

Optimal escapement in stage-structured fisheries with environmental stochasticity



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ARTICLE INFO

Article history:

Received 3 March 2015

Revised 25 August 2015

Accepted 28 August 2015

Available online 9 September 2015

Keywords:

Bioeconomics

Fisheries management

Optimal harvest

Age-structure

Environmental stochasticity

Mercenaria mercenaria

ABSTRACT

Stage-structured population models are commonly used to understand fish population dynamics and additionally for stock assessment. Unfortunately, there is little theory on the optimal harvest of stage-structured populations, especially in the presence of stochastic fluctuations. In this paper, we find closed form optimal equilibrium escapement policies for a three-dimensional, discrete-time, stage-structured population model with linear growth, post-harvest nonlinear recruitment, and stage-specific pricing and extend the analytic results to structured populations with environmental stochasticity. When only fishing reproductive adults, stochasticity does not affect optimal escapement policies. However, when harvesting immature fish, the addition of stochasticity can increase or decrease optimal escapement depending on the second and third derivative of the recruitment function. For logistic recruitment, stochasticity reduces optimal immature escapement by a multiplicative factor of one over one plus the variance of the environmental noise. Using hard clam, *Mercenaria mercenaria*, as an example and assuming Beverton–Holt recruitment, we show that optimal fishing of hard clam targets the immature stage class exclusively and that environmental stochasticity increases optimal escapement for low discount rates and decreases optimal escapement for high discount rates.

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1. Introduction

Fisheries biologists, managers and economists widely recognize that traditional one-dimensional bioeconomic models are too simple for developing management guidelines for the majority of real-life fisheries [1], as policies derived from such models can drastically reduce profits and stock sizes when naively applied to age-structured populations [2]. While determining optimal age-specific harvest policies is a classic problem in bioeconomics [3–8], and an active area of both theoretical and applied research [9–16], the effect of stage structure and environmental stochasticity on optimal fisheries management is poorly understood.

Stage-structured models are often used to understand fish population dynamics and perform stock assessment [17,18]. It is usually more convenient for managers to obtain data on fish size or life stage rather than age. Techniques for aging organisms can be expensive and time consuming and in extreme cases logistically infeasible [19]. In addition, fish prices are often based on discrete size classes or life stages [20,21]. While developing optimal harvest rules for size and stage-structured populations can potentially improve fisheries

management, it is more challenging to solve for optimal strategies in this framework due to the lack of sparsity in the equations for stock dynamics.

Past studies have simplified the problem by limiting transitions between stage classes [22,23] or using continuous time models, including two-dimensional ordinary differential equations (e.g. [24]) and partial differential equations [25,26]. However, fisheries biologists usually use discrete-time models for stock assessment [27] and variability among individuals within a population can lead to a wide range of stage transitions, previously unexplored with respect to optimization.

Tahvonen's model [23] is the most similar to our deterministic setup, but differs in a few key ways. We assume that harvest occurs prior to growth and recruitment, as is usually the case for migrating fish populations such as eel and salmon [28,29] and that individuals can skip stages. However, the biggest difference between our two approaches is that we consider the addition of environmental stochasticity.

While the effect of environmental stochasticity on optimal harvest has been widely studied for one-dimensional bioeconomic models (e.g. [30]), little is known about how stochasticity affects optimal harvest in structured populations. Of the few studies that exist, stochasticity is typically only included in the form of random recruitment,

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and usually independent of spawning biomass [12,22]. In addition, solutions heavily rely on numerical simulation and error-bound approximation [22,31].

In this paper, to our knowledge, we provide the first analytic optimal stationary escapement solution for a demographically structured population model with endogenous, nonlinear recruitment and environmental stochasticity affecting all classes. We find that with the addition of environmental stochasticity, the optimal escapement of reproductive adults remains unchanged from the deterministic case, if harvest occurs prior to recruitment. However, in the case of immature harvest, fishing should either be more aggressive or conservative than the deterministic case depending on the second and third derivatives of the recruitment function. For example, if the recruitment function is logistic, escapement should decrease by a factor of one over one plus the variance of the environmental noise. We use historical data from New York state’s hard clam fishery to provide a concrete example of our theoretical results.

