshoe crab fishery. The degree to which fishery rents are being dissipated in the regulated open access fishery is an empirical question that we save for future research.

We also find that the value of red knots is a key driver of the optimal harvest policy. However, the gains from transitioning from BIO-EBFM to ECON-EBFM are sensitive to the parameters in the red knot value function. The current literature provides two point estimates of the average willingness to pay for a birding trip to the Delaware Bay area. Estimates of the marginal red knot value function are more appropriate for a policy analysis such as ours, but absent from the literature. Therefore, to better understand the gains from efficient EBFM, future work is needed to measure societal values for the red knot population and other shorebird populations dependent on horseshoe crabs in Delaware Bay.

³³We mean the harvest rate maximizing the instantaneous profit. Due to the delay in recruitment of horseshoe crabs and discounting, the sustained harvest rate under ECON-EBFM does not maximize the instantaneous profit.

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Appendix

In this appendix we derive the first-order necessary optimality conditions for the fishery manager's delayed optimal control problem under ECON-EBFM defined in (8–12). We assume all conditions required by Theorem 4.2 in [Göllmann et al. \(2009\)](#) are satisfied so that the theorem applies.³⁴ We first work with the present-value Hamiltonian and then turn to the current-value Hamiltonian.

³⁴We ignore the $R < R_m$ branch of the red knot value function (7) since the infinite derivative at $R = R_m$ would keep the optimal trajectory of R_t away from R_m . This immediately renders the nonnegativity constraint on R_t and the subsequent introduction of the multiplier $\zeta_{r,t}^p$ redundant. Yet we keep $\zeta_{r,t}^p$ in the Hamiltonian for the sake of completeness. Alternatively, we could have set up the optimal control problem with the constraint $R_t \geq R_m$, $t \in [0, T]$, or $R_t \geq R_m + \epsilon$, $t \in [0, T]$, where ϵ is a sufficiently small positive number. Additionally, it can be easily verified that the rank condition ([Göllmann et al. 2009](#), Equation 10) for the nonnegativity constraints (11) is satisfied.

Construct the present-value Hamiltonian as

$$\begin{aligned}
& \mathcal{H}^P(t, C_t, C_{t-\tau}, R_t, E_t, \lambda_t^P, \xi_t^P, \zeta_{e,t}^P, \zeta_{c,t}^P, \zeta_{r,t}^P) \\
&= e^{-\rho t} [pqC_t E_t - \delta E_t^2 + w(R_t - R_m)^\alpha] \\
&\quad + \lambda_t^P [g_c C_{t-\tau} \exp(-C_{t-\tau}/K_c^*) - \eta_c C_t - qC_t E_t] \\
&\quad + \xi_t^P g_r R_t \{1 - R_t/K_r/a \cdot [1 + \exp(b_0 + b_1 C_t)]\} \\
&\quad + \zeta_{e,t}^P E_t + \zeta_{c,t}^P C_t + \zeta_{r,t}^P R_t,
\end{aligned}$$

where a superscript p indicates association with the present-value Hamiltonian, λ_t^P and ξ_t^P are the two costate variables associated respectively with (9) and (10), and $\zeta_{e,t}^P$, $\zeta_{c,t}^P$, and $\zeta_{r,t}^P$ are multipliers associated with the nonnegativity constraints (11).

The first-order necessary optimality conditions are then given by

$$0 = \frac{\partial \mathcal{H}^P}{\partial E_t} = e^{-\rho t} (pqC_t - 2\delta E_t) - \lambda_t^P qC_t + \zeta_{e,t}^P, \quad 0 \leq t \leq T, \quad (23)$$

$$\begin{aligned}
-\dot{\lambda}_t^P &= \frac{\partial \mathcal{H}^P}{\partial C_t} + \frac{\partial \mathcal{H}^P}{\partial C_{t-\tau}} \\
&= e^{-\rho t} pqE_t - \lambda_t^P (\eta_c + qE_t) - \xi_t^P g_r R_t^2 / K_r / a \cdot b_1 \exp(b_0 + b_1 C_t) + \zeta_{c,t}^P \\
&\quad + \lambda_{t+\tau}^P g_c (1 - C_t / K_c^*) \exp(-C_t / K_c^*), \quad 0 \leq t < T - \tau,
\end{aligned} \quad (24)$$

$$\begin{aligned}
-\dot{\lambda}_t^P &= \frac{\partial \mathcal{H}^P}{\partial C_t} = e^{-\rho t} pqE_t - \lambda_t^P (\eta_c + qE_t) - \xi_t^P g_r R_t^2 / K_r / a \cdot b_1 \exp(b_0 + b_1 C_t) \\
&\quad + \zeta_{c,t}^P, \quad T - \tau \leq t \leq T,
\end{aligned} \quad (25)$$

and

$$\begin{aligned}
-\dot{\xi}_t^P &= \frac{\partial \mathcal{H}^P}{\partial R_t} = e^{-\rho t} w \alpha (R_t - R_m)^{\alpha-1} \\
&\quad + \xi_t^P g_r \{1 - 2R_t / K_r / a \cdot [1 + \exp(b_0 + b_1 C_t)]\} \\
&\quad + \zeta_{r,t}^P, \quad 0 \leq t \leq T.
\end{aligned} \quad (26)$$

Also, the optimal solution should maximize the Hamiltonian among all admissible

control and state trajectories that satisfy the nonnegativity constraints (11). The transversality condition is simply

$$\lambda_T^P = 0. \quad (27)$$

Nonnegativity of multipliers and the complementarity condition guarantee

$$\zeta_{e,t}^P, \zeta_{c,t}^P, \zeta_{r,t}^P \geq 0 \quad \text{and} \quad \zeta_{e,t}^P E_t = \zeta_{c,t}^P C_t = \zeta_{r,t}^P R_t = 0. \quad (28)$$

We now turn to the current-value Hamiltonian, defined simply as $\mathcal{H} = e^{\rho t} \mathcal{H}^P$. The current-value costate variables and current-value multipliers are defined accordingly as

$$\lambda_t = e^{\rho t} \lambda_t^P, \quad \xi_t = e^{\rho t} \xi_t^P, \quad (29)$$

and

$$\zeta_{e,t} = e^{\rho t} \zeta_{e,t}^P, \quad \zeta_{c,t} = e^{\rho t} \zeta_{c,t}^P, \quad \zeta_{r,t} = e^{\rho t} \zeta_{r,t}^P. \quad (30)$$

Differentiation with respect to time in (29) yields

$$\dot{\lambda}_t = \rho \lambda_t + e^{\rho t} \dot{\lambda}_t^P \quad \text{and} \quad \dot{\xi}_t = \rho \xi_t + e^{\rho t} \dot{\xi}_t^P. \quad (31)$$

Substitute (29–31) into (23–28) and then we obtain the conditions in current-value terms. (23–26) become

$$\begin{aligned} E_t &= [qC_t(p - \lambda_t) + \zeta_{e,t}]/(2\delta), \quad 0 \leq t \leq T, \\ -\dot{\lambda}_t + \rho \lambda_t &= pqE_t - \lambda_t(\eta_c + qE_t) - \xi_t g_r R_t^2 / K_r / a \cdot b_1 \exp(b_0 + b_1 C_t) + \zeta_{c,t} \\ &\quad + e^{-\rho \tau} \lambda_{t+\tau} g_c (1 - C_t / K_c^*) \exp(-C_t / K_c^*), \quad 0 \leq t < T - \tau, \\ -\dot{\lambda}_t + \rho \lambda_t &= pqE_t - \lambda_t(\eta_c + qE_t) - \xi_t g_r R_t^2 / K_r / a \cdot b_1 \exp(b_0 + b_1 C_t) \\ &\quad + \zeta_{c,t}, \quad T - \tau \leq t \leq T, \quad \text{and} \end{aligned}$$

$$-\dot{\xi}_t + \rho \xi_t = w\alpha(R_t - R_m)^{\alpha-1} + \xi_t g_r \left\{ 1 - 2R_t/K_r/a \cdot [1 + \exp(b_0 + b_1 C_t)] \right\} + \zeta_{r,t}, \quad 0 \leq t \leq T.$$

(27) becomes $\lambda_T = 0$. (28) becomes

$$\zeta_{e,t}, \zeta_{c,t}, \zeta_{r,t} \geq 0 \quad \text{and} \quad \zeta_{e,t} E_t = \zeta_{c,t} C_t = \zeta_{r,t} R_t = 0.$$

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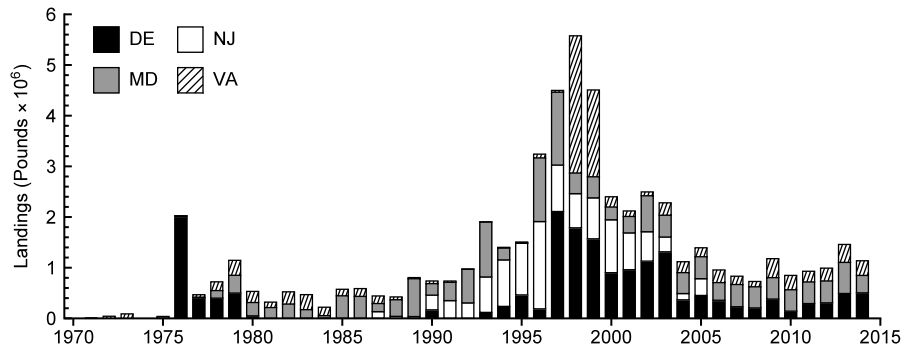


Fig. 1 Reported and imputed commercial landings of horseshoe crabs in Delaware Bay-region states (Delaware, New Jersey, Maryland, and Virginia), 1970–2014.

Note. All data except Maryland’s in 2002–2013 are from ACCSP (2016). Maryland’s data in 2002–2013 are based on ACCSP (2016), ASMFC (2013a, Table 2; 2015, Table 1), and authors’ calculations. See the online supplementary material for detail.

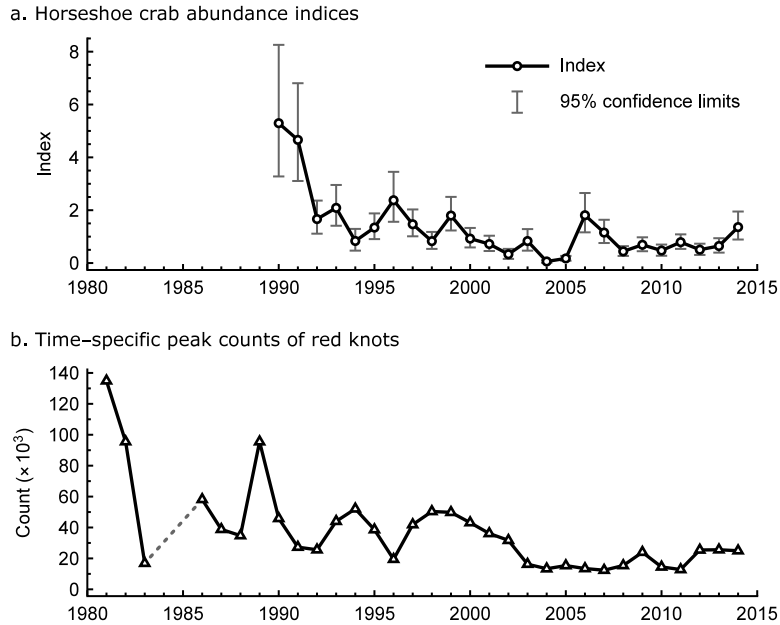


Fig. 2 a. Abundance indices of horseshoe crabs in Delaware Bay from the Delaware 30-foot trawl survey (all months), 1990–2014. b. Time-specific peak counts of red knots in Delaware Bay from aerial and/or ground surveys, 1981–1983 and 1986–2014.

