CrossMark

Considering Economic Efficiency in Ecosystem-Based Management: The Case of Horseshoe Crabs in Delaware Bay

Yue Tan[1] · **Sunny L. Jardine**[2]

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.

✉ Yue Tan
yue.tan.yt@gmail.com

Sunny L. Jardine
jardine@uw.edu

[1] Charles Schwab & Co., Inc. and Charles Schwab Bank, 9800 Schwab Way, Lone Tree, CO 80124, USA

[2] School of Marine and Environmental Affairs, University of Washington, 3707 Brooklyn Ave NE, Seattle, WA 98105, USA

Springer

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. 13,547[1], 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 principle 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 2017), 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 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

---

[1] 3 C.F.R. 227 (2010), *reprinted in* 33 U.S.C. §857–19 (2015).

[2] As 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.

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 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. 13,547[1], 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 analyze the sensitivity of our results to our empirically derived estimate of the red knot value function. We then discuss our findings and conclude.
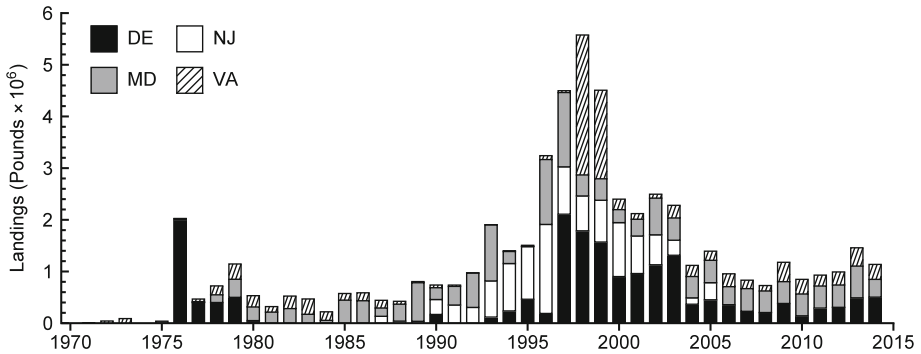
Fig. 1 Reported and imputed commercial landings of horseshoe crabs in Delaware Bay–region states (Delaware, New Jersey, Maryland, and Virginia), 1970–2014. All data except Maryland's in 2002–2013 are from ACCSP (2016). Maryland's data in 2002–2013 are based on ACCSP (2016), ASMFC (2013a, Table 2; 2015, Table 1), and authors' calculations. See the online supplementary material for detail

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,[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 at 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).

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

---

[3] 79 Fed. Reg. 73,705 (11 Dec 2014).

[4] For 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.

[5] There were limited existing restrictions in New Jersey, Delaware, and Maryland (see ASMFC 1998b for more detail).
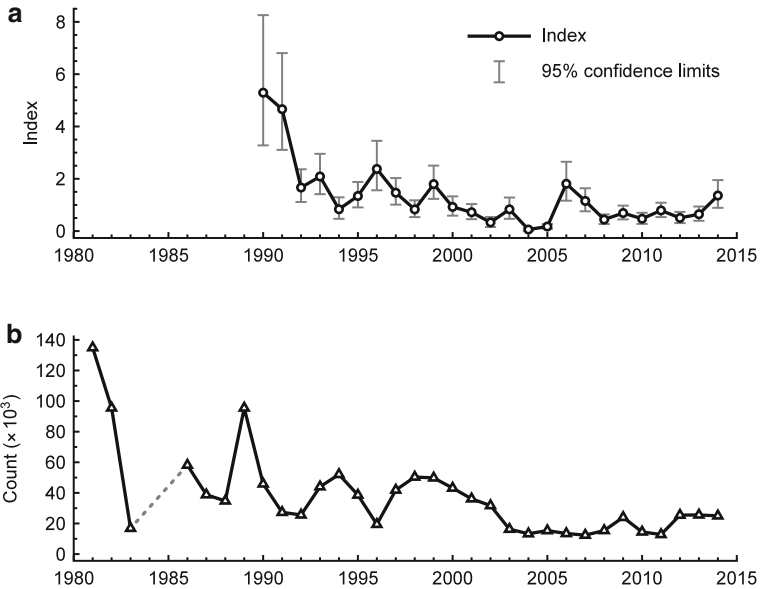
Fig. 2 a Abundance indices of horseshoe crabs in Delaware Bay from the Delaware 30-foot trawl survey (all months), 1990–2014. **b** Time-specific peak counts of red knots in Delaware Bay from aerial and/or ground surveys, 1981–1983 and 1986–2014. Horseshoe crab abundance data are from staff at the Delaware Department of Natural Resources and Environmental Control. Red knot count data 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

access) are derived from a 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 population threshold of 11.2 million female horseshoe crabs or 81,900 red knots[6] (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

---

[6] The 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.

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

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 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. Then we briefly describe parameterization of the model. 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 the variable, e.g. $\dot{C}_t = dC_t/dt$, the horseshoe crab population dynamics are governed by

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

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

---

[8] Empirical 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).

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

[10] Because 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.

instantaneous harvest rate. The growth Eq. 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

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

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]

$$K_r^*(C) = \frac{a}{1 + \exp(b_0 + b_1 C)} K_r,$$ (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, Eq. 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 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]

---

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

[12] This 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, < 180g) to heavy-weight (departure weight ≥ 180g) during the stopover as a logistic function of the abundance of spawning female horseshoe crabs.

[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.

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

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:

$$h_t = qC_tE_t. \tag{4}$$

Therefore, instantaneous industry rents are given by

$$\Pi_t(C_t, E_t) = pqC_tE_t - \delta E_t^2, \tag{5}$$

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 (1990) specification of industry sluggishness:

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

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 (Eq. 1) with the initial condition $C_t = K_c, \forall t \le -T_1$, the population dynamics of red knots (Eq. 2) with the initial condition $R_{-T_1} = K_r$, and the effort dynamics (Eq. 6) with the initial condition $E_{-T_1} = \bar{E}$.