2. The deterministic model

Consider a harvested stage-structured fish population, where events occur in the following order: (1) census (2) harvest, (3) reproduction, and (4) natural mortality and growth. That is,

$$B_{1,t+1} = R(B_{3,t} - h_t) + a_{11}B_{1,t} \tag{1}$$

$$B_{2,t+1} = a_{21}B_{1,t} + a_{22}(B_{2,t} - \eta_t) \tag{2}$$

$$B_{3,t+1} = a_{31}B_{1,t} + a_{32}(B_{2,t} - \eta_t) + a_{33}(B_{3,t} - h_t), \tag{3}$$

where $B_{1,t}$, $B_{2,t}$, and $B_{3,t}$ are the biomass of juvenile (stage 1), immature (stage 2) and adult (stage 3) fish at time t , respectively. The juvenile stage consists of fish too small to reproduce or catch. The immature stage consists of all fish large enough to catch, but still cannot reproduce. At time t , h_t and η_t units of biomass are harvested from the adult and immature fish population and we define $\sigma_t \equiv B_{3,t} - h_t$ and $s_t \equiv B_{2,t} - \eta_t$ as the corresponding amount of adult and immature biomass that escape harvest. The remaining fish survive and grow, where a_{ij} is the per unit biomass contribution, from the biomass that escaped harvest in stage j , at time t , to the biomass in stage i , at time $t + 1$.

We assume, $0 \leq a_{ij} \leq m_i/m_j$, for all $i > j$, where m_i is the average mass of a stage i individual and that $a_{ij} < 1$ for all $i = j$. This means that the population’s biomass can only increase through reproduction and transitioning between different stages. If a_{ij} were greater than one for some i , then, in the absence of harvest, an initial amount of biomass in the i th stage would grow to infinity, even if there was no reproduction.

Adults that escape harvest, reproduce, generating offspring with total biomass described by a bounded, positive, smooth, concave, density-dependent recruitment function $R(\sigma_t)$, where σ_t is the spawning biomass at time t and $R(0) = 0$. We can write the model in matrix notation as

$$\vec{B}_{t+1} = A(\vec{B}_t - \vec{h}_t) + \vec{R}_t, \tag{4}$$

where

$$\vec{B}_t = \begin{pmatrix} B_{1,t} \\ B_{2,t} \\ B_{3,t} \end{pmatrix}, A = \begin{pmatrix} a_{11} & 0 & 0 \\ a_{21} & a_{22} & 0 \\ a_{31} & a_{32} & a_{33} \end{pmatrix},$$

$$\vec{h}_t = \begin{pmatrix} 0 \\ \eta_t \\ h_t \end{pmatrix}, \vec{R}_t = \begin{pmatrix} R(B_{3,t} - h_t) \\ 0 \\ 0 \end{pmatrix}.$$

$B_{1,t}$ is bounded for all time, because R is bounded and $a_{11} < 1$. It follows that $B_{2,t}$ and $B_{3,t}$ are bounded since $a_{ij} < 1$ for $i = j$.

Note, the model unconventionally tracks biomass rather than population abundance. In classic stage-structured models of abundance, a_{ij} is the probability of an individual surviving and transitioning from stage j to stage i . However, in our model, a_{ij} is a composite parameter which additionally includes growth. Because of our assumptions on R and a_{ij} , a simple rescaling, from biomass to abundance, of any admissible parameterization of (4) yields a valid parameterization of the classic stage-structured model presented in [32, Chs. 3, 4 and 16]. For example, if \hat{a}_{ij} is an entry in the classic transition matrix model, then $\hat{a}_{ij} = a_{ij}m_j/m_i$, where m_i is the average mass of a stage i individual.

We wish to maximize total discounted revenue, where revenue is a linear function of harvest,

$$\max_{h_t, \eta_t} \left\{ \sum_{t=0}^{\infty} \rho^t (p_3 h_t + p_2 \eta_t) \right\}, \tag{5}$$

with p_2 and p_3 , the price per unit biomass of immature and adult fish, respectively, and $\rho = 1/(1 + \delta)$, the discrete discount factor, with discount rate $\delta \geq 0$. Harvest is also subject to the constraints $0 \leq h_t \leq B_{3,t}$ and $0 \leq \eta_t \leq B_{2,t}$.