Note. Data on horseshoe crabs are from staff at the Delaware Department of Natural Resources and Environmental Control. Data on red knots are from [USFWS \(2014, Table 10\)](#), [ASMFC \(2013b, Appendix A, Table 1\)](#), and A. Dey (personal communication 2 Jul 2016). Per a footnote under the aforementioned Table 10, the red knot count in 1981 shown here is the recorded count doubled.

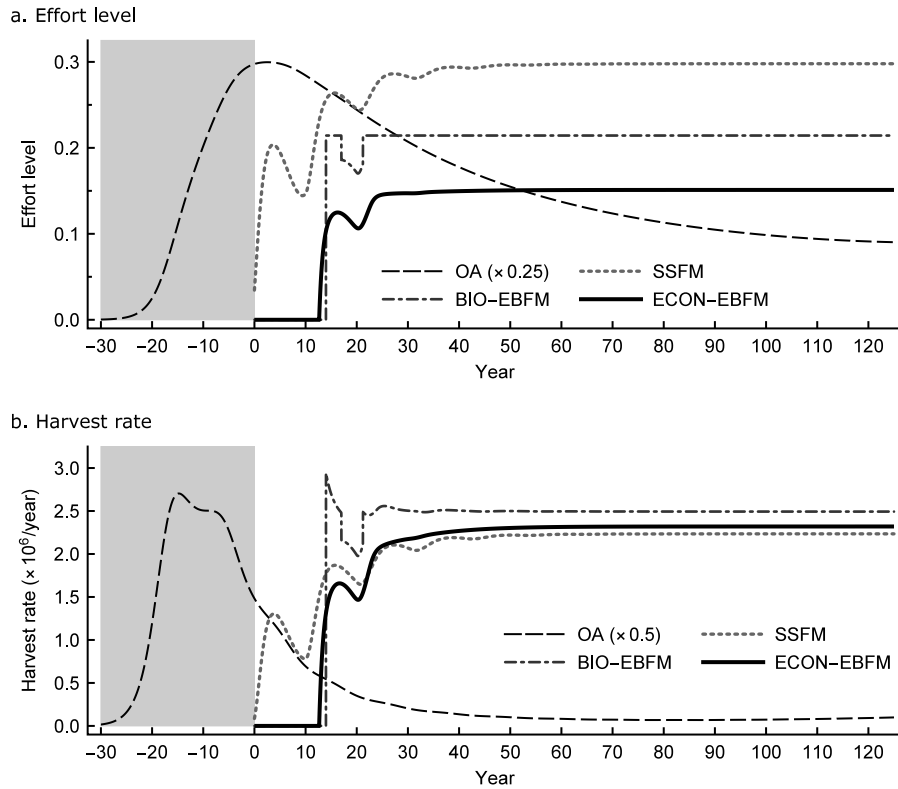


Fig. 3 Trajectories of the effort levels and the harvest rates under continued open access (OA; the dashed lines), single-species fishery management (SSFM; the dotted lines), biological ecosystem-based fishery management (BIO-EBFM; the dot-dashed lines), and efficient ecosystem-based fishery management (ECON-EBFM; the thick, solid lines).

Note. The shade indicates the modeled open access period. All fishery management plans start at $t = 0$. We speculate that the trajectories towards $t = 125$ here approximate what the optimal trajectories would have been as $t \rightarrow \infty$ over an infinite management horizon, and therefore trajectories after $t = 125$ are not shown. See also [fn. 28](#).

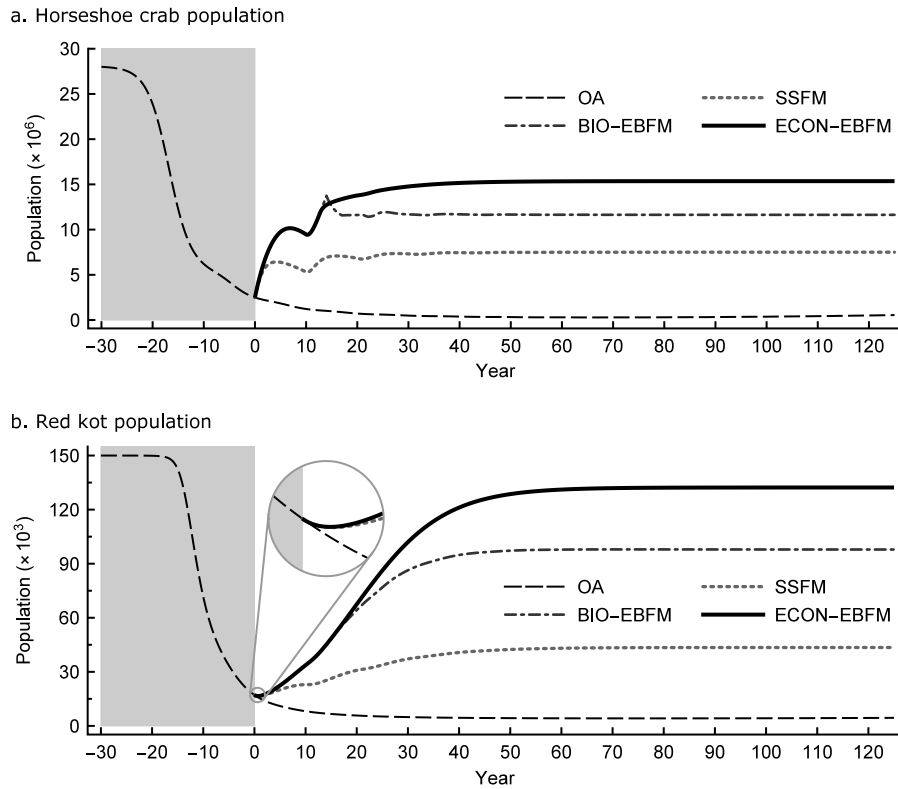


Fig. 4 Trajectories of population sizes of horseshoe crabs and red knots under continued open access (OA; the dashed lines), single-species fishery management (SSFM; the dotted lines), biological ecosystem-based fishery management (BIO-EBFM; the dot-dashed lines), and efficient ecosystem-based fishery management (ECON-EBFM; the thick, solid lines).

Note. The shade indicates the modeled open access period. All fishery management plans start at $t = 0$. We speculate that the trajectories towards $t = 125$ here approximate what the optimal trajectories would have been as $t \rightarrow \infty$ over an infinite management horizon, and therefore trajectories after $t = 125$ are not shown. See also [fn. 28](#).

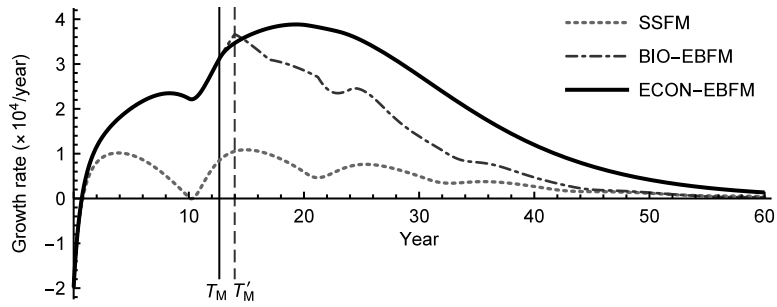


Fig. 5 Instantaneous growth rates of the red knot population in the first six decades of the management horizon under single-species fishery management (SSFM; the dotted line), biological ecosystem-based fishery management (BIO-EBFM; the dot-dashed line), and efficient ecosystem-based fishery management (ECON-EBFM; the thick, solid line).

Note. The solid vertical line at $t = T_M \approx 12.6$ and the dashed vertical line at $t = T'_M \approx 14.0$ mark the ends of moratoriums under ECON-EBFM and BIO-EBFM, respectively.

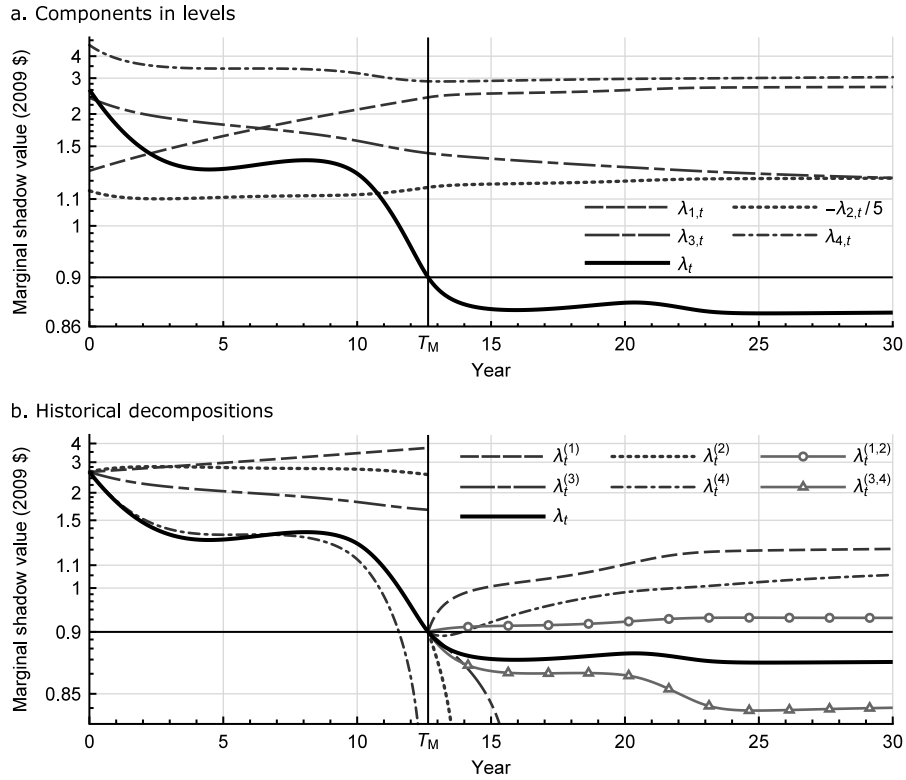
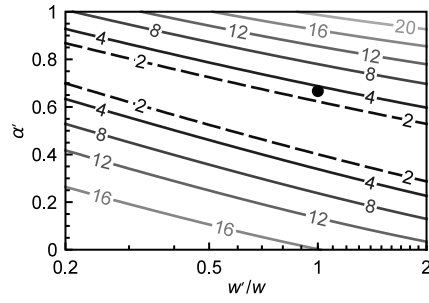
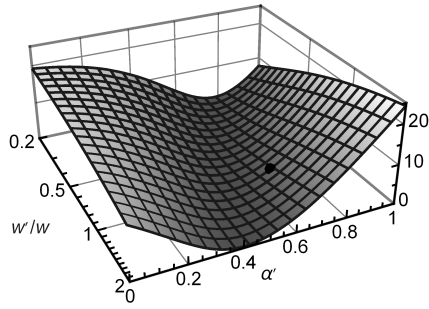


Fig. 6 Decompositions of the costate variable λ_t , i.e. the current shadow price of horseshoe crabs, in the first three decades of efficient ecosystem-based fishery management (ECON-EBFM).

Note. See Sect. 5.1 for definitions of the decompositions and the components. The y-axes are in customized logarithmic scales. The horizontal black line in each panel marks the ex-vessel price of horseshoe crabs $p = 0.90$. The vertical black line at $t = T_M \approx 12.6$ in each panel marks the end of the moratorium. In Panel b, historical decomposition is performed separately on two time intervals, $[0, T_M]$ and $[T_M, 30]$.

a. No rent dissipation under BIO-EBFM



b. Complete rent dissipation under BIO-EBFM

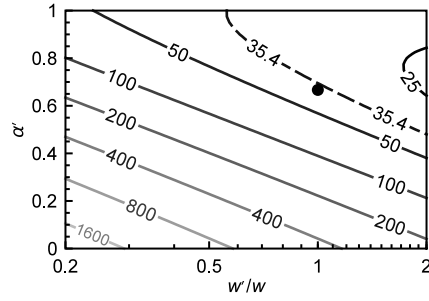
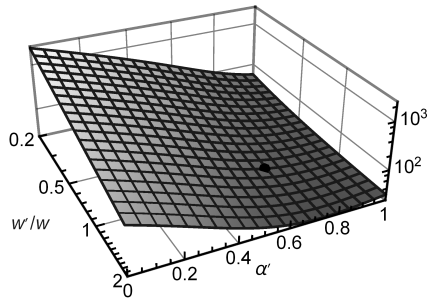


Fig. 7 Surface plots (left) and contour plots (right) of the percentage gains in net present values (NPVs) by efficient ecosystem-based fishery management (ECON-EBFM) over biological ecosystem-based fishery management (BIO-EBFM) as the parameters w' and α' vary, assuming either no rent dissipation or complete rent dissipation occurring under BIO-EBFM.