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. (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:

---

[15] Our 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.

[16] We 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.

[17] While 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.

$$V_t(R_t) = \begin{cases} w(R_t - R_{\mathrm{m}})^{\alpha}, & R_t \geq R_{\mathrm{m}}, \\ 0, & R_t < R_{\mathrm{m}}, \end{cases} \tag{7}$$

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 the harvest effort E_t over the horizon $[0, T]$ to maximize the NPV of the sum of rents in the 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, Eqs. 1 and 2, respectively. Essentially, the manager solves a delayed optimal control problem:

$$\max_{E_t,\, t \in [0,T]} \int_0^T e^{-\rho t} \left(\Pi_t(C_t, E_t) + V_t(R_t) \right) \mathrm{d}t \tag{8}$$

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

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

$$E_t, C_t, R_t \geq 0, \quad t \in [0, T], \tag{11}$$

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

where ρ is the discount factor, $\Pi_t(\cdot, \cdot)$, $V_t(\cdot)$, and $K_{r,t}^*(\cdot)$ are defined respectively in Eqs. 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 where 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.

---

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

[19] Additionally, 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 calculated with observed data was \$118.5 (2009 dollars).

[20] We 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 weight.

Additionally, consistent with National Standard 1 of the Magnuson–Stevens Fishery Conservation and Management Act[21], 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 to ensure the red knot target is met and harvest does not exceed MSY. 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] The preceding discussion implies that our results provide an upper bound on fishery rents that can be generated under current policy and that 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.

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

$$\max_{E_t,\, t \in [0,T]} \int_0^T q C_t E_t \, dt$$

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

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

$$q E_t \le F_{\text{MSY}}, \quad t \in [0, T],$$

$$E_t \le 0 \quad \text{if } R_t < \Theta_r, \quad t \in [0, T],$$

$$E_t, C_t, R_t \ge 0, \quad t \in [0, T],$$

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

4 Methods

In this section, we briefly describe how we calibrate the bioeconomic models and how we obtain numerical solutions to the models. A more detailed discussion on the model calibration and the numerical algorithms used in the calibration process is included in the online supplementary material.

---

[21] 16 U.S.C. §1851(a)(1) (2015); see also 50 C.F.R. §600.310 (2015).

[22] To determine F_{MSY} in our model, we first solve Eq. 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 $F_{\text{MSY}} = h_{\text{MSY}}/C_{\text{MSY}}$.

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

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

4.1 Calibration

For the majority of the biological parameters, we either take their values directly from the literature or calculate their values from literature estimates of related life history parameters. The period of time needed for horseshoe crabs to reach maturity is from Shuster and Sekiguchi (2003). We derive horseshoe crabs' maximum per capita rate of egg production, corrected for egg-to-adult survival, as well as the adult death rate from estimates of their fecundity, egg-to-hatch survival rate, and age-specific survival rates from Sweka et al. (2007) and ASMFC (2009a). Horseshoe crabs' carrying capacity is inferred from ASMFC (2009a). The red knots' carrying capacity potential (when not limited by horseshoe crab abundance) is taken from McGowan et al. (2011b). We calculate red knots' intrinsic growth rate from fecundity and survival rates estimated or set by Baker et al. (2004) and McGowan et al. (2011b).

The data used to calculate the economic model parameters also come from a variety of sources. We compute the per capita ex-vessel price of horseshoe crabs from data on the reported value of annual landings from ACCSP (2016) and the reported counts of horseshoe crabs landed from ASMFC (2013a, Table 2; 2004, Table 1). We estimate the red knot value function from 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).

We used a data-fitting exercise to estimate the bioeconomic parameters that could not be derived from the existing literature, including harvest cost, the parameters defining the red knots' dependence on horseshoe crabs, the speed of effort adjustment under open access, and the initial effort level under open access. In the data-fitting exercise, we augment the open access model in Sect. 3.2.1 with a post–open access period in which harvest of horseshoe crabs is regulated and mimics the observed pattern of harvest in Delaware Bay since 2004. We then "fit" the augmented open access model to time series of observed population and harvest levels, by selecting the parameter values for which the augmented open access model can reproduce key features of the observed time series. Specifically, the features we attempt to reproduce include the magnitude of decline in population levels of red knots and horseshoe crabs, the increase in harvest over the open access period, and the trend of population recovery in the post–open access period.

Finally, we take the manager's red knot target level from ASMFC (2009a). We assume an optimization horizon of 200 years and an annual discount rate of 5%. Table 1 summarizes the model parameters, their values, and empirical support.

4.2 Solution Methods

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. The essence of Göllmann's et al.'s (2009) numerical method is to convert a finite-horizon optimal control problem to a nonlinear programming problem whose solution approximates the solution to the optimal control problem, by discretization of the objective function, the state equations, and the constraints. We outline the conversion applied in our case in the online supplementary

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)	30	Assumed
γ	Speed of effort adjustment (units of effort/million 2009 \$)	0.01832	Data fitting[e]
$\bar{E}$	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)

material. The resulting nonlinear programming problems are then solved numerically using the fmincon solver from the Optimization Toolbox in MATLAB R2015b.[25] We used a grid size of 400,000 and error tolerances of 10^{-10} or smaller for our main results.

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

5 Results

Our analysis highlights the key drivers of optimal horseshoe crab management in Delaware Bay and the potential gains from 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, Eqs. 8–12, temporarily ignoring the non-negativity constraints Eq. 11,[26] is

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

where λ_t and ξ_t are the two costate variables associated with Eqs. 9 and 10, respectively. Necessary optimality conditions include[27]

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

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

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

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

---

[25] MATLAB code is available from the authors upon request.