3. Analysis of the deterministic model

3.1. Optimal equilibrium escapement

We use the Karush–Kuhn–Tucker theorem (p. 61 of [1]) to solve for the equilibrium optimal harvest policy. The Lagrangian for the problem is

$$\begin{aligned} \mathcal{L} = \sum_{t=0}^{\infty} \rho^t \{ & p_3 h_t + p_2 \eta_t + \rho \lambda_{1,t+1} [R(B_{3,t} - h_t) + a_{11}B_{1,t} - B_{1,t+1}] \\ & + \rho \lambda_{2,t+1} [a_{21}B_{1,t} + a_{22}(B_{2,t} - \eta_t) - B_{2,t+1}] \\ & + \rho \lambda_{3,t+1} [a_{31}B_{1,t} + a_{32}(B_{2,t} - \eta_t) + a_{33}(B_{3,t} - h_t) - B_{3,t+1}] \\ & + \mu_{1,t} h_t + \mu_{2,t} [B_{3,t} - h_t] + \mu_{3,t} \eta_t + \mu_{4,t} [B_{2,t} - \eta_t] \} \end{aligned} \tag{6}$$

where $\rho \lambda_{i,t+1}$ is the current value shadow price for $B_{i,t}$, the money someone would pay for a small additional amount of biomass in the i th stage at time $t + 1$ and $\mu_{i,t}$ are the multipliers for the inequality constraints on harvest. The Karush–Kuhn–Tucker necessary conditions for and optimal solution are

$$\rho a_{11} \lambda_{1,t+1} + \rho a_{21} \lambda_{2,t+1} + \rho a_{31} \lambda_{3,t+1} - \lambda_{1,t} = 0, \tag{7}$$

$$\rho a_{22} \lambda_{2,t+1} + \rho a_{32} \lambda_{3,t+1} - \lambda_{2,t} + \mu_{4,t} = 0, \tag{8}$$

$$\rho a_{33} \lambda_{3,t+1} + \rho R'(B_{3,t} - h_t) \lambda_{1,t+1} - \lambda_{3,t} + \mu_{2,t} = 0, \tag{9}$$

$$p_2 - \rho a_{22} \lambda_{2,t+1} - \rho a_{32} \lambda_{3,t+1} + \mu_{3,t} - \mu_{4,t} = 0, \tag{10}$$

$$p_3 - \rho R'(B_{3,t} - h_t) \lambda_{1,t+1} - \rho a_{33} \lambda_{3,t+1} + \mu_{1,t} - \mu_{2,t} = 0, \tag{11}$$

$$\mu_{1,t} h_t = 0 \text{ and } \mu_{2,t} [B_{3,t} - h_t] = 0, \tag{12}$$

$$\mu_{3,t} \eta_t = 0 \text{ and } \mu_{4,t} [B_{2,t} - \eta_t] = 0, \tag{13}$$

$$\text{and } \mu_{i,t} \geq 0 \text{ for all } i \in \{1, 2, 3, 4\}. \tag{14}$$

At steady state, the above system can be solved analytically, yielding optimal equilibrium escapement rules for immature and adult biomass, which we define as s^* and σ^* , respectively. We use the star superscript (*) and the omission of the time subscript to denote steady state values for each variable under the optimal equilibrium

escapement rule (e.g. B_3^* is the optimal pre-harvest adult biomass at steady state). Solving (7)–(14), at steady state, yields three optimal regimes depending on the parameters.

In the first regime (Case 1), the discounted value of immature fish, as a result of survival and growth, is greater than the marginal value of harvesting immature fish today, $\rho(a_{22}p_2 + a_{32}p_3) > p_2$. In other words, fish are more valuable in the water than on the dock. Therefore, it is optimal to only fish adults. Alternatively, if $\rho(a_{22}p_2 + a_{32}p_3) < p_2$, it is optimal to exclusively fish immatures (Case 2), but in such a way that the same amount of adult biomass escapes to reproduce as in Case 1. However, provided a large enough fraction of juveniles skip a stage to become adults ($a_{31} > 0$) and sufficient escaped adults also survive ($a_{33} > 0$), there can be a surplus of adults above optimal adult equilibrium escapement, even when harvesting all of the immatures (Case 3). In this regime, it is optimal to harvest all of the immatures and some of the surplus adult biomass. However, optimal adult equilibrium escapement is higher in this case than in Case 1 because the manager is forced to harvest some adults despite them being less valuable than immatures. Since increasing adult biomass increases the more valuable immature biomass prior to harvest, it is optimal to leave more adults in the water. To state these cases precisely it is useful to define the following quantity,