Note. NPV calculations include the first 125 years of the management horizon. The black dot locates the baseline point where $w' = w$ and $\alpha' = \alpha$.

Table 1 Summary of parameters in the bioeconomic model.^a

Parameter and definition		Value	Source
A. Population dynamics of horseshoe crabs			
τ	Time to sexual maturity (years)	10	Shuster and Sekiguchi (2003)
K_c	Carrying capacity (millions)	28	Authors' calculation ^b
g_c	Maximum per capita rate of egg production corrected for egg-to-adult survival	0.6955	Authors' calculation ^c
η_c	Adult per capita death rate	0.2006	Sweka et al. (2007)
B. Population dynamics of red knots			
K_r	Full carrying capacity (thousands)	150	McGowan et al. (2011b)
g_r	Intrinsic growth rate	0.13	Authors' calculation ^d
a	Parameter of dependence on horseshoe crabs	1.001	Data fitting ^e
b_0	Parameter of dependence on horseshoe crabs	3.662	Data fitting ^e
b_1	Parameter of dependence on horseshoe crabs	-0.3686	Data fitting ^e
C. Revenue and cost structures of the horseshoe crabs fishery			
p	Per capita ex-vessel price (2009 \$)	0.90	Estimated ^f
q	Catchability coefficient	1	Assumed
δ	Cost coefficient (millions of 2009 \$/unit of effort)	1.6	Data fitting ^e
D. Value function of red knots			
w	Value per thousand red knots (millions of 2009 \$)	0.2739	Estimated ^g
R_m	Minimal number of red knots valued (thousands)	8.719	Estimated ^g
α	Shape parameter	2/3	Assumed
E. Model of open access			
T_1	Length of open access (years)	29	Assumed
γ	Speed of effort adjustment (units of effort/million 2009 \$)	0.01832	Data fitting ^e
E_{-T_1}	Initial effort level	0.001167	Data fitting ^e
F. Models of fishery management			
T	Horizon of management (years)	200	Assumed
ρ	Discount rate	0.05	Assumed
Θ_r	Red knot population target (thousands)	45	ASMFC (2009a)

^a See the online supplementary material for details on calibration of the bioeconomic model.

^b Based on ASMFC (2009a).

^c Based on fecundity, egg-to-hatch survival, and age-specific mortality estimates by Sweka et al. (2007).

^d Based on fecundity and survival estimated or set by Baker et al. (2004) and McGowan et al. (2011b).

^e Derived from fitting an augmented open access model with observed trends in harvest of horseshoe crabs and population sizes of horseshoe crabs and red knots.

^f Estimated with data on the value of landings from ACCSP (2016) and data on the number of horseshoe crabs landed from ASMFC (2013a, Table 2; 2004, Table 1).

^g Estimated with estimates of willingness to pay for birding trips to the Delaware Bay area and the number of birders visiting birding sites by Eubanks et al. (2000), Myers et al. (2010), and Edwards et al. (2011).

Table 2 Net present values (NPVs) of the horseshoe crab fishery rents and the red knot conservation value in the first 125 years of continued open access (OA), single-species fishery management (SSFM), biological ecosystem-based fishery management (BIO-EBFM), and efficient ecosystem-based fishery management (ECON-EBFM).

Open access or management plan	Horseshoe crab fishery rents		Red knot conservation value		Combined NPV
	NPV	% of combined	NPV	% of combined	
OA	-10.56	—	4.23	—	-6.32
SSFM	25.44	39.9	38.28	60.1	63.72
BIO-EBFM	0-21.17	0-25.0	63.65	75.0-100	63.65-84.82
ECON-EBFM	17.95	20.5	69.64	79.5	87.59

Note. All NPVs are in millions of 2009 dollars. The first 125 years of the management horizon account for at least 99.5% of the total combined NPV in the entire horizon of T years under any of the three management plans.

SUPPLEMENT TO

**“Considering economic efficiency in ecosystem-based management:
the case of horseshoe crabs in Delaware Bay”**

by

29 Aug 2016

S1 Model Calibration

In this supplement we describe how we estimate or select the parameter values used in our bioeconomic model. Please refer to Table 1 for a summary of all the parameters. Some of our parameters are taken directly from the literature. The remainder, which are either estimated, assumed, or obtained through a data-fitting exercise, are described in what follows.

S1.1 Parameters of the population dynamics of horseshoe crabs

Carrying capacity. We calculate the carrying capacity of the Delaware Bay horseshoe crab population from [ASMFC \(Atlantic States Marine Fisheries Commission; 2009\)](#), who stated that the female horseshoe crabs of the Delaware Bay population had a predicted carrying capacity of 14 million. Since we assume a 1:1 sex ratio, we set $K_c = 28$ (in millions).

Productivity. The maximum per capita rate of egg production, corrected for egg-to-adult survival, g_c , is calculated from estimates of fecundity, egg-to-hatch survival, and age-specific mortality from [Sweka et al. \(2007\)](#) as follows:

$$g_c = 0.5 \times \text{fecundity} \times \text{egg-to-hatch survival} \times \text{age-0-to-adult survival}.$$

The first multiplicative factor of 0.5 on the right-hand side is due to the assumed 1:1 sex ratio (in both adults and eggs).

We start with an average fecundity of 80,300 eggs per female horseshoe crab (Sweka et al. 2007). Sweka et al. (2007) developed three density-dependent egg mortality curves assuming low, medium, and high mortality rates. ASMFC (2009) and McGowan et al. (2011) adopted Sweka et al.'s (2007) low-mortality curve in their model for horseshoe crabs because the other two curves would have “unrealistic implications” on the size of the horseshoe crab population. Following ASMFC (2009) and McGowan et al. (2011) we derive our egg-to-hatch survival rate from Sweka et al.'s (2007) low-mortality curve. Note that in Equation 1 the maximum rate of egg production, g_c , is a density-independent parameter while the multiplicative exponential term $\exp(-C_{t-\tau}/K_c^*)$ following $g_c C_{t-\tau}$ accounts for recruitment's density dependence. This suggests removal of any density dependence when calculating g_c . We hence take the leftmost point on Sweka et al.'s (2007, Fig. 1) low-mortality curve. Assuming the number of spawning female horseshoe crabs is 0.1×10^6 , the estimated (maximum) egg-to-hatch survival rate is

$$1 - (0.0957 \ln(0.1 \times 10^6) - 0.9950) = 0.8932.$$

Since we assume horseshoe crabs' length of maturation is ten years, we obtain the age-0-to-adult survival rate as the product of the age-specific survival rates for ages 0–9 reported by Sweka et al. (2007, Table 1):

$$0.00003 \times 0.9738^8 \times 0.7994 = 0.00001939.$$

Hence we obtain

$$g_c = 0.5 \times 80,300 \times 0.8932 \times 0.00001939 = 0.6955.$$

Remark. We note here that the intrinsic growth rate of horseshoe crabs implied by the two parameters g_c and η_c that we have is $g_c - \eta_c = 0.4949$, which is in line with the predictions of some theoretical models and empirical data. Theoretical models developed by [Gibson and Olszewski \(2001\)](#) predicted an intrinsic growth rate of horseshoe crabs in the neighborhood of 0.5. [Smith et al. \(2009\)](#) reported that the rate of increase for horseshoe crabs computed with data from trawl surveys in Narragansett Bay during 1968–1975 was 0.52.¹

S1.2 Parameters of the population dynamics of red knots

Intrinsic growth rate. We assume red knots breed in their second year ([Harrington and Morrison 1980](#)). We set fecundity to 0.33 females produced per breeding female, which is between 0.29, used by [Baker et al. \(2004\)](#), and 0.4, used by [McGowan et al. \(2011\)](#).² Following [McGowan et al. \(2011\)](#), we set adult annual survival to 0.92 and first-year survival to 70% of adult survival. Therefore, we calculate the intrinsic growth rate of red knots as

$$\begin{aligned} g_r &= \text{fecundity} \times \text{first-year survival} - \text{adult death rate} \\ &= 0.33 \times (0.92 \times 0.7) - (1 - 0.92) \\ &\approx 0.13. \end{aligned}$$

Density-dependent carrying capacity. To determine the parameters a , b_0 , and b_1 in the density-dependent carrying capacity of red knots (Equation 3), we assume that

¹[Smith et al. \(2009\)](#) also pointed out the discrepancy between intrinsic growth rates of horseshoe crabs derived with different approaches and that some authors derived intrinsic growth rates considerably lower than 0.5.

²Specifically, [McGowan et al. \(2011\)](#) used a fecundity rate of 0.4 for heavy-weight (departure weight, i.e. weight upon departing Delaware Bay, ≥ 180 g) red knots. However, we do not distinguish between heavy-weight and light-weight (departure weight < 180 g) red knots.

the density-dependent carrying capacity curve passes through three “anchoring” points on the CR -plane. Specifically, we assume that

$$K_r^*(\rho_0 K_c) = \theta_0 a K_r, \quad K_r^*(\rho_1 K_c) = \theta_1 a K_r, \quad \text{and} \quad K_r^*(K_c) = K_r,$$

where (ρ_0, θ_0) and (ρ_1, θ_1) are two pairs of additional parameters. The last equality above ensures that the density-dependent carrying capacity is compatible with the steady state $C_t = K_c$ and $R_t = K_r, \forall t$. The two pairs of additional parameters can be interpreted as follows: A horseshoe crab population $\rho_0 \times 100\%$ of its carrying capacity can support a red knot population $\theta_0 a \times 100\%$ of its full carrying capacity and a horseshoe crab population $\rho_1 \times 100\%$ of its carrying capacity can support a red knot population $\theta_1 a \times 100\%$ of its full carrying capacity. We rely on this interpretation in setting the values of the two pairs of additional parameters. The parameters a, b_0 , and b_1 can be recovered as

$$a = 1 + \left(\frac{\theta_0}{1 - \theta_0} \right)^{\frac{1 - \rho_1}{\rho_1 - \rho_0}} \left(\frac{1 - \theta_1}{\theta_1} \right)^{\frac{1 - \rho_0}{\rho_1 - \rho_0}}, \quad (\text{S1})$$

$$b_0 = \frac{1}{\rho_1 - \rho_0} \left(\rho_1 \ln \frac{1 - \theta_0}{\theta_0} - \rho_0 \ln \frac{1 - \theta_1}{\theta_1} \right), \quad \text{and} \quad (\text{S2})$$

$$b_1 = \frac{1}{K_c} \frac{1}{\rho_1 - \rho_0} \left(\ln \frac{1 - \theta_1}{\theta_1} - \ln \frac{1 - \theta_0}{\theta_0} \right). \quad (\text{S3})$$

There seems no consensus on the strength of red knots’ dependence on horseshoe crab eggs from empirical studies. For example, basing on energy requirements of shorebirds, [Botton et al. \(1994\)](#) estimated that the entire shorebird population may be sustained on an average egg density of 44,000 eggs/m², which is a relatively low number compared to the observed egg density of more than 200,000 eggs/m² at some locations on the Delaware Bay shore in the early 1990s ([Botton et al. 1994](#), [Niles et al. 2009a](#)). Yet, citing [Hernández \(2005\)](#), [Niles et al. \(2008\)](#) stated that field studies in Delaware Bay suggested “a minimum density of at least 300,000 eggs/m²

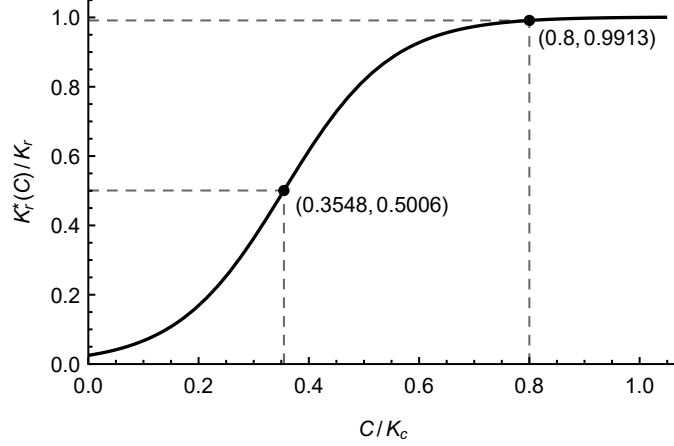


Figure S1 The assumed relationship between normalized horseshoe crab population size (C/K_c) and normalized density-dependent carrying capacity of red knots ($K_r^*(C)/K_r$).

was needed for Red Knots to completely maximize foraging efficiency on buried eggs” (p. 38).