[26] The non-negativity constraint on effort level E_t binds when $\lambda_t > p$, at which point effort level is no longer determined by Eq. 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".

[27] Full set of necessary optimality conditions is included in the "Appendix".

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

Since the costate variable λ_t can be interpreted as the current-value shadow price (the marginal shadow value) of horseshoe crabs, Eq. 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:

$$-\dot{\lambda}_{1,t} + \rho\lambda_{1,t} = pqE_t, \qquad\qquad\qquad 0 \le t \le T, \tag{17}$$
$$-\dot{\lambda}_{2,t} + \rho\lambda_{2,t} = -\lambda_t(\eta_c + qE_t), \qquad\qquad 0 \le t \le T, \tag{18}$$
$$-\dot{\lambda}_{3,t} + \rho\lambda_{3,t} = e^{-\rho\tau}\lambda_{t+\tau}g_c(1 - C_t/K_c^*)\exp(-C_t/K_c^*), \quad 0 \le t \le T - \tau, \tag{19}$$
$$-\dot{\lambda}_{4,t} + \rho\lambda_{4,t} = -\xi_t g_r R_t^2/K_r/a \cdot b_1\exp(b_0 + b_1 C_t), \quad 0 \le t \le T, \tag{20}$$

and

$$\lambda_{1,T} = \lambda_{2,T} = \lambda_{4,T} = 0, \quad \lambda_{3,t} = 0, \quad T - \tau \le t \le T, \tag{21}$$

such that

$$\lambda_t = \lambda_{1,t} + \lambda_{2,t} + \lambda_{3,t} + \lambda_{4,t}, \quad 0 \le t \le T. \tag{22}$$

The right-hand-side terms in Eqs. 17–20 are found on the right-hand sides of Eqs. 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

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

and

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

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
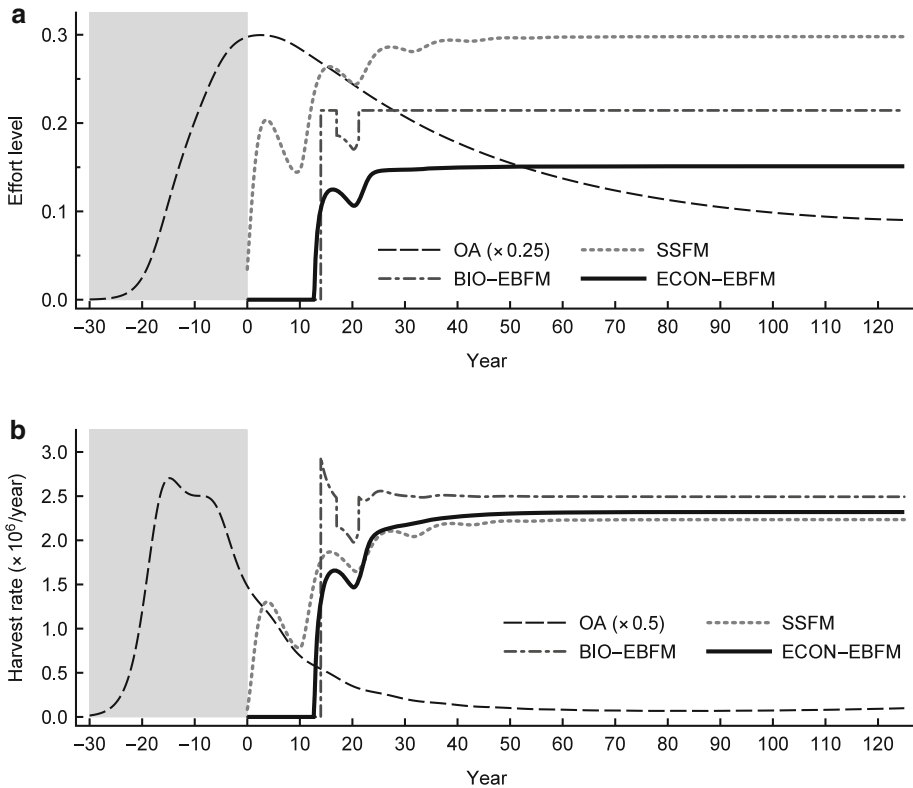
Fig. 3 Trajectories of the effort levels and the harvest rates under continued open access (OA; the dashed lines), single-species fishery management (SSFM; the dotted lines), biological ecosystem-based fishery management (BIO-EBFM; the dot-dashed lines), and efficient ecosystem-based fishery management (ECON-EBFM; the thick, solid lines). **a** Effort levels, **b** Harvest rates. 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 $t \to \infty$ over an infinite management horizon, and therefore trajectories after $t = 125$ are not shown. See also footnote 29

the various components in shaping λ_t. It is similar to the purpose of historical decomposition in vector autoregression models.[28]

In what follows we examine the decomposition and its mutations numerically to 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. Figures 3 and 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