$$\alpha \equiv \frac{(1 - \rho a_{11})(1 - \rho a_{22})(1 - \rho a_{33})}{\rho^3 a_{21} a_{32} + \rho^2 a_{31}(1 - \rho a_{22})}. \tag{15}$$

Case 1. If $\rho(a_{22}p_2 + a_{32}p_3) > p_2$, then it is optimal, at steady state, to only harvest adults, letting σ^* adult biomass escape harvest, where σ^* is the solution to $R'(\sigma^*) = \alpha$. In this case the equilibrium biomasses, shadow prices, harvests and multipliers are

$$B_1^* = \frac{R(\sigma^*)}{1 - a_{11}}, \quad B_2^* = \frac{a_{21}R(\sigma^*)}{(1 - a_{11})(1 - a_{22})},$$

$$B_3^* = \left[a_{31} + \frac{a_{21}a_{32}}{1 - a_{22}} \right] \frac{R(\sigma^*)}{1 - a_{11}} + a_{33}\sigma^*, \tag{16}$$

$$\lambda_1^* = \frac{\rho^2 p_3 a_{21} a_{32} + \rho p_3 a_{31} (1 - \rho a_{22})}{(1 - \rho a_{11})(1 - \rho a_{22})},$$

$$\lambda_2^* = \frac{\rho p_3 a_{32}}{1 - \rho a_{22}}, \quad \lambda_3^* = p_3, \tag{17}$$

$$h^* = \frac{(a_{31} - a_{31}a_{22} + a_{21}a_{32})R(\sigma^*)}{(1 - a_{11})(1 - a_{22})} - (1 - a_{33})\sigma^*, \quad \eta^* = 0, \tag{18}$$

$$\mu_1^* = \mu_2^* = \mu_4^* = 0, \quad \mu_3^* = \frac{\rho(a_{22}p_2 + a_{32}p_3) - p_2}{1 - \rho a_{22}} > 0. \tag{19}$$

For the following two cases it is useful to define the quantity

$$\beta \equiv \frac{(1 - a_{33})\sigma^*}{a_{32}} - \frac{a_{31}R(\sigma^*)}{a_{32}(1 - a_{11})}, \tag{20}$$

where σ^* is the solution to $R'(\sigma^*) = \alpha$.

Case 2. If $\rho(a_{22}p_2 + a_{32}p_3) < p_2$ and $\beta \geq 0$, then it is optimal, at steady state, to harvest only immatures, letting $s^* = \beta$ immature biomass escape harvest, so that adult spawning biomass is σ^* . The equilibrium biomasses, shadow prices, harvests and multipliers are

$$B_1^* = \frac{R(\sigma^*)}{1 - a_{11}},$$

$$B_2^* = \frac{(a_{21}a_{32} - a_{31}a_{22})R(\sigma^*)}{a_{32}(1 - a_{11})} + \frac{a_{22}(1 - a_{33})\sigma^*}{a_{32}}, \quad B_3^* = \sigma^* \tag{21}$$

$$\lambda_1^* = \frac{\rho p_2 a_{21} a_{32} + p_2 a_{31} (1 - \rho a_{22})}{a_{32}(1 - \rho a_{11})},$$

$$\lambda_2^* = p_2, \quad \lambda_3^* = \frac{p_2(1 - \rho a_{22})}{\rho a_{32}}, \tag{22}$$

$$h^* = 0,$$

$$\eta^* = \frac{(a_{21}a_{32} - a_{31}a_{22} + a_{31})R(\sigma^*)}{a_{32}(1 - a_{11})} - \frac{(1 - a_{22})(1 - a_{33})\sigma^*}{a_{32}}, \tag{23}$$

$$\mu_2^* = \mu_3^* = \mu_4^* = 0, \quad \mu_1^* = p_2 - \rho(a_{22}p_2 + a_{32}p_3) > 0. \tag{24}$$