In [ASMFC’s \(2009\)](#) model, harvest of horseshoe crabs was allowed when the population size of female horseshoe crabs was above 80% of its assumed carrying capacity, and the threshold was “intended to allow harvest if horseshoe crabs are sufficiently abundant that they are not likely to limit red knot population” (p. 4). We take the assumption by [ASMFC \(2009\)](#) and set $\rho_1 = 0.8$ and $\theta_1 = 0.99$. We have insufficient information to directly set values for the other pair of parameters (ρ_0, θ_0) and decide to resort to a data-fitting exercise (see [Section S1.6](#)). We fix $\theta_0 = 0.5$ in the data-fitting exercise and the resulting value of ρ_0 is 0.3548. [Figure S1](#) plots the density-dependent carrying capacity curve we assume.

S1.3 Parameters of the revenue and cost structures of the horseshoe crab fishery

Normalization. Note first that in our bioeconomic model the absolute level of the ex-vessel price of horseshoe crabs, p , and the cost coefficient, δ , do not matter. What matters is the relative price p/δ (or more precisely $p/(\delta/q^2)$). This is because we can always define $\tilde{E}_t = qE_t$, $\tilde{p} = p/(\delta/q^2)$, $\tilde{\gamma} = \gamma\delta/q$, and $\tilde{w} = w/(\delta/q^2)$ so that the

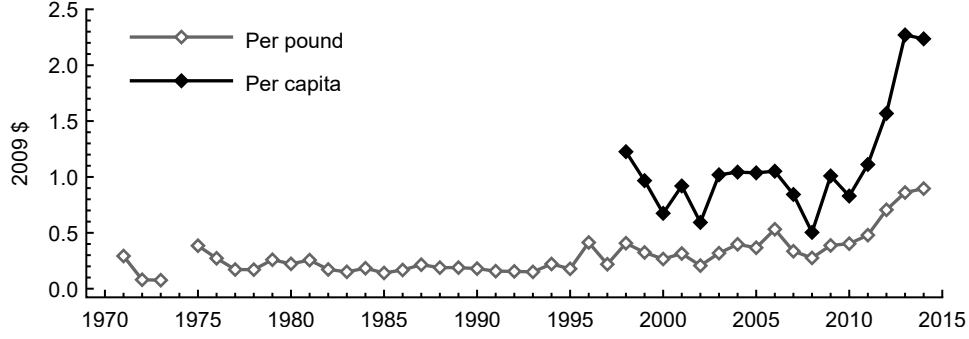


Figure S2 Inflation-adjusted per pound and per capita ex-vessel prices (in 2009 dollars) of horseshoe crabs, averaged across Delaware Bay–region states including Delaware, New Jersey, Maryland, and Virginia, 1971–2014.

Note. Authors’ calculation. Data on landings in pounds and value of landings in current dollars are from ACCSP (2016). Data on the number of horseshoe crabs landed are from ASMFC (2013a, Table 2), ASMFC (2015, Table 1), and ASMFC (2004a, Table 1). The ACCSP’s data for Maryland for the years 2002–2013 are excluded in calculating the average prices in 2002–2013 due to issues with data quality; See Section S1.6.5 for details. Prices are deflated with the gross domestic product deflator from BEA (2016).

equation of adjustment of effort in the open access period, i.e. Equation 6, becomes

$$\dot{\tilde{E}}_t = \tilde{\gamma} \tilde{E}_t (\tilde{p} C_t - \tilde{E}_t),$$

which is exactly the same equation with $p = \tilde{p}$, $\delta = 1$, and $\gamma = \tilde{\gamma}$. Furthermore, the optimal control problems to be solved by the fishery manager with parameters p , q , δ , and w are equivalent to the ones with the respective parameters replaced by \tilde{p} , 1, 1, and \tilde{w} . With that in mind, we nonetheless try to set p and δ separately.

Ex-vessel price of horseshoe crabs. We calculate inflation-adjusted per pound and per capita ex-vessel prices of horseshoe crabs averaged across Delaware Bay–region states including Delaware, New Jersey, Maryland, and Virginia since the 1970s, wherever data are available (Figure S2). We see that historically the inflation-adjusted ex-vessel prices had been fairly low and stable in the 1980s and the early 1990s. The mean per pound price was 0.18 (2009 dollars) for 1980–1995 with a coefficient of variation of 17%. The prices rose in the late 1990s and the early 2000s,

and have risen more substantially since the late 2000s. However, compared with landings in Delaware Bay–region states (see Figure 1), the prices had much less variation in the late 1990s and the early 2000s. For the period of 1996–2008, the coefficient of variation of landings was 78%, while that of per pound prices was 26%. For the period of 1998–2008, the coefficient of variation of per capita prices was 25%.

We calculate the per capita ex-vessel price of horseshoe crabs in our model, p , as the mean of the yearly inflation-adjusted per capita ex-vessel price averaged across Delaware Bay–region states in 1998–2008, which results in $p = 0.90$ (2009 dollars). We choose the year range of 1998–2008 because our red knot value function will be derived from estimates of consumer surplus from two surveys, one conducted in 1998 and the other in 2008 (see Section S1.4) and choosing a matching year range may better reflect the relative value between horseshoe crabs and red knots at the time when ecosystem-based fishery management for horseshoe crabs in Delaware Bay was initiated.

Cost coefficient. We have insufficient information to set a value for the cost parameter δ , and we resort to a data-fitting exercise (see Section S1.6). However, we expect the cost of harvesting horseshoe crabs to be low (see Section 2).

S1.4 The value function of red knots

The functional form of our red knot value function (Equation 7) is motivated by Kellner et al. (2011), who modeled the non-fishing value proportional to the square root of fish density. Compared to Kellner et al.’s (2011) functional form, ours introduces two additional features besides diminishing returns: a threshold under which red knots are no longer valued (the parameter R_m) and a shape parameter α . The feature of a minimal number of red knots valued is motivated by Eubanks et al.’s (2000) finding from surveying New Jersey birders in 1997 that average survey

respondents “would be willing to tolerate no more than a 50.7% decline in horseshoe crabs and migrate shorebirds before they would cease visiting the DBSA [Delaware Bay study area]” (p. 7).

We now proceed to estimate the parameters w , which is the value per thousand red knots, and R_m , which is the minimal number of red knots valued, with literature estimates of birders’ consumer surplus (or willingness to pay, WTP). Eubanks et al. (2000) estimated that the consumer surplus of an average birder visiting birding sites on the New Jersey side of the Delaware Bay shore (referred to as a New Jersey birder) in May of 1998 was 259.49 in 1998 dollars or 329.07 in 2009 dollars.³ Additionally, Eubanks et al. (2000) estimated that the total number of New Jersey birders in the birding season of 1998 was 6,000–10,000. Assuming an average of 8,000 New Jersey birders, we calculate the real total surplus of New Jersey birders in the 1998 season to be $\$329.07 \times 8,000 = \2.63 million (2009 dollars).

Myers et al. (2010) and Edwards et al. (2011) estimated that the total number of household-days for birders visiting birding sites on the Delaware side of the Delaware Bay shore (referred to as Delaware birders) during the 2008 birding season was about 3,363. Additionally, Edwards et al. (2011) estimated that the average WTP of Delaware birders during the 2008 season was 63.69 in 2008 dollars or 64.17 in 2009 dollars per day trip per household. Therefore, we calculate the real total surplus of Delaware birders in the 2008 season to be $\$64.15 \times 3,363 = \0.216 million (2009 dollars).

Because there is no information on the surplus of Delaware birders in the 1998 season or the surplus of New Jersey birders in the 2008 season, we assume that in the 1998 season the total surplus of Delaware birders was 25% of the total surplus of New Jersey birders, and that in the 2008 season the total surplus of

³In adjusting for inflation we make use of the gross domestic product deflator from BEA (2016).

Table S1 Calculation of the combined real total surplus of Delaware and New Jersey birders in the 1998 and the 2008 birding seasons.^a

Year	Real total surplus (V)		
	Delaware	New Jersey	Combined
1998	$V_{11} = V_{12} \times 0.25^b$ = \$0.658 million	$V_{12} = \$329.07 \times 8,000^c$ = \$2.63 million	$V_1 = V_{11} + V_{12}$ = \$3.29 million
2008	$V_{21} = \$64.17 \times 3,363^d$ = \$0.216 million	$V_{22} = V_{21} \times 3.5^b$ = \$0.755 million	$V_2 = V_{21} + V_{22}$ = \$0.971 million

^a All monetary values have been converted to 2009 dollars with the gross domestic product deflator (BEA 2016).

^b Authors' assumptions.

^c Based on estimates by Eubanks et al. (2000).

^d Based on estimates by Myers et al. (2010) and Edwards et al. (2011).

New Jersey birders was 3.5 times the total surplus of Delaware birders.⁴ These assumptions imply that the real total surplus of Delaware birders in the 1998 season was $\$2.63 \text{ million} \times 0.25 = \0.658 million (2009 dollars), and that the real total surplus of New Jersey birders in the 2008 season was $\$0.216 \text{ million} \times 3.5 = \0.755 million (2009 dollars).

Therefore, the real total surplus of Delaware and New Jersey birders combined in the 1998 season was $\$0.658 \text{ million} + \$2.63 \text{ million} = \$3.29 \text{ million}$ (2009 dollars), and the real total surplus of Delaware and New Jersey birders combined in the 2008 season was $\$0.216 \text{ million} + \$0.755 \text{ million} = \0.971 million (2009 dollars). Table S1 summarizes all calculations done. We note that the estimates imply that from 1998 to 2008, Delaware birders' real total surplus dropped by about 67%, while New Jersey birders' real total surplus dropped by about 71%. During the same period, the peak aerial count of red knots in Delaware Bay dropped by about 69% (see

⁴According to USFWS (2014, Table 12), the peak count of red knots in New Jersey was roughly 3.8 times the count in Delaware on average between 2006 and 2012 (except 2009). One footnote accompanying Table 10 in USFWS (2014) suggested that red knots in Delaware Bay were "relatively evenly distributed between New Jersey and Delaware from 1986 to 1992" (p. 49).