---

[28] The technique of historical decomposition in vector autoregression models was pioneered by Sims (1980) and subsequently developed by Burbidge and Harrison (1985).
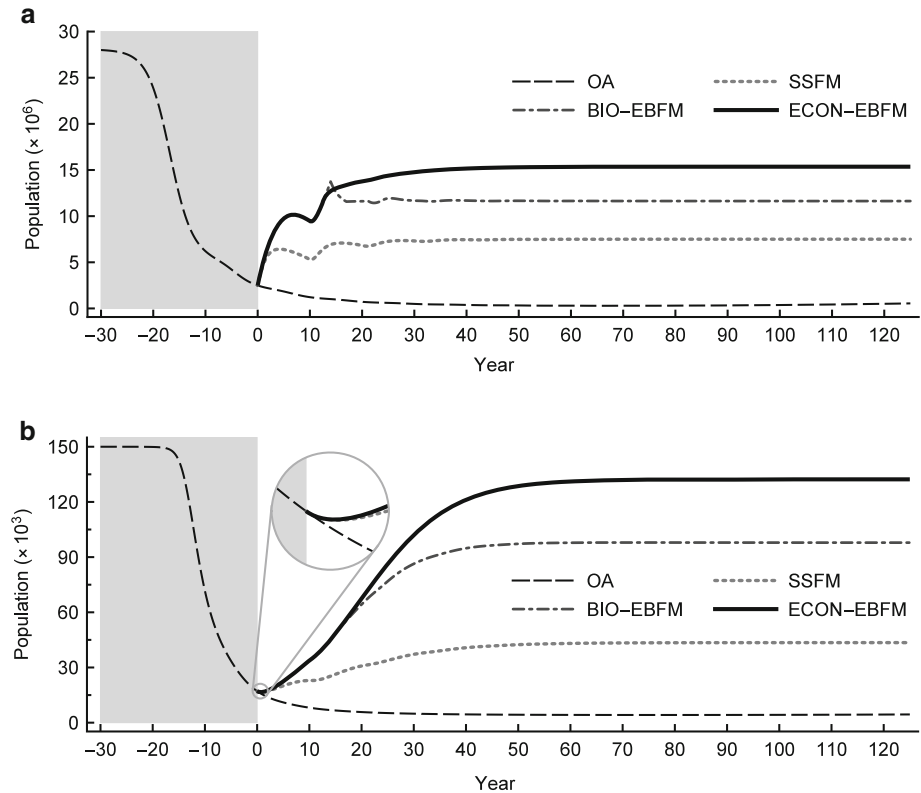
Fig. 4 Trajectories of population sizes of horseshoe crabs and red knots under continued open access (OA; the dashed lines), single-species fishery management (SSFM; the dotted lines), biological ecosystem-based fishery management (BIO-EBFM; the dot-dashed lines), and efficient ecosystem-based fishery management (ECON-EBFM; the thick, solid lines). **a** Horseshoe crab population, **b** Red knot population. 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 $t \to \infty$ over an infinite management horizon, and therefore trajectories after $t = 125$ are not shown. See also footnote [29]

of less interest to us and we speculate that the trajectories towards $t = 125$ here approximate what the optimal trajectories would have been as $t \to \infty$ over an infinite horizon.[29]

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

---

[29] To 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.

to reach sexual maturity. For example, recruitment of horseshoe crabs fifteen years into the open access period 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.[30] The result is driven by the low 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 the 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.[31] 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.[32]

---

[30] Such 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.

[31] By "stabilize" or "sustain," we mean that subsequent changes in the population or harvest level are by less than 1% (except towards the terminal periods).

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

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 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 see also Fig. 5. This decline 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 (Figs. 3, 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 (Figs. 3, 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, the harvest rate rises quickly from zero to a local maximum of about 67% of MSY in about 4 years. After that the 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. Figure 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.

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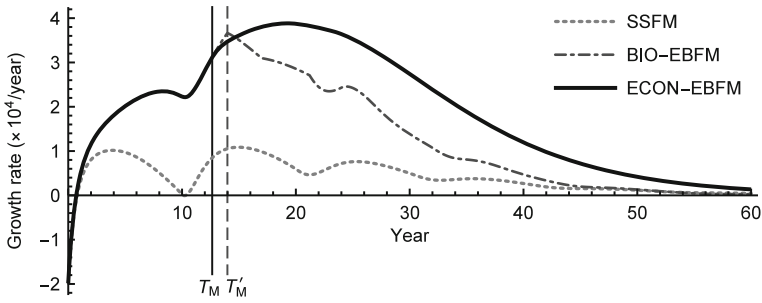
Fig. 5 Instantaneous growth rates of the red knot population in the first six decades of the management horizon under single-species fishery management (SSFM; the dotted line), biological ecosystem-based fishery management (BIO-EBFM; the dot-dashed line), and efficient ecosystem-based fishery management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

Eqs. 17–21. Figure 6 shows the decompositions in the first three decades of management. Note that in this period the horseshoe crab population is generally increasing.

Figure 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.

Figure 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, it 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 values in various scenarios. Under continued open access, the
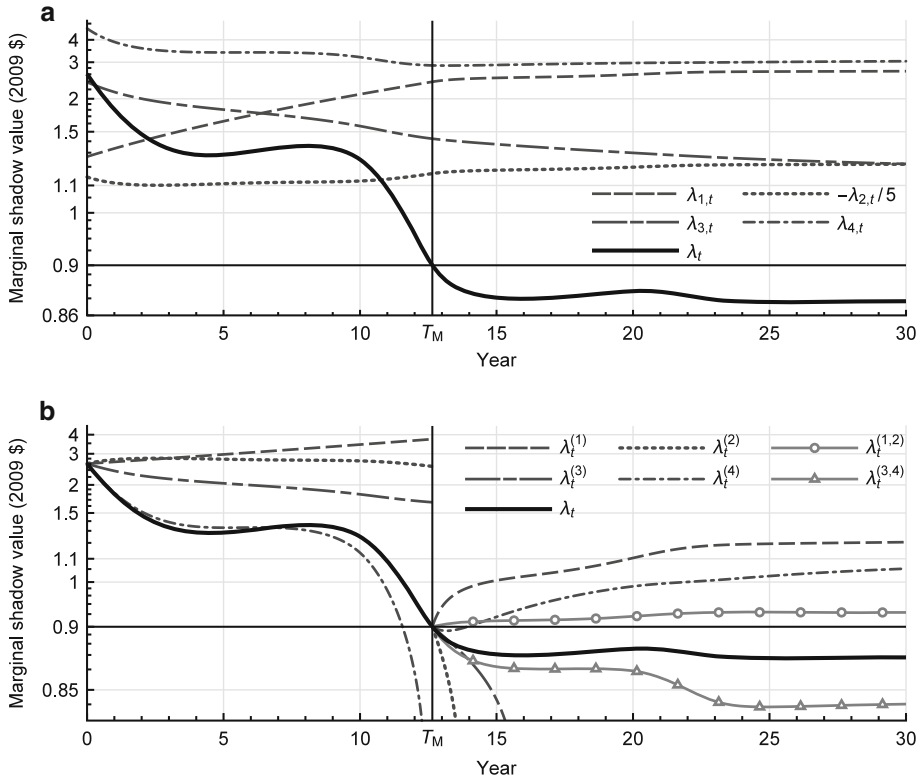
Fig. 6 Decompositions of the costate variable λ_t, i.e. the current shadow price of horseshoe crabs, in the first three decades of efficient ecosystem-based fishery management (ECON-EBFM). **a** Components in level, **b** Historical decompositions. See Sect. 5.1 for definitions of the decompositions 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 $[T_M, 30]$