Case 3. If $\rho(a_{22}p_2 + a_{32}p_3) < p_2$ and $\beta < 0$, then it is optimal, at steady state, to harvest all immatures ($s^* = 0$), and in addition harvest some adults such that $\hat{\sigma}^*$ adult biomass escapes harvest, where $\hat{\sigma}^*$ is the solution to

$$R'(\hat{\sigma}^*) = \frac{p_3(1 - \rho a_{33})(1 - \rho a_{11})}{\rho^2(p_2 a_{21} + p_3 a_{31})}. \tag{25}$$

In this case the equilibrium biomasses, shadow prices, harvests and multipliers are

$$B_1^* = \frac{R(\hat{\sigma}^*)}{1 - a_{11}}, \quad B_2^* = \frac{a_{21}R(\hat{\sigma}^*)}{1 - a_{11}}, \quad B_3^* = \frac{a_{31}R(\hat{\sigma}^*)}{1 - a_{11}} + a_{33}\hat{\sigma}^* \tag{26}$$

$$\lambda_1^* = \frac{\rho(a_{21}p_2 + a_{31}p_3)}{1 - \rho a_{11}}, \quad \lambda_2^* = p_2, \quad \lambda_3^* = p_3, \tag{27}$$

$$h^* = \frac{a_{31}R(\hat{\sigma}^*)}{1 - a_{11}} + (a_{33} - 1)\hat{\sigma}^*, \quad \eta^* = B_2^*, \tag{28}$$

$$\mu_1^* = \mu_2^* = \mu_3^* = 0, \quad \mu_4^* = p_2 - \rho(a_{22}p_2 + a_{32}p_3) > 0. \tag{29}$$

Note that if $\rho(a_{22}p_2 + a_{32}p_3) = p_2$, exactly, then it is equally profitable to harvest immatures or adults. In this case, it suffices to use the strategy defined in Case 1 to maximize discounted net revenue, at steady state, and hence we do not write this as a separate case.

Because R is bounded and smooth, by the intermediate value theorem applied to the function $\alpha x - R(x)$, the optimal equilibrium, presented above, always exists if $R'(0) > \alpha$. This condition guarantees that at low population biomasses a fish in the water is worth more than the revenue generated from harvesting that fish.

3.2. Closed form solutions for logistic and Beverton–Holt recruitment

Depending on the functional form of the recruitment function, $R(\sigma)$, it is possible to obtain closed form solutions for the optimal escapement at equilibrium. For example, Let R be the logistic map with carrying capacity k , and growth rate r ,

$$R(\sigma) = r\sigma \left(1 - \frac{\sigma}{k} \right), \tag{30}$$

under the restriction that $0 < \sigma < k$, $k > 0$, and $r > \alpha$. In this case, if $\rho(a_{22}p_2 + a_{32}p_3) > p_2$, optimal adult escapement is

$$\sigma^* = \frac{k}{2r} \left[r - \frac{(1 - \rho a_{11})(1 - \rho a_{22})(1 - \rho a_{33})}{\rho^3 a_{21} a_{32} + \rho^2 a_{31} (1 - \rho a_{22})} \right]. \tag{31}$$

If $\rho(a_{22}p_2 + a_{32}p_3) < p_2$ and $\beta \geq 0$, we harvest no adults and let $s^* = \beta$ immatures escape harvest to achieve a spawning biomass of σ^* . If $\rho(a_{22}p_2 + a_{32}p_3) < p_2$ and $\beta < 0$, then we harvest all of the immatures and some adults, letting

$$\hat{\sigma}^* = \frac{k}{2r} \left[r - \frac{(1 - \rho a_{11})(1 - \rho a_{33})}{\rho^2(a_{21} + a_{31})} \right] \tag{32}$$

adult biomass escape harvest. As a second example, consider the Beverton–Holt recruitment function,

$$R(\sigma) = \frac{b_1 \sigma}{1 + b_2 \sigma}, \tag{33}$$

with parameters $b_1 > \alpha$ and $b_2 > 0$. In this case,

$$\sigma^* = \frac{1}{b_2} \left[\sqrt{\frac{\rho^2 b_1 [\rho a_{21} a_{32} + a_{31} (1 - \rho a_{22})]}{(1 - \rho a_{11})(1 - \rho a_{22})(1 - \rho a_{33})}} - 1 \right]. \tag{34}$$