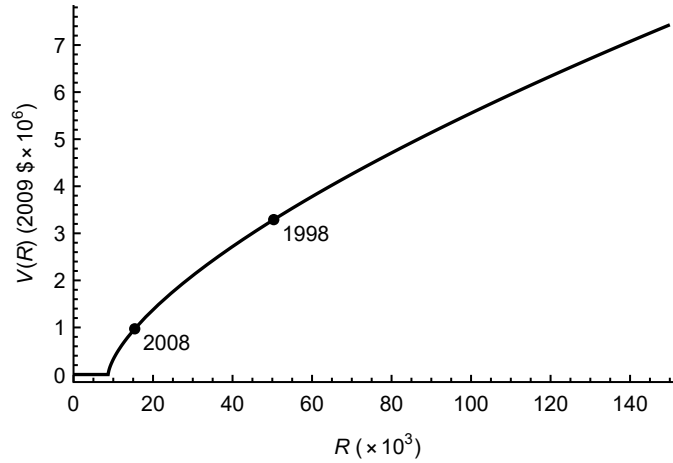


Figure S3 The estimated red knot value function (solid line) along with the two data points (dots; labelled with the year of the data) used in estimation $R(\times 10^3)$.

below).

Data from aerial surveys in Delaware Bay show that the peak counts of red knots in 1998 and 2008 were 50,360 and 15,395, respectively (USFWS 2014, Table 10). We set $\alpha = 2/3$ and then fit the assumed functional form $V(R) = w(R - R_m)^\alpha$ with the two data points on (R, V) : (50.360, 3.29) and (15.395, 0.971) (red knot counts have been put in thousands and surplus values have been put in millions of 2009 dollars). The resulting parameter values of w and R_m are

$$w = 0.2739 \quad \text{and} \quad R_m = 8.719,$$

where w is in millions of 2009 dollars per thousand red knots and R_m is in thousand red knots. Figure S3 plots our estimated red knot value function along with the two data points used in estimation.

Due to limited data availability, our estimation of the red knot value function relies heavily on our assumptions about the shape parameter α and the distribution of consumer surplus between New Jersey birders and Delaware birders. We therefore conduct a sensitivity analysis on the red knot value function; See Section 5.2.7.

S1.5 Other parameters in the models of open access and fishery management

Length and mapping of the open access period. We set the length of the open access period to $T_1 = 30$ (years) basing on the history of the horseshoe crab fishery and regulation of the fishery in Delaware Bay and along the Atlantic coast. Commercial harvest of horseshoe crabs in Delaware Bay dates back to the 19th century, when harvested horseshoe crabs were primarily used as fertilizers and livestock feed (Kreamer and Michels 2009, Shuster 2003). Records show that the average annual harvest per decade from Delaware Bay was more than one million in the late 19th century and the early 20th century (Shuster 2003). With the advent of alternative fertilizers, reliance on horseshoe crabs for fertilizing diminished and commercial harvest became minimal in the 1960s (Kreamer and Michels 2009, Shuster 2003). Demand for horseshoe crabs was renewed in the late 1970s, and then resurged in the 1990s as the American eel (*Anguilla rostrata*) and the whelk (*Busycon carica* and *Busycotypus canaliculatus*) fisheries, which used horseshoe crabs as bait, expanded (Kreamer and Michels 2009). The harvest of horseshoe crabs in the Delaware Bay area had been increasing in general since the late 1970s until the late 1990s (see Figure 1). It seems that the end of 1960s and the beginning of the 1970s separated two eras in the history of the horseshoe crab fishery in the Delaware Bay area. With that in mind, we map the first year of the open access period in our bioeconomic model to the year of 1974.

Horseshoe crab fisheries on the Atlantic coast had remained largely unregulated until recently. The ASMFC approved the Interstate Fishery Management Plan for Horseshoe Crab (FMP henceforth) in 1998 (ASMFC 1998), which was a first initiative on coast-wide management of horseshoe crabs. In 2000, Addendum I to the FMP (ASMFC 2000) established coast-wide state-level annual quotas. In 2001, the 3,885-square-kilometers Carl N. Shuster Jr. Horseshoe Crab Reserve off the mouth of

Delaware Bay was created, in which harvest of horseshoe crabs is prohibited.⁵ Addendum III to the FMP (ASMFC 2004b) in 2004 substantially reduced the quotas for Delaware, New Jersey, and Maryland. The quotas were further reduced by subsequent Addenda (ASMFC 2012). Some Atlantic states have had voluntarily reduced quotas. For example, New Jersey have enforced a moratorium on bait harvest of horseshoe crabs since 2007 (ASMFC 2012, 2015). Addendum III and subsequent Addenda to the FMP also established or extended season and/or area closure, and/or imposed other restrictions on the horseshoe crab fishery.

We choose to map the last year of the open access period in our bioeconomic model to the year of 2003 for multiple reasons. First, despite established quotas through Addendum I in 2000, landings of horseshoe crabs in Delaware and New Jersey in 2000–2003 were not necessarily lower than landings in the early- to mid-1990s, when horseshoe crabs seemed to be more abundant in Delaware Bay (see Figure 1 and Figure 2a). Delaware’s landings were even increasing from 2000 to 2004. New Jersey’s landings in 2000 were higher than those in 1998 and 1999. Niles et al. (2009a) concluded that “[a]s numerous ASMFC reports have demonstrated, the horseshoe crab harvests of the 1990s were not sustainable, nor were the lower harvests of later periods, because the population continued to decline” (p. 162). After Addendum III in 2004 harvest was brought down to much lower levels.

Second and more importantly, according to the horseshoe crab abundance indices from the Delaware 30-foot trawl survey and the time-specific peak counts of red knots in Delaware Bay from aerial and/or ground surveys (see Figure 2), the stocks of horseshoe crabs and red knots were in a historically relatively low point around 2004. Since in our bioeconomic model optimal fishery management follows immediately after the end of open access, mapping the end of open access in our model to the year of 2003 makes the hypothetical fishery manager in our model face

⁵50 C.F.R. §697.23(f) (2015). See also 66 Fed. Reg. 8,906 (5 Feb 2001).

the same depleted stocks of horseshoe crabs and red knots as the real-world fishery managers did when they decided to further reduce harvest of horseshoe crabs in 2004 and later developed the adaptive resource management (ARM) framework (see [ASMFC 2009](#)).

To summarize, we map the open access period in our bioeconomic model to the period of 1974–2003, which has $T_1 = 30$ years.

Parameters in models of fishery management. We assume a sufficiently long management horizon of $T = 200$ years and a moderate annual discount rate of $\rho = 0.05$.

The red knot population target of $\Theta_r = 45$ (thousand birds) in our BIO-EBFM model is taken from [ASMFC \(2009\)](#). In [ASMFC's \(2009\)](#) model, harvest of female horseshoe crabs was not rewarded unless the number of red knots exceeded the threshold of 45,000.⁶

S1.6 Fitting an augmented open access model with data

We use a data-fitting exercise to estimate or select values for the remaining parameters not available in the literature, including γ , which is the speed of effort adjustment in the open access model, E_{-T_1} , which is the initial effort level in the open access model, ρ_0 , which is one of the “anchoring” points in determining the red knot’s density-dependent carrying capacity curve, and δ , which is the cost parameter.

In the data-fitting exercise, we consider an augmented open access model where the open access period (modeled the same as in our bioeconomic model) is not followed by optimal fishery management. Instead, post–open access harvest is set equal to a scaled harvest function that mimics observed harvest patterns. The

⁶In fact, [ASMFC's \(2009\)](#) model would reward harvest if the number of red knots was below 45,000 but the number of female horseshoe crabs exceeded 11.2×10^6 . However, the horseshoe crab population threshold is redundant in our model and is not included as a constraint.

data-fitting procedure includes multiple steps. We first select a value of δ to be fixed in the subsequent minimization. We then choose the remaining parameter values to minimize the “distance” between population trends that emerge from our augmented open access model and the observed population and harvest trends. We then check whether the first open-access expansion of the horseshoe crab fishery lasts at least 30 years (see detail below). If not, we re-select the value of δ and repeat the minimization step until the length of the open-access expansion is roughly equal to the observed one of 30 years.

Because our data are noisy, we smooth the time series of stock sizes of horseshoe crabs and red knots and use the smoothed time series for fitting. In addition, we tend to set “milder” targets and avoid extreme predictions when we construct the objective function to be used in the minimization problem (see [Section S1.6.3](#)).

Additionally, because our simple bioeconomic model cannot replicate all features of our data, we focus on replicating general trends in the data. For example, the relative abundance of horseshoe crabs displayed its largest decline in the early 1990s (Figure 2a) while the reported bait landings of horseshoe crabs in the Delaware Bay region peaked in the late 1990s (Figure 1). This feature cannot be replicated in our model where fishery harvest is the primary driver of horseshoe crab abundance.

We emphasize that this data-fitting exercise is intended as an auxiliary procedure in our model calibration to set reasonable values for certain parameters, not a separate modeling effort to explain the dynamics in the time series of recent population sizes of horseshoe crabs and red knots and landings of horseshoe crabs.

S1.6.1 Timing conventions

We denote the model’s time variable by t . As has been discussed in [Section S1.5](#), we map the time interval $[-T_1, 0]$ in our open access model to the real-world period of 1974–2003. So $t = 0$ represents to the end of 2003 and the beginning of 2004.

We denote the model's year variable by i and year i represents the time interval $[i, i + 1)$. Thus, year j ($j = 1974, \dots, 2014$) in the real world is mapped back to the time interval $[j - 2004, j - 2003)$.

We assume that the time series of population sizes of horseshoe crabs and red knots are mid-year observations. For instance, the horseshoe crab abundance index in 2003 is assumed to reflect the size of the Delaware Bay horseshoe crab population in the middle of 2003, which is mapped back to $t = -0.5$ in our model, and the time-specific peak aerial count of red knots in 2004 is assumed to reflect the size of the stopover red knot population at Delaware Bay in the middle of 2004, which is mapped back to $t = 0.5$ in our model.

S1.6.2 The scaled harvest function

In order to obtain the trajectories of population sizes in the post-open access period (i.e. to solve Equations 1–3 when $t \geq 0$), we need to know the harvest as a function of time in the post-open access period. Since we are fitting the model's predicted trajectories of population sizes to the observed ones, we construct a scaled harvest function h_t ($t \geq 0$) that mimics observed harvest patterns after 2003.⁷

Denote the real-world annual harvest (landings) of horseshoe crabs in model year i by L_i ($i = -T_1, \dots, 10$). Define the model's annual harvest of horseshoe crabs in model year i as

$$H_i = \int_i^{i+1} h_t dt, \quad i = -T_1, \dots, 10,$$

where h_t is the instantaneous harvest rate at time t in the model. The scaled harvest

⁷Recall that $h_t = qC_tE_t$ in the open access period ($t \in [-T_1, 0)$).

function is constructed⁸ such that

$$H_i/H_{-T_1} \approx L_i/L_{-T_1}, \quad i = 0, 1, \dots, 10,$$

which means that for each year from 2004 to 2014, the two ratios of harvest in that year to harvest in 1974, one calculated with real-world data⁹ and the other calculated with the harvest function and the model's harvest in model year $-T_1$, are approximately the same, and thus the scaled harvest function mimics observed harvest patterns in the post-open access period.¹⁰

S1.6.3 *Targets and metrics*

For the open access period, we fit the model to general trends in harvest and population sizes of horseshoe crabs and red knots in 1974–2003. For the post-open access period, we fit the model to the whole segment of smoothed time series of population sizes in 2003–2014.

We set three primary targets that we expect the model to achieve or approach over the open access period: (1) the magnitude of decline of the horseshoe crab population relative to its carrying capacity be roughly 91.5% (i.e. $C_0/K_c \approx 0.085$), according to the smoothed data; (2) the magnitude of decline of the red knot population relative to its full carrying capacity be roughly 88.5% (i.e. $R_0/K_r \approx 0.115$), according to the smoothed data; and (3) the magnitude of expansion of the horseshoe crab fishery,

⁸by piecewise cubic interpolation of the data points $\{(i + 0.5, L_i/L_{-T_1} \cdot H_{-T_1})\}_{i=-1}^{10}$ via the `interp1` function from MATLAB R2015b with the `pchip` method.