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.

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.

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 200 years under any of the three management plans.
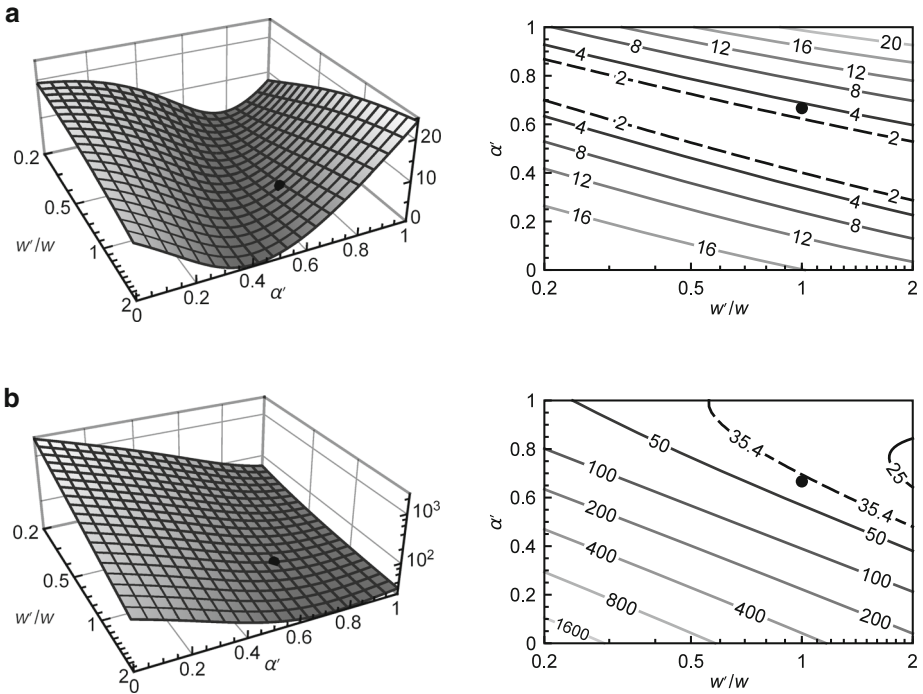

Fig. 7 Surface plots (left) and contour plots (right) of the percentage gains in net present values (NPVs) by efficient ecosystem-based fishery management (ECON-EBFM) over biological ecosystem-based fishery management (BIO-EBFM) as the parameters w' and α' vary, assuming either no rent dissipation or complete rent dissipation occurring under BIO-EBFM. **a** No rent dissipation under BIO-EBFM, **b** Complete rent dissipation under BIO-EBFM. NPV calculations include the first 125 years of the management horizon. The black dots locate the baseline point where $w' = w$ and $\alpha' = \alpha$

5.2.7 Sensitivity Analysis on the Red Knot Value Function

Because the red knot use value plays such a dominant role and because there is limited information regarding the red knot value function Eq. 7,[33] 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 w' or α' implies increasing the value of red knots in general.[34] We track the NPVs as w' and α' vary. Figure 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).

While our main results show only modest gains from moving from BIO-EBFM to 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 2327% (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 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 the economically efficient harvest rate[35] 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

---

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

[34] This statement holds when the stock size is larger than $R_{\text{m}} + 1$, which is always true in our case.

[35] We 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.

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.

Additionally, while we explore EBFM in a deterministic setting, both horseshoe crabs and red knot populations are subject to stochasticity. Fishery managers have identified four key areas of uncertainty: uncertainty in horseshoe crab spawning, uncertainty in juvenile horseshoe crab survival, uncertainty in red knot survival, and uncertainty in red knot fecundity (ASMFC 2009a). If fishery managers are risk averse, considering key drivers of stochasticity in the system will be important for policy purposes. Therefore, important areas of future work include obtaining valuation estimates that are compatible with a bioeconomic model (non-use valuation functions rather than point estimates) and considering optimal EBFM under uncertainty.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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 Eqs. 8–12. We assume all conditions required by Theorem 4.2 in Göllmann et al. (2009) are satisfied so that the theorem applies.[36] We first work with the present-value Hamiltonian and then turn to the current-value Hamiltonian.