In Case 3,

$$\hat{\sigma}^* = \frac{1}{b_2} \left[\sqrt{\frac{\rho^2 b_1 [a_{21} + a_{31}]}{(1 - \rho a_{11})(1 - \rho a_{33})}} - 1 \right]. \tag{35}$$

To confirm that our above analysis is in fact producing the best constant escapement policy, at steady state, we compared our analytic solutions to the best escapement strategies found via numerical optimization (see online supplementary information).

3.3. Stability

Note that the positive biomass equilibrium of system (1) is not always stable. For example, in the absence of harvest, if $a_{32} = a_{21} = 1$, $a_{11} = a_{22} = a_{33} = a_{31} = 0$, and R is given by the logistic Eq. (30), the population dynamics of a single cohort, sampled every three years as adults, reduces to the one-dimensional logistic map, whose trajectories exhibit periodic and chaotic behavior for growth rates between three and four [33]. However, it can be shown that the Jacobian of the linearized biomass system dynamics, evaluated at optimal adult escapement, has a dominant eigenvalue between one and zero if we assume $a_{11} = a_{22} = a_{33} < \rho$ and $a_{31} = 0$. This case actually includes the logistic case described above, which is not a contradiction because optimal escapement in that example is always below one half of the unstable positive biomass equilibrium for $B_{3,t}$ in the absence of harvest.

Unfortunately, when $a_{31} \neq 0$, computing the roots of the characteristic equation can be quite complicated, and therefore we leave a full, rigorous, stability analysis of the population dynamics (1)–(3) and optimality system (7)–(14) as an open area of research. For all numerical examples provided in this paper, we confirmed that from several different initial conditions, the biomass of the three classes approached optimal economic equilibrium when deploying the appropriate escapement rule, out of those described in Cases (1)–(3).

4. Stochastic model and analysis

In simple one-dimensional bioeconomic models, constant escapement policies can be optimal even when the biomass dynamics are stochastic. In this section, we explore these policies for structured populations. To simplify the analysis we consider two cases, one where only adult fish are harvested and the other where only immatures are harvested (which we justify after analyzing the stochastic models). We show that environmental stochasticity affects optimal harvest in the two stage classes differently. Within each of these cases we first consider the age-structured case with $a_{31} = a_{11} = a_{22} = a_{33} = 0$, and for the case of adult harvest extend the analysis to models closer to (1).

4.1. When harvesting only adults

Consider a simplified age-structured model where adults die after spawning and only adult fish are harvested,

$$\begin{aligned} B_{1,t+1} &= z_{1,t+1} R(B_{3,t} - h_t) \\ B_{2,t+1} &= z_{2,t+1} a_{21} B_{1,t} \\ B_{3,t+1} &= z_{3,t+1} a_{32} B_{2,t}. \end{aligned} \tag{36}$$

The random variables $z_{i,t}$ are chosen such that the sequences $\{z_{i,t}\}_{t \geq 1}$ are each independently and identically distributed on a closed interval contained in $(0, \infty)$ with $\mathbb{E}[z_{i,t}] = 1$, in such a way that $z_{i,t}$ and $z_{j,t+m}$ are independent for all $i, j \in \{1, 2, 3\}$ and $m > 0$. In other words, we are allowing for correlation between age classes, but no temporal autocorrelation. For example, one possibility for modeling the noise is $z_{i,t} = \bar{z}_i + \epsilon_{i,t}$, with $\mathbb{E}[\bar{z}_i] = q$, and $\mathbb{E}[\epsilon_{i,t}] = 1 - q$, where $0 \leq q \leq 1$. When $q = 0$, the age classes experience independent, random

fluctuations. When $q = 1$, the noise is perfectly correlated between age classes.