⁹Because no data for landings in Delaware Bay–region states in 1974 are available from our data sources, we substitute the harvest in 1974 with the average harvest in 1973 and 1975.

¹⁰It is entirely possible to construct a harvest function that makes the two ratios precisely equal. Such construction would be more complicated. Yet, we think our simple construction suffices for our modeling purpose. Relative differences between the two ratios are mostly below 4% in our case.

or the greatest annual harvest relative to the initial annual harvest, be roughly 106.9 (i.e. $H_{\max}/H_{-T_1} \approx 106.9$, where $H_{\max} = \max\{H_i\}_{i=-T_1}^{-1}$), according to the harvest data.

We have another two primary targets to assess how well our augmented open access model fits the trends of population sizes in the post-open access period. Denote the smoothed horseshoe crab abundance index (see Section S1.6.5) in model year i by C_i^s . We run the simple linear regression

$$C_i^s = \beta_c C_t|_{t=i+0.5} + \epsilon_{c,i}, \quad i = -1, 0, \dots, 10, \quad (\text{S4})$$

where C_t is the population size of horseshoe crabs in the model at time t , β_c is the slope coefficient, and $\epsilon_{c,i}$ is the error term. Recall our timing convention that we assume data on population sizes are observed in the middle of each year. Note that the constant term (the intercept) is excluded, because we want to preserve the relative magnitude of the fitted values in the regression across years. For instance, if the smoothed abundance index (the dependent variable) rises by 30% from year 1 to year 2, then the fitted value in the regression also rises by 30% from year 1 to year 2. Let

$$Z_c = 1 - \frac{\sum_{i=-1}^{10} \hat{\epsilon}_{c,i}^2}{\sum_{i=-1}^{10} (C_i^s)^2},$$

where $\hat{\epsilon}_{c,i}$ is the year- i residual from regression (S4). Z_c is essentially the uncentered R^2 in regression (S4). We use Z_c as the fourth primary target.

To describe our fifth target, denote the smoothed time-specific peak count of red knots (see Section S1.6.5) in model year i by R_i^s . Similarly, we run the simple linear regression

$$R_i^s = \beta_r R_t|_{t=i+0.5} + \epsilon_{r,i}, \quad i = -1, 0, \dots, 10, \quad (\text{S5})$$

where R_t is the population size of red knots in the model at time t , β_r is the slope

coefficient, and $\epsilon_{r,i}$ is the error term. Let

$$Z_r = 1 - \frac{\sum_{i=-1}^{10} \hat{\epsilon}_{r,i}^2}{\sum_{i=-1}^{10} (R_i^s)^2},$$

where $\hat{\epsilon}_{r,i}$ is the year- i residual from regression (S5). Z_r is essentially the uncentered R^2 in regression (S5). We use Z_r as the fifth primary target.

We define a secondary target, which is the time length of the first expansion of the horseshoe crab fishery. Our simple open access model predicts that the horseshoe crab fishery under open access exhibits cycles, with expansion signaled by increasing effort and often increasing harvest and contraction signaled by decreasing effort and often decreasing harvest. According to the time series of landings of horseshoe crabs in Delaware Bay–region states (see Figure 1), landings increased in general from the early 1970s till the late 1990s. We do not know if landings would have continued to increase if the FMP had not been approved in 1998 and state level quotas had not been enforced since 2000. But it seems reasonable to assume that the horseshoe crab fishery in the Delaware Bay area had been expanding for 25–30 years since the early 1970s before management actions were taken to restrict harvest. Therefore, we assume that the first expansion of the fishery in our open access model lasts at least 30 years.

Additionally, we also have multiple secondary metrics designed to assess how well our augmented open access model can capture specific patterns in (smoothed) time series of observed harvest and populations sizes in the open access period as well as the post–open access period, including the time at which the maximum rate of decline in the horseshoe crab population size occurs ($\arg \min_t \dot{C}_t$), the time at which the horseshoe crab population bottoms ($\arg \min_t C_t$), relative change in the horseshoe crab population size from 2003 to 2014 ($C_{10.5}/C_{-0.5} - 1$), the time at which the maximum rate of decline in the red knot population size occurs ($\arg \min_t \dot{R}_t$),

the time at which the red knot population size bottoms ($\arg \min_t R_t$), relative change in the red knot population size from 2003 to its bottom ($\min_t R_t/R_{-0.5} - 1$), relative change in the red knot population size from 2003 to 2014 ($R_{10.5}/R_{-0.5} - 1$), the year in which annual harvest peaks ($\arg \max_i H_i$), and the ratio of peak to average annual harvest ($H_{\max}T_1/\sum_{i=-T_1}^{-1} H_i$, where $H_{\max} = \max\{H_i\}_{i=-T_1}^{-1}$). See [Table S2](#).

S1.6.4 *The minimization problem*

At its core the data-fitting exercise is solving a minimization problem in which we choose certain parameter values to minimize a “distance” function characterizing goodness of fit.

The objective function. Since we have multiple primary targets, we try to combine them into one objective function.¹¹ Secondary targets and metrics are not included in the objective function.

The objective function F consists of five components, corresponding to the five primary targets. The first component, F_1 , is the squared relative deviation of the model’s C_0 -to- K_c ratio from its target of 0.085, i.e. $F_1 = [(C_0/K_c - 0.085)/0.085]^2$. The second component, F_2 , is the squared relative deviation of the model’s R_0 -to- K_r ratio from its target of 0.115, i.e. $F_2 = [(R_0/K_r - 0.115)/0.115]^2$. The third component, F_3 , is the squared relative deviation of the model’s peak-to-initial harvest ratio from its target of 106.9, i.e. $F_3 = [(H_{\max}/H_{-T_1} - 106.9)/106.9]^2$. The fourth and the fifth

¹¹The first three primary targets could have been implemented as constraints (and thus excluded from the objective function) in the minimization problem. For example, we could have set up constraints such as $C_0/K_c \leq 0.09$, $0.098 \leq R_0/K_c \leq 0.132$, and $H_{\max}/H_{-T_1} \geq 106.9$. However, including them in the objective function turns out to work well. On the contrary, implementing them as constraints might cause difficulty for the numerical minimizer to find feasible solutions and to approach the optimal solution.

components are $F_4 = 1 - Z_c$ and $F_5 = 1 - Z_r$. Then, the objective function is

$$F = \sum_{i=1}^5 \omega_i F_i,$$

where ω_i is the weight for F_i ($i = 1, \dots, 5$).

We assign the weights as $\omega_1 = \omega_2 = 1$, $\omega_3 = 0.1$, $\omega_4 = 1/3$, and $\omega_5 = 3$. We assign a low weight for F_3 for two reasons. First, there is noise in the landings data (due to both non-mandatory reporting prior to 1998 and the way we convert weights of horseshoe crabs landed to counts) and this noise has not been accounted for so far. We have tried to account for noises in the time series of population sizes of horseshoe crabs and red knots by applying smoothing and fitting to general trends instead of specific patterns. We do not smooth the time series of harvest, but instead allow some deviation from the target on the harvest ratio by lowering the weight ω_3 relative to ω_1 and ω_2 , to the extent that such deviation may improve the model's goodness of fit. The resulting H_{\max}/H_{-T_1} is about 22% larger than the preset target.

We assign a lower ω_4 and a higher ω_5 to balance the contributions of F_4 and F_5 to the objective function. Since the model tends to produce a relatively poorer fit on the trend in the population size of horseshoe crabs than it does on the trend in the population size of red knots, it is necessary to lower ω_4 relative to ω_5 to prevent F_4 from dominating F_5 in the objective function. The fitted model has $\omega_4 F_4 / (\omega_4 F_4 + \omega_5 F_5) \approx 0.5$.

The choice variables. We include three parameters as the choice variables in the minimization problem: the speed of adjustment parameter in the open access model, γ , the initial effort level in the open access model, E_{-T_1} , and one parameter used to construct the density-dependent carrying capacity curve of red knots, ρ_0 . While the cost parameter, δ , is not a choice variable in the minimization problem it is set to ensure that the primary targets on decline of population sizes of horseshoe crabs

and red knots over the open access period and the secondary target on the length of the first expansion of the horseshoe crab fishery can be met.

Formulation. The minimization problem can be formulated as follows:

$$\begin{aligned}
& \min_{\gamma, E_{-T_1}, \rho_0; \delta} F(\gamma, E_{-T_1}, \rho_0; \delta) \\
& \text{subject to } \dot{C}_t = g_c C_{t-\tau} \exp(-C_{t-\tau}/K_c^*) - \eta_c C_t - h_t, \quad t \in [-T_1, +\infty), \\
& \quad \dot{R}_t = g_r R_t \left(1 - \frac{R_t}{K_{r,t}^*(C_t; \rho_0)}\right), \quad t \in [-T_1, +\infty), \\
& \quad \dot{E}_t = \gamma E_t (pq C_t - \delta E_t), \quad t \in [-T_1, 0], \quad \delta \text{ given}, \\
& \quad h_t = q C_t E_t, \quad t \in [-T_1, 0), \\
& \quad h_t = \text{the scaled harvest function}, \quad t \in [0, +\infty), \\
& \quad \min\{t \mid pq C_t E_t - \delta E_t^2 = 0\} \geq 0, \\
& \quad C_t = K_c, \quad R_t = K_r, \quad t \in (-\infty, -T_1], \quad E_{-T_1} \text{ as chosen}, \\
& \quad C_t, R_t, E_t, h_t \geq 0, \quad \forall t.
\end{aligned}$$

$K_{r,t}^*(C_t)$ is given by Equation 3 with the parameters a , b_0 , and b_1 given by (S1–S3).

S1.6.5 Data

We now describe our data. The data-fitting exercise requires three time series: the size of the Delaware Bay horseshoe population, the size of the red knot population stopping over at Delaware Bay, and the harvest of horseshoe crabs from the Delaware Bay population. Smoothing is to be applied to the time series of population sizes. The landings data are transformed to reflect the proportion of horseshoe crabs harvested by the fishery in each of the Delaware Bay–region states that are from the Delaware Bay population.

Time series. We use the abundance indices (geometric means of the number of horseshoe crabs caught per tow, all months) from the Delaware 30-foot trawl survey conducted by the Delaware Division of Fish and Wildlife as the time series of the size of the Delaware Bay horseshoe crab population.¹² Niles et al. (2009a) stated that “This survey [the Delaware Bay 30-foot trawl survey] was criticized . . . because, as a finfish survey, it was not designed specifically for horseshoe crabs. However, it is the only reliable long-term survey of horseshoe crab numbers in Delaware Bay” (p. 156). Despite numerous other surveys of horseshoe crabs in the Delaware Bay region, Niles et al. (2009b) stated that “[o]verwhelmingly, they [several surveys] show the same decline as the Delaware 30-foot trawl survey did, which is most relevant as it measures trends within the Delaware Bay” (p. 542).

We use the time-specific peak counts of red knots in Delaware Bay from aerial and/or ground surveys as the time series of the size of the red knot population stopping over at Delaware Bay. The time-specific peak aerial/ground counts were originally used to construct the state variable for the abundance of stopover adult red knots in the ARM model (ASMFC 2009). In 2013, estimates via a mark–resight method that accounted for population turnover replaced the peak aerial/ground counts for estimating the abundance of stopover adult red knots in the ARM model (ASMFC 2013b). However, time series of the mark–resight estimates are too short for our model calibration purpose.

We use a weighted sum of bait landings in the four Delaware Bay–region states including Delaware, New Jersey, Maryland, and Virginia as the time series of the harvest of horseshoe crabs from the Delaware Bay population. The four states are included because, based on tagging and genetic evidence, horseshoe crabs from the Delaware Bay population are most likely to be caught by fisheries in these four states

¹²Our results are robust to whether we use the indices constructed from tow results in all months (March–December) or the index months (April–July).