Construct the present-value Hamiltonian as

$$\mathcal{H}^{\mathrm{p}}(t, C_t, C_{t-\tau}, R_t, E_t, \lambda_t^{\mathrm{p}}, \xi_t^{\mathrm{p}}, \zeta_{e,t}^{\mathrm{p}}, \zeta_{c,t}^{\mathrm{p}}, \zeta_{r,t}^{\mathrm{p}})$$
$$= e^{-\rho t} \left[p q C_t E_t - \delta E_t^2 + w(R_t - R_{\mathrm{m}})^\alpha \right]$$
$$+ \lambda_t^{\mathrm{p}} \left[g_c C_{t-\tau} \exp(-C_{t-\tau}/K_c^*) - \eta_c C_t - q C_t E_t \right]$$

---

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

$$+ \xi_t^{\mathrm{p}} g_r R_t \left\{ 1 - R_t / K_r / a \cdot [1 + \exp(b_0 + b_1 C_t)] \right\}$$

$$+ \zeta_{e,t}^{\mathrm{p}} E_t + \zeta_{c,t}^{\mathrm{p}} C_t + \zeta_{r,t}^{\mathrm{p}} R_t,$$

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 Eqs. 9 and 10, and $\zeta_{e,t}^{\mathrm{p}}$, $\zeta_{c,t}^{\mathrm{p}}$, and $\zeta_{r,t}^{\mathrm{p}}$ are multipliers associated with the nonnegativity constraints Eq. 11.

The first-order necessary optimality conditions are then given by

$$0 = \frac{\partial \mathcal{H}^{\mathrm{p}}}{\partial E_t} = e^{-\rho t}(pqC_t - 2\delta E_t) - \lambda_t^{\mathrm{p}} q C_t + \zeta_{e,t}^{\mathrm{p}}, \quad 0 \le t \le T, \tag{23}$$

$$\begin{aligned}
-\dot{\lambda}_t^{\mathrm{p}} = \frac{\partial \mathcal{H}^{\mathrm{p}}}{\partial C_t} + \left. \frac{\partial \mathcal{H}^{\mathrm{p}}}{\partial C_{t-\tau}} \right|_{t+\tau} &= e^{-\rho t} pq E_t - \lambda_t^{\mathrm{p}} (\eta_c + q E_t) \\
&\quad - \xi_t^{\mathrm{p}} g_r R_t^2 / K_r / a \cdot b_1 \exp(b_0 + b_1 C_t) + \zeta_{c,t}^{\mathrm{p}} \\
&\quad + \lambda_{t+\tau}^{\mathrm{p}} g_c (1 - C_t / K_c^*) \exp(-C_t / K_c^*), \quad 0 \le t < T - \tau,
\end{aligned} \tag{24}$$

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

and

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

Also, the optimal solution should maximize the Hamiltonian among all admissible control and state trajectories that satisfy the nonnegativity constraints Eq. 11. The transversality condition is simply

$$\lambda_T^{\mathrm{p}} = 0. \tag{27}$$

Nonnegativity of multipliers and the complementarity condition guarantee

$$\zeta_{e,t}^{\mathrm{p}}, \zeta_{c,t}^{\mathrm{p}}, \zeta_{r,t}^{\mathrm{p}} \ge 0 \quad \text{and} \quad \zeta_{e,t}^{\mathrm{p}} E_t = \zeta_{c,t}^{\mathrm{p}} C_t = \zeta_{r,t}^{\mathrm{p}} R_t = 0. \tag{28}$$

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

$$\lambda_t = e^{\rho t} \lambda_t^{\mathrm{p}}, \quad \xi_t = e^{\rho t} \xi_t^{\mathrm{p}}, \tag{29}$$

and

$$\zeta_{e,t} = e^{\rho t} \zeta_{e,t}^{\mathrm{p}}, \quad \zeta_{c,t} = e^{\rho t} \zeta_{c,t}^{\mathrm{p}}, \quad \zeta_{r,t} = e^{\rho t} \zeta_{r,t}^{\mathrm{p}}. \tag{30}$$

Differentiation with respect to time in Eq. 29 yields

$$\dot{\lambda}_t = \rho \lambda_t + e^{\rho t} \dot{\lambda}_t^{\mathrm{p}} \quad \text{and} \quad \dot{\xi}_t = \rho \xi_t + e^{\rho t} \dot{\xi}_t^{\mathrm{p}}. \tag{31}$$

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

$$E_t = [qC_t(p - \lambda_t) + \zeta_{e,t}]/(2\delta), \quad 0 \le t \le T,$$

$$-\dot{\lambda}_t + \rho\lambda_t = pqE_t - \lambda_t(\eta_c + qE_t) - \xi_t g_r R_t^2/K_r/a \cdot b_1 \exp(b_0 + b_1 C_t) + \zeta_{c,t}$$
$$+ e^{-\rho\tau}\lambda_{t+\tau} g_c(1 - C_t/K_c^*) \exp(-C_t/K_c^*), \quad 0 \le t < T - \tau,$$

$$-\dot{\lambda}_t + \rho\lambda_t = pqE_t - \lambda_t(\eta_c + qE_t) - \xi_t g_r R_t^2/K_r/a \cdot b_1 \exp(b_0 + b_1 C_t)$$
$$+ \zeta_{c,t}, \quad T - \tau \le t \le T, \quad \text{and}$$

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

Equation 27 becomes $\lambda_T = 0$. Equation 28 becomes

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

References

ACCSP (Atlantic Coastal Cooperative Statistics Program) (2016) Non-confidential commercial landings database. http://www.accsp.org/data-warehouse. Cited 21 July 2016

ASMFC (Atlantic States Marine Fisheries Commission) (1998) Interstate fishery management plan for horseshoe crab. Fishery Management Report No. 32, Atlantic States Marine Fisheries Commission, Washington, DC

ASMFC (Atlantic States Marine Fisheries Commission) (2004) 2003 review of the fishery management plan for horseshoe crab (*Limulus polyphemus*). http://www.asmfc.org/uploads/file/fmpreview2004.pdf