Note that in the equation for $B_{1,t+1}$, in (36), there is no random variable in the argument of the recruitment function, R . We are assuming that stochasticity affects reproductive adult biomass prior to harvest, but that stochasticity does not affect adult biomass between harvest and reproduction. This is a standard assumption in one-dimensional bioeconomic models [1,30].

Lastly, we assume that the population is “self-sustaining” at the optimal escapement level. For example, in the case where $a_{31} = a_{11} = a_{22} = a_{33} = 0$, σ^* self-sustaining means that $z_1 z_2 z_3 a_{32} a_{21} R(\sigma^*) \geq \sigma^*$, where z_i is the lowest value $z_{i,t}$ can attain. This assumption is standard in stochastic, one-dimensional bioeconomic models [1] because it guarantees, $B_{3,t} - \sigma_t > 0$, when the system is in stationary distribution, and allows for solutions achieved through stochastic dynamic programming arguments.

While the stochastic realizations of juvenile and immature biomass in years $t - 2$ and $t - 1$ influence $B_{3,t}$, under the above assumptions, the lagged effect of stochasticity on the future recruitment of juveniles is eliminated when using a self-sustaining adult escapement rule.

Because juvenile and immature fish always grow or die, and mature fish die after spawning, Eq. (36) yields three independent cohorts. Therefore, it suffices to find the optimal equilibrium escapement for a single cohort, only tracking the population in the harvested age class. Without loss of generality, consider the cohort, that is initially in the adult age class. The cohort’s dynamics are given by

$$\begin{aligned} x_{\tau+1} &= \zeta_{\tau+1} a_{21} a_{32} R(x_{\tau} - h_{\tau}), \\ x_0 &= B_{3,0} \end{aligned} \tag{37}$$

where $x_{\tau} = B_{3,3\tau}$ is the adult biomass in the τ th generation and $\zeta_{\tau+1} = z_{3,3\tau+3} z_{2,3\tau+2} z_{1,3\tau+1}$. The escapement policy that maximizes

$$\mathbb{E} \left\{ \sum_{\tau=0}^{\infty} \rho^{3\tau} p_3 h_{3\tau} \right\} \tag{38}$$

is

$$R'(\sigma_t) = \frac{(1 + \delta)^3}{a_{32} a_{21}}, \tag{39}$$

since this formulation satisfies the one-dimensional optimization problem with fixed per unit cost and concave positive recruitment in [34]. Note that the optimal escapement is the same as in the deterministic case, $R'(\sigma^*) = \alpha$, when substituting $a_{31} = a_{11} = a_{22} = a_{33} = 0$ into Eq. (15).

Now consider the full stage-structured model, but again assume fishing can only occur in the adult age class. The model for adult harvest is

$$\begin{aligned} B_{1,t+1} &= z_{1,t+1} [R(\sigma_t) + a_{11} B_{1,t}] \\ B_{2,t+1} &= z_{2,t+1} [a_{21} B_{1,t} + a_{22} B_{2,t}] \\ B_{3,t+1} &= z_{3,t+1} [a_{31} B_{1,t} + a_{32} B_{2,t} + a_{33} \sigma_t]. \end{aligned} \tag{40}$$

First we maximize expected discounted net revenue over a fixed time horizon T ,

$$\mathbb{E} \left\{ \sum_{t=0}^T \rho^t p_3 h_t \right\}, \tag{41}$$

and then let $T \rightarrow \infty$. We proceed with a calculation similar to the one in Section 7.3 of [1], but extend it to our three-dimensional framework. Define the value function

$$V(\vec{B}_t) = \max_{\sigma_t} \{ p_3 (B_{3,t} - \sigma_t) + \rho \mathbb{E}\{V(\vec{B}_{t+1})\} \}. \tag{42}$$

At the final time, it is clearly optimal to harvest everything. Hence, $\sigma_T^* = 0$, yielding $V(\vec{B}_T) = p_3 B_{3,T}$. Therefore,

$$V(\vec{B}_{T-1}) = \max_{\sigma_{T-1}} \{ p_3 (B_{3,T-1} - \sigma_{T-1}) + \rho \mathbb{E}\{p_3 B_{3,T}\} \}. \tag{43}$$