(ASMFC 2011, 2013a). The ASMFC distributes state-level quotas among the four Delaware Bay–region states after the quota for the Delaware Bay horseshoe crab population is determined through the ARM model (ASMFC 2012). The weights we use in summing states’ landings are the “lambdas” assigned to the four Delaware Bay–region states by the ASMFC, which “[indicate] how much of a state’s harvest is of Delaware Bay-origin (i.e. has spawned at least once in Delaware Bay)” (ASMFC 2012, p. 5).

Beside being harvested as bait, horseshoe crabs have been captured for use in the biomedical industry as well. In particular, horseshoe crabs have been captured to have their blood extracted to produce *Limulus* amebocyte lysate (LAL), which is used to test the presence of endotoxin for bacterial contamination (Novitsky 2009). After blood extraction the crabs are either returned to their habitat or given to the bait industry (and thus counted towards the ASMFC’s bait quota). We do not include harvest of horseshoe crabs for biomedical uses in our time series of harvest because mortality associated with biomedical harvest is unknown but estimated to be small relative to mortality associated with bait harvest coast-wide (ASMFC 2013a, 2015).

Smoothing. We smooth the time series of population sizes using locally weighted scatterplot smoothing (LOWESS; Cleveland 1979).^{13,14} Figure S4 visually compares the smoothed time series with the original data.

Construction of the time series of harvest. To construct the time series of the total number of horseshoe crabs harvested from the Delaware Bay population, we first need time series of states’ landings in numbers, which are not available prior to 1998.

¹³via the smooth function in Curve Fitting Toolbox R2015b from MathWorks with the lowess method and the default span of 5.

¹⁴We also tried another smoother, which is the 3-year centered moving geometric mean. However, our fitted parameter values are robust to the method of smoothing the data.

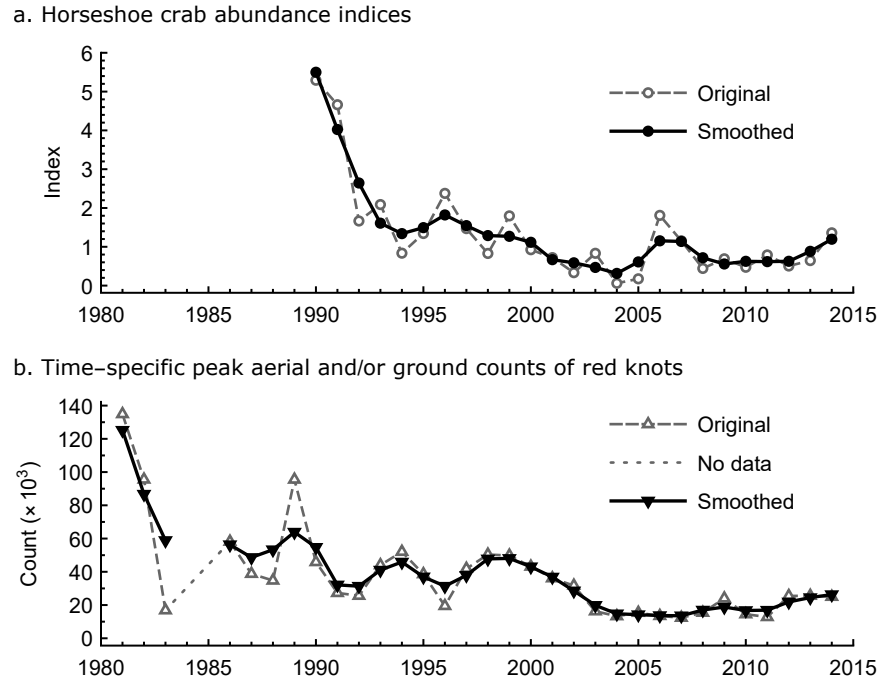


Figure S4 Visual comparison between the original and the smoothed time series of population sizes of horseshoe crabs and red knots.

Hence we attempt to impute the annual numbers of horseshoe crabs landed in the four Delaware Bay–region states prior to 1998 from these states’ annual landings in pounds.

We derive our conversion factors from data from the Atlantic Coastal Cooperative Statistics Program (ACCSP) and the ASMFC. Since data on both annual landings in pounds (from the ACCSP) and annual counts of horseshoe crabs landed (from the ASMFC) in each Delaware Bay–region state are available for the years 1998–2014, we first compute for each year from 1998 to 2014 and each Delaware Bay–region state the average weight per horseshoe crab of horseshoe crabs landed by dividing the amount of landings in pounds by the number landed, and then for each state take the mean of the yearly average weights in selected years as the conversion factor for that state.

The years used in calculating the conversion factors are 1998–2006 for Delaware and New Jersey, 1998–2012 for Virginia, and 1998–2001 for Maryland. In the case of

Delaware, a moratorium on bait harvest of female horseshoe crabs has been in effect since 2007. As a result, the sex composition of bait landings in Delaware after 2006 is likely to be different from and unrepresentative of the historical sex composition of landings in Delaware prior to 1998, and thus the years after 2006 are excluded in calculating the conversion factor for Delaware.¹⁵ Similarly, in the case of Virginia, a male-only harvest east of the COLREGS line¹⁶ has been in effect since 2013, and thus the years 2013–2014 are excluded in calculating the conversion factor for Virginia. In the case of New Jersey, a moratorium on bait harvest of all horseshoe crabs has been in effect since 2007, so years after 2006 are naturally excluded in calculating the conversion factor for New Jersey. In the case of Maryland, only the years 1998–2001 are used because we consider data on Maryland’s reported landings in 2002–2012 from the ACCSP unreliable¹⁷ and Maryland has had a male-only bait harvest policy since 2013. The resulting conversion factors for Delaware, New Jersey, Maryland, and Virginia are 3.40 pounds/crab, 2.73 pounds/crab, 2.55 pounds/crab, and 1.98 pounds/crab, respectively. Additionally, we impute the amount of Maryland’s landings in pounds in 2002–2013, which are used to draw Maryland’s bars for the years 2002–2013 in Figure 1, by multiplying the counts of horseshoe crabs landed (the ASMFC’s data) by the computed conversion factor.

We then impute the annual number of horseshoe crabs landed in each Delaware Bay–region state in each year prior to 1998 by dividing the annual landings in pounds for each state in each year by the computed conversion factor for that state. Finally, we construct the time series of the number of horseshoe crabs harvested from the Delaware Bay population as a weighted sum of the numbers of horseshoe

¹⁵Sex composition of landings is important in calculating the conversion factor because female horseshoe crabs typically weigh more than males (see e.g. [Graham et al. 2009](#)).

¹⁶33 C.F.R. §80 (2015).

¹⁷For instance, Maryland’s reported annual landings in 2011 were 167,053 crabs according to the ASMFC, but the weight was only 11 pounds according to the ACCSP.

crabs landed in the four Delaware Bay–region states:

$$L_i = \lambda_{\text{DE}}L_{\text{DE},i} + \lambda_{\text{NJ}}L_{\text{NJ},i} + \lambda_{\text{MD}}L_{\text{MD},i} + \lambda_{\text{VA}}L_{\text{VA},i},$$

where i is the model year ($i = -30, -29, \dots, 10$) and $\lambda_{\text{DE}} = \lambda_{\text{NJ}} = 1.0$, $\lambda_{\text{MD}} = 0.51$, and $\lambda_{\text{VA}} = 0.35$ are the “lambdas” assigned by the ASMFC (ASMFC 2012).

S1.6.6 Results and assessment

The parameter values resulted from the data-fitting exercise are

$$\delta = 1.6, \quad \rho_0 = 0.3548, \quad \gamma = 0.01832, \quad \text{and} \quad E_{-T_1} = 0.001167.$$

Table S2 summarizes the performance of our data-fitting exercise. We see that the three primary targets on the overall declines in population sizes of horseshoe crabs and red knots (Items A1 and B1) and on the peak-to-initial harvest ratio (Item C2) have been achieved or approached. The secondary target on the length of the first expansion cycle of the horseshoe crab fishery (Item C4) has been achieved, too. Table S2 also assesses goodness of fit in the post–open access period by the other two primary targets (Items A5 and B6). The two (uncentered) R^2 statistics are high, potentially indicating a good fit.

In addition, Table S2 assesses how well the fitted augmented open access model replicates observed trends and specific patterns in population sizes and harvest in the post–open access period. The fitted model successfully predicts a prolonged decline in the population size of red knots (Items B3 and B4), though, compared to the observed ones, the predicted length is shorter and the predicted magnitude is smaller. The fitted model also succeeds in predicting the approximate magnitude of recoveries in both the horseshoe crab and the red knot populations (Items A4 and B5).

Table S2 Assessment of goodness of fit of the augmented open access model.^a

Target or metric	Target or observed	Model prediction
A. Population size of horseshoe crabs^b		
1. Decline over the open access period ($1 - C_0/K_c$)	91.5% ^c	91.1%
2. Time at which the maximum rate of decline occurs ($\arg \min_t \dot{C}_t$)	-13.2 ^d	-16.8
3. Time at which the stock size bottoms ($\arg \min_t C_t$)	0.5 ^e	0
4. Relative change from 2003 to 2014 ($C_{10.5}/C_{-0.5} - 1$)	+155%	+105%
5. R^2 (uncentered) in regression (S4) (Z_c)		0.869 ^c
B. Population size of red knots^f		
1. Decline over the open access period ($1 - R_0/K_r$)	88.5% ^c	88.6%
2. Time at which the maximum rate of decline occurs ($\arg \min_t \dot{R}_t$)	-13.1 ^g	-12.2
3. Time at which the stock size bottoms ($\arg \min_t R_t$)	3.5 ^h	1.3
4. Relative change from 2003 to the bottom ($\min_t R_t/R_{-0.5} - 1$)	-32% ^h	-11%
5. Relative change from 2003 to 2014 ($R_{10.5}/R_{-0.5} - 1$)	+33%	+31%
6. R^2 (uncentered) in regression (S5) (Z_r)		0.985 ^c
C. Harvest of horseshoe crabs in the open access periodⁱ		
1. Year in which annual harvest peaks ($\arg \max_i H_i$)	-7 ^j	-15
2. Ratio of peak to first-year harvest (H_{\max}/H_{-T_1})	107 ^{cj}	130
3. Ratio of peak to average harvest ($H_{\max}T_1/\sum_{i=-T_1}^{-1} H_i$)	3.3 ^j	1.7
4. Time at which fishery rents reach zero for the first time if open access is to continue beyond $t = 0$ ($\min\{t \mid \Pi_t = 0\}$)	≥ 0 ^k	2.5

^a In this table, “time” and “year” refer to the value of the time variable (t) and the year variable (i) in the model, respectively. See Section S1.6.1 for the timing conventions. See Section S1.6.5 for details on the data used to calculate the observed values in this table.

^b C_t denotes the population size of horseshoe crabs at time t in the model. Observed values are calculated with the smoothed time series of the horseshoe crab abundance index in Delaware Bay in 1990–2014, unless otherwise noted.

^c Primary targets. See Section S1.6.3.

^d Estimated via numerical differentiation of spline interpolation of the smoothed abundance indices.

^e Lowest smoothed horseshoe crab abundance index was observed in 2004.

^f R_t denotes the population size of red knots at time t in the model. Observed values are calculated with the smoothed time series of the time-specific peak aerial/ground counts of red knots in Delaware Bay in 1986–2014, unless otherwise noted.

^g Estimated via numerical differentiation of spline interpolation of the smoothed peak aerial counts since 1986. The counts prior to 1986 are excluded due to the partial survey in 1981 and interruptions in 1984 and 1985.

^h Lowest smoothed peak aerial count was observed in 2007.