ASMFC (Atlantic States Marine Fisheries Commission) (2009a) A framework for adaptive management of horseshoe crab harvest in the Delaware Bay constrained by red knot conservation. Stock Assessment Report No. 09-02 (Supplement B), Atlantic States Marine Fisheries Commission, Washington, DC

ASMFC (Atlantic States Marine Fisheries Commission) (2009b) Horseshoe crab stock assessment for peer review. Stock Assessment Report No. 09-02 (Supplement A), Atlantic States Marine Fisheries Commission, Washington, DC

ASMFC (Atlantic States Marine Fisheries Commission) (2013a) 2013 horseshoe crab stock assessment update. http://www.asmfc.org/uploads/file//52a88db82013HSC_StockAssessmentUpdate.pdf

ASMFC (Atlantic States Marine Fisheries Commission) (2013b) Horseshoe crab Delaware Bay Ecosystem Technical Committee meeting summary, Arlington, VA, September 24, 2013. http://www.asmfc.org/uploads/file/DBETCMeetingSummary_Sept2013.pdf

ASMFC (Atlantic States Marine Fisheries Commission) (2015) 2015 review of the Atlantic States Marine Fisheries Commission fishery management plan for horseshoe crab (*Limulus polyphemus*), 2014 fishing year. http://www.asmfc.org/uploads/file/56d76a40hscFMPReview2015.pdf

Atkinson PW, Baker AJ, Bevan RM, Clark NA, Cole KB, Gonzalez PM, Newton J, Niles LJ, Robinson RA (2005) Unravelling the migration and moult strategies of a long-distance migrant using stable isotopes: Red Knot *Calidris canutus* movements in the Americas. Ibis 147(4):738–749

Baker AJ, González PM, Piersma T, Niles LJ, de Lima Serrano do Nascimento I, Atkinson PW, Clark NA, Minton CDT, Peck MK, Aarts G, (2004) Rapid population decline in red knots: fitness consequences of decreased refuelling rates and late arrival in Delaware Bay. Proc R Soc Lond B Biol Sci 271(1541):875–882

Bertram C, Quaas MF (2017) Biodiversity and optimal multi-species ecosystem management. Environ Resour Econ 67(2):321–350

Botsford LW, Castilla JC, Peterson CH (1997) The management of fisheries and marine ecosystems. Science 277(5325):509–515

Botton ML, Loveland RE (2003) Abundance and dispersal potential of horseshoe crab (*Limulus polyphemus*) larvae in the Delaware estuary. Estuar Coasts 26(6):1472–1479

Brodziak J, Link J (2002) Ecosystem-based fishery management: What is it and how can we do it? Bull Mar Sci 70(2):589–611

Burbidge J, Harrison A (1985) An historical decomposition of the great depression to determine the role of money. J Monet Econ 16(1):45–54

Clark CW (1990) Mathematical bioeconomics: the optimal management of renewable resources, 2nd edn. Wiley, New York

Deacon RT, Finnoff D, Tschirhart J (2011) Restricted capacity and rent dissipation in a regulated open access fishery. Resour Energy Econ 33(2):366–380

Edwards PET, Parsons GR, Myers KH (2011) The economic value of viewing migratory shorebirds on the Delaware Bay: an application of the single site travel cost model using on-site data. Hum Dimens Wildl 16(6):435–444

Essington TE (2001) The precautionary approach in fisheries management: the devil is in the details. Trends Ecol Evol 16(3):121–122

Eubanks TL Jr., Stoll JR, Kerlinger P (2000) The economic impact of tourism based on the horseshoe crab–shorebird migration in New Jersey. Report to New Jersey Division of Fish and Wildlife, Fermata, Inc

Falk-Petersen J, Armstrong CW (2013) To have one's cake and eat it too: managing the alien invasive red king crab. Mar Resour Econ 28(1):65–81

Gerrodette T, Dayton PK, Macinko S, Fogarty MJ (2002) Precautionary management of marine fisheries: moving beyond burden of proof. Bull Mar Sci 70(2):657–668

Göllmann L, Kern D, Maurer H (2009) Optimal control problems with delays in state and control variables subject to mixed control-state constraints. Optim Control Appl Methods 30(4):341–365

Gurney WSC, Blythe SP, Nisbet RM (1980) Nicholson's blowflies revisited. Nature 287:17–21

Guttormsen AG, Kristoffersson D, Nævdal E (2008) Optimal management of renewable resources with Darwinian selection induced by harvesting. J Environ Econ Manag 56(2):167–179

Hannesson R (1983) Optimal harvesting of ecologically interdependent fish species. J Environ Econ Manag 10(4):329–345

Haramis GM, Link WA, Osenton PC, Carter DB, Weber RG, Clark NA, Teece MA, Mizrahi DS (2007) Stable isotope and pen feeding trial studies confirm the value of horseshoe crab *Limulus polyphemus* eggs to spring migrant shorebirds in Delaware Bay. J Avian Biol 38(3):367–376

Harrington BA, Morrison RIG (1980) An investigation of wintering areas of red knots (*Calidris canutus*) and hudsonian godwits (*Limosa haemastica*) in Argentina. Report to World Wildlife Federation. Washington D.C. and Toronto, ON, Canada

Hilborn R (2004) Ecosystem-based fisheries management: The carrot or the stick? In: Perspectives on ecosystem-based approaches to the management of marine resources. Mar Ecol Prog Ser 274:275–278

Holland D, Schnier KE (2006) Individual habitat quotas for fisheries. J Environ Econ Manag 51(1):72–92

Homans FR, Wilen JE (1997) A model of regulated open access resource use. J Environ Econ Manag 32(1):1–21

Homans FR, Wilen JE (2005) Markets and rent dissipation in regulated open access fisheries. J Environ Econ Manag 49(2):381–404

Jardine SL, Sanchirico JN (2015) Fishermen, markets, and population diversity. J Environ Econ Manag 10:125

Kamien MI, Schwartz NL (1991) Dynamic optimization: the calculus of variations and optimal control in economics and management, 2nd edn. Elsevier, Amsterdam

Kellner JB, Sanchirico JN, Hastings A, Mumby PJ (2011) Optimizing for multiple species and multiple values: tradeoffs inherent in ecosystem-based fisheries management. Conserv Lett 4(1):21–30

Levin PS, Fogarty MJ, Murawski SA, Fluharty D (2009) Integrated ecosystem assessments: developing the scientific basis for ecosystem-based management of the ocean. PLoS Biol 7(1):e1000,014

Link JS (2002) What does ecosystem-based fisheries management mean. Fisheries 27(4):18–21

Lubchenco J, Sutley N (2010) Proposed U.S. policy for ocean, coast, and great lakes stewardship. Science 328(5985):1485–1486

McGowan CP, Hines JE, Nichols JD, Lyons JE, Smith DR, Kalasz KS, Niles LJ, Dey AD, Clark NA, Atkinson PW, Minton CDT, Kendall W (2011a) Demographic consequences of migratory stopover: linking red knot survival to horseshoe crab spawning abundance. Ecosphere 2(6):1–22

McGowan CP, Smith DR, Sweka JA, Martin J, Nichols JD, Wong R, Lyons JE, Niles LJ, Kalasz K, Brust J, Klopfer M, Spear B (2011b) Multispecies modeling for adaptive management of horseshoe crabs and red knots in the Delaware Bay. Nat Resour Model 24(1):117–156

Myers JP, Morrison RIG, Antas PZ, Harrington BA, Lovejoy TE, Sallaberry M, Senner SE, Tarak A (1987) Conservation strategy for migratory species. Am Sci 75:18–26

Myers KH, Parsons GR, Edwards PET (2010) Measuring the recreational use value of migratory shorebirds on the Delaware Bay. Mar Resour Econ 25(3):247–264

Niles LJ, Sitters HP, Dey AD, Atkinson PW, Baker AJ, Bennett KA, Carmona R, Clark KE, Clark NA, Espoz C, González PM, Harrington BA, Hernández DE, Kalasz KS, Lathrop RG, Matus RN, Minton CDT, Morrison RIG, Peck MK, William P, Robinson RA, Serrano IL (2008) Status of the Red Knot (*Calidris canutus rufa*) in the Western Hemisphere. No. 36 in Studies in Avian Biology, Cooper Ornithological Society

Niles LJ, Bart J, Sitters HP, Dey AD, Clark KE, Atkinson PW, Baker AJ, Bennett KA, Kalasz KS, Clark NA, Clark J, Gillings S, Gates AS, González PM, Hernandez DE, Minton CDT, Morrison RIG, Porter RR,

Ross RK, Veitch CR (2009) Effects of horseshoe crab harvest in Delaware Bay on red knots: Are harvest restrictions working? BioScience 59(2):153–164

Pierce JC, Tan G, Gaffney PM (2000) Delaware bay and Chesapeake Bay populations of the horseshoe crab (*Limulus polyphemus*) are genetically distinct. Estuaries 23(5):690–698

Pikitch EK, Santora C, Babcock EA, Bakun A, Bonfil R, Conover DO, Dayton P, Doukakis P, Fluharty D, Heneman B, Houde ED, Link J, Livingston PA, Mangel M, McAllister MK, Pope J, Sainsbury KJ (2004) Ecosystem-based fishery management. Science 305(5682):346–347

Schaefer MB (1954) Some aspects of the dynamics of populations important to the management of the commercial marine fisheries. Inter Am Trop Tuna Comm Bull 1(2):23–56

Shuster CN Jr, Sekiguchi K (2003) Growing up takes about ten years and eighteen stages. In: Shuster CN Jr, Brockmann HJ, Barlow RB (eds) The American Horseshoe Crab. Harvard University Press, Cambridge, pp 103–132

Sims CA (1980) Macroeconomics and reality. Econometrica 48(1):1–48

Singh R, Weninger Q (2009) Bioeconomies of scope and the discard problem in multiple-species fisheries. J Environ Econ Manag 58(1):72–92

Smith DR (2007a) Effect of horseshoe crab spawning density on nest disturbance and exhumation of eggs: a simulation study. Estuar Coasts 30(2):287–295

Smith DR, Millard MJ, Carmichael RH (2009) Comparative status and assessment of *Limulus polyphemus* with emphasis on the New England and Delaware Bay populations. In: Tanacredi JT, Botton ML, Smith DR (eds) Biology and Conservation of Horseshoe Crabs. Springer, Berlin, pp 361–386

Smith MD (2007b) Generating value in habitat-dependent fisheries: the importance of fishery management institutions. Land Econ 83(1):59–73

Smith VL (1968) Economics of production from natural resources. Am Econ Rev 58(3):409–431

Swan BL (2005) Migrations of adult horseshoe crabs, *Limulus polyphemus*, in the Middle Atlantic Bight: a 17-year tagging study. Estuaries 28(1):28–40

Sweka JA, Smith DR, Millard MJ (2007) An age-structured population model for horseshoe crabs in the Delaware Bay area to assess harvest and egg availability for shorebirds. Estuar Coasts 30(2):277–286

USFWS (United States Fish and Wildlife Service) (2014) Rufa red knot ecology and abundance, supplement to Endangered and Threatened Wildlife and Plants; Proposed Threatened status for the rufa red knot (*Calidris canutus rufa*)