ⁱ H_i denotes the annual landings in year i in the model. Observed values are calculated with the time series of annual harvest of horseshoe crabs from the Delaware Bay horseshoe crab population in 1974–2014, unless otherwise noted. The harvest in 1974 has been substituted with the average harvest in 1973 and 1975.

^j Highest annual harvest was observed in 1997.

^k A secondary target. See Section S1.6.3.

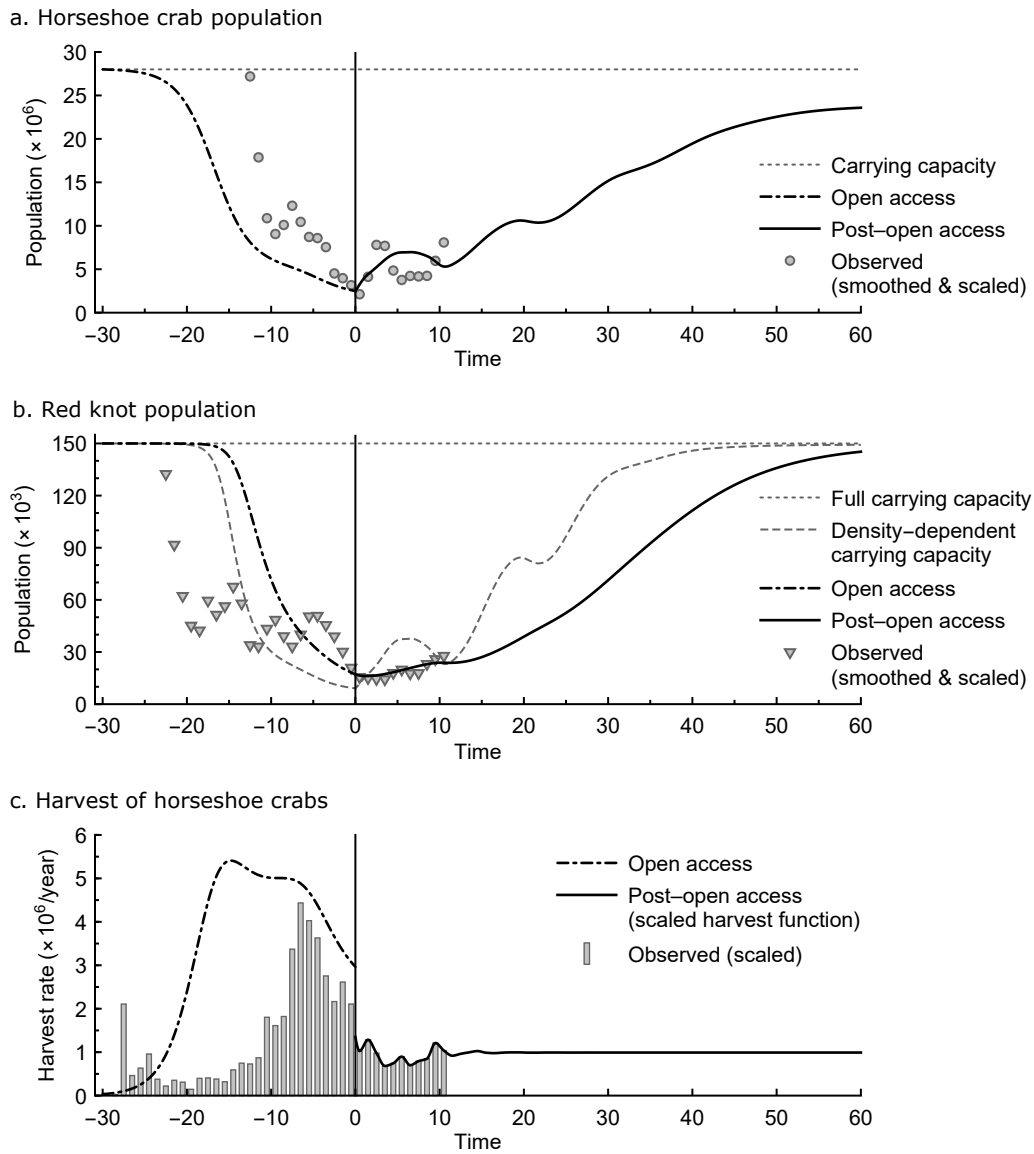


Figure S5 Visual assessment of goodness of fit of the augmented open access model.

Note. See Section S1.6.1 for timing conventions. We project long-term trends in population sizes of horseshoe crabs and red knots by assuming the current trend in harvest persists. Specifically, we expand the set of data points used to construct the scaled harvest function into $\{(i + 0.5, \hat{L}_i / L_{-T_1} \cdot H_{-T_1})\}_{i=-1}^{60}$, where $\hat{L}_i = L_i$ for $i = -1, \dots, 10$ and $\hat{L}_i = \sum_{j=1}^5 L_{i-j}$ for $i > 10$. Scaling in Panels a and b is done by multiplying the smoothed time series by the respective scaling factors. The scaling factor for the population size of horseshoe crabs is the estimated coefficient in the no-intercept regression of the model's predicted population sizes of horseshoe crab at $t = -0.5, 0.5, \dots, 10.5$ on the smoothed horseshoe crab abundance indices in 2003–2014. The scaling factor for the population size of red knots is the estimated coefficient in the no-intercept regression of the model's predicted population sizes of red knots at $t = -0.5, 0.5, \dots, 10.5$ on the smoothed time-specific peak aerial and/or ground counts of red knots in 2003–2014. The smoothed and scaled observed population size of horseshoe crabs in 1990 is 37.2×10^6 and is not shown in Panel a. The bars in Panel c represent annual harvests from the Delaware Bay horseshoe crab population scaled by the ratio of the model's first-year harvest to the average observed harvest in 1973 and 1975, i.e. H_{-T_1} / L_{-T_1} . See Section S1.6.5 for details on the data.

Figure S5 plots the predicted trajectories of harvest and population sizes under open access, the scaled harvest function, and the predicted trajectories of population sizes under the scaled harvest function in the post–open access period, along with smoothed and scaled time series of observed population sizes and the scaled time series of observed harvest. Figure S5 serves as a visual assessment of goodness of fit of the augmented open access model and confirms the findings in Table S2.

In conclusion, we consider the fitted augmented open access model having produced a reasonable fit to the data in general, and thus the data-fitting exercise supplies reasonable values for the parameters γ , E_{-T_1} , ρ_0 , and δ .

S1.6.7 Additional simulation assessment

In the previously discussed data-fitting exercise, a system of three components—a horseshoe crab population, a red knot population, and harvest of horseshoe crabs—is fitted to the data. In this three-component system, dynamics of the red knot population is linked through the density-dependent carrying capacity to dynamics of the horseshoe crab population, which is ultimately driven by dynamics of harvest of horseshoe crabs. We now decouple the two populations from harvest and focus on the two-population system, in which we try to assess whether the assumed density-dependent carrying capacity curve is able to capture the relationship between the time series of observed population sizes of horseshoe crabs and red knots.

Note that such assessment has been partially done as we fit the augmented open access model to the data in the post–open access period, and the fit turns out to be reasonable. However, not all the data in the open access period were included in fitting. In this additional assessment, we include more data in the open access period.

Since we decouple the two populations from harvest, we simulate the trajectory of the population size of red knots taking the trajectory of the population size of

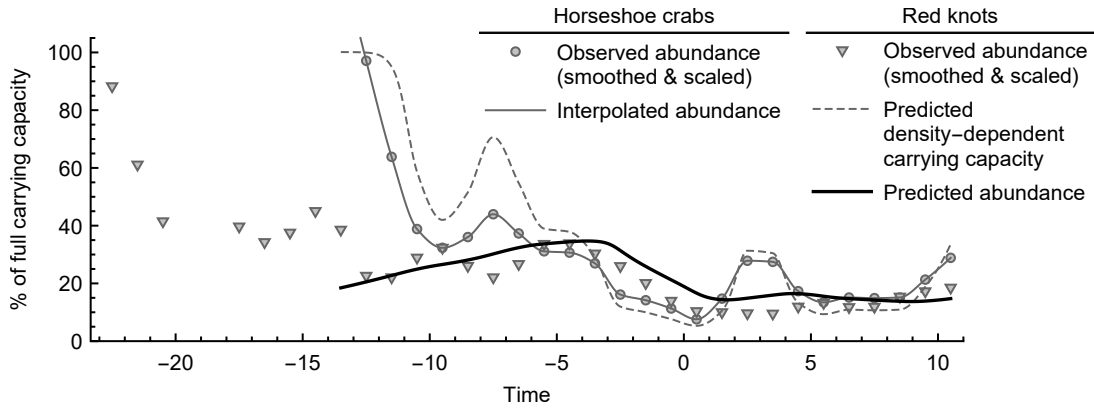


Figure S6 Visual comparison between observed and predicted abundance of red knots in the harvest-decoupled two-population system.

Note. The smoothed and scaled time series of abundance of horseshoe crabs and red knots are the same ones used in Figure S5, except that the time series here have been put in percentages of respective populations' assumed full carrying capacities. See the note accompanying Figure S5. The smoothed and scaled population size of horseshoe crabs in 1990 is 132% of the carrying capacity of horseshoe crabs and is not shown in the graph. The predicted trajectories are generated from solving Equation 2 on $[-13.5, 10.5]$ with the assumed parameter values, the initial condition $R_{-13.5} = 26.16$, and the trajectory of the population size of horseshoe crabs interpolated from the smoothed and scaled time series of abundance indices of horseshoe crabs taken as given.

horseshoe crabs as given. Moreover, since our model is in continuous time while the data are in discrete time, we construct a continuous-time function of the population size of horseshoe crabs by interpolating the smoothed and scaled time series of the observed horseshoe crab abundance index in 1990–2014.¹⁸ Taking C_t as given, we solve Equation 2 (together with Equation 3) numerically on the time interval $[-13.5, 10.5]$ with the parameter values we have selected and the initial condition $R_{-13.5} = 26.16$.¹⁹

Figure S6 compares the predicted trajectory of red knot abundance with the smoothed and scaled time series of the time-specific peak aerial/ground count of red knots. Visually the former seems to stay close to the latter in general.

¹⁸See footnote 13 for the smoothing procedure. See the note accompanying Figure S5 for the scaling procedure. Piecewise cubic interpolation is applied to the scaled and smoothed time series via the `interp1` function from MATLAB R2015b with the `pchip` method.

¹⁹This initial condition has been chosen to minimize the root mean square prediction error.

Furthermore, we can compute some statistics to assist assessment. Let R_i^{ss} be the smoothed and scaled peak count of red knots in model year i ($i = -13, \dots, 10$). Let $\tilde{R}_t|_{t=i+0.5}$ be the predicted red knot abundance in model year i ($i = -13, \dots, 10$). We calculate the coefficient of variation (CV) of the root mean square error (RMSE) of the predictions:

$$CV(RMSE) = \frac{\sqrt{\sum_{i=-13}^{10} (\tilde{R}_t|_{t=i+0.5} - R_i^{ss})^2 / 24}}{\sum_{i=-13}^{10} R_i^{ss} / 24} = 0.201.$$

We also calculate the mean absolute percentage error (MAPE) of the predictions:

$$MAPE = \sum_{i=-13}^{10} \frac{\tilde{R}_t|_{t=i+0.5} - R_i^{ss}}{R_i^{ss}} = 0.219.$$

The two statistics can be interpreted as that the parameterized decoupled model (Equations 2–3) makes a relative error of 20% or 22% (depending on the statistic) on average in predicting the smoothed and scaled peak counts of red knots from model year -13 to model year 10 (i.e. the years 1991–2014), when the (smoothed and scaled) trajectory of the population size of horseshoe crabs is given.

To summarize, both the visual comparison and the statistics suggest that the parameterized density-dependent carrying capacity curve reasonably captures the relationship between the population sizes of horseshoe crabs and red knots observed in the data we have.

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