Using the dynamic model (40) to write $B_{3,T}$ in terms of adult, immature and juvenile biomass at time $T - 1$, and noting that these values are constants, we get $\sigma_{T-1}^* = 0$ as well. To calculate σ_{T-2}^* , we continue iterating backwards, substituting $V(\vec{B}_{T-1})$ into the formula for $V(\vec{B}_{T-2})$. It can be shown, via simple algebra, that finding σ_{T-2}^* is equivalent to maximizing the function

$$w_{T-2}(\sigma_{T-2}) \equiv (\rho a_{33} - 1)\sigma_{T-2} + \rho^2 a_{31} R(\sigma_{T-2}), \tag{44}$$

and hence σ_{T-2}^* is the solution to

$$R'(\sigma_{T-2}^*) = \frac{1 - \rho a_{33}}{\rho^2 a_{31}}. \tag{45}$$

As we proceed backwards in time, to calculate the optimal escapement strategy at time $T - n$, σ_{T-n}^* , a pattern emerges for $w_{T-n}(\sigma_{T-n})$. That is, for $n \geq 3$,

$$w_{T-n}(\sigma_{T-n}) = -\sigma_{T-n} + \rho a_{33} \sigma_{T-n} + a_{31} R(\sigma_{T-n}) \sum_{j=2}^n \rho^j a_{11}^{j-2} + a_{32} a_{21} R(\sigma_{T-n}) \sum_{j=3}^n \sum_{i=0}^{j-3} \rho^j a_{22}^i a_{11}^{j-i-3}. \tag{46}$$

As $n \rightarrow \infty$, with $n < T$, the above sequence of functions converges to

$$w(\sigma) = -\sigma + \rho a_{33} \sigma + \frac{\rho^2 a_{31}}{1 - a_{11} \rho} R(\sigma) + \frac{\rho^3 a_{32} a_{21}}{(1 - \rho a_{22})(1 - \rho a_{11})} R(\sigma). \tag{47}$$

Therefore, at a stationary distribution, the optimal escapement strategy is given by $R'(\sigma) = \alpha$, the same as in Case (1) of our deterministic analysis.

4.2. When harvesting immatures

Now consider the simplified, stochastic, age-structured model, where adults die after spawning and only immatures are harvested.

$$\begin{aligned} B_{1,t+1} &= z_{1,t+1} R(B_{3,t}) \\ B_{2,t+1} &= z_{2,t+1} a_{21} B_{1,t} \\ B_{3,t+1} &= z_{3,t+1} a_{32} (B_{2,t} - \eta_t). \end{aligned} \tag{48}$$

In this case the single cohort dynamics are given by

$$\begin{aligned} y_{\tau+1} &= \xi_{\tau+1} a_{21} R(v_{\tau+1} a_{32} [y_{\tau} - \eta_{\tau}]), \\ y_0 &= B_{2,0} \end{aligned} \tag{49}$$

where $y_{\tau} = B_{2,3\tau}$ is the immature biomass in the τ th generation of a cohort which started as immatures, $\xi_{\tau+1} = z_{2,3\tau+3} z_{1,3\tau+2}$, and $v_{\tau+1} = z_{3,3\tau+1}$. We wish to find the escapement that maximizes

$$\mathbb{E} \left\{ \sum_{\tau=0}^T \rho^{3\tau} p_2 \eta_{3\tau} \right\}. \tag{50}$$

A similar stochastic dynamic programming argument, to the one in the previous section, can be used to show that the optimal immature escapement policy, s^* is the solution to

$$\mathbb{E} [v_{\tau+1} R'(v_{\tau+1} a_{32} s)] = \frac{(1 + \delta)^3}{a_{32} a_{21}}. \tag{51}$$

For the logistic recruitment function, this equation has the closed form solution,

$$s^* = \left[\frac{k}{2ra_{32}} \right] \left[r - \frac{(1 + \delta)^3}{a_{32} a_{21}} \right] \left[\frac{1}{1 + \text{var}(v_{\tau+1})} \right], \tag{52}$$

which is just $1/(1 + \text{var}[z_{3,t}])$ times the optimal escapement policy for a deterministic model with logistic recruitment. Therefore, when recruitment and survival vary randomly over time, if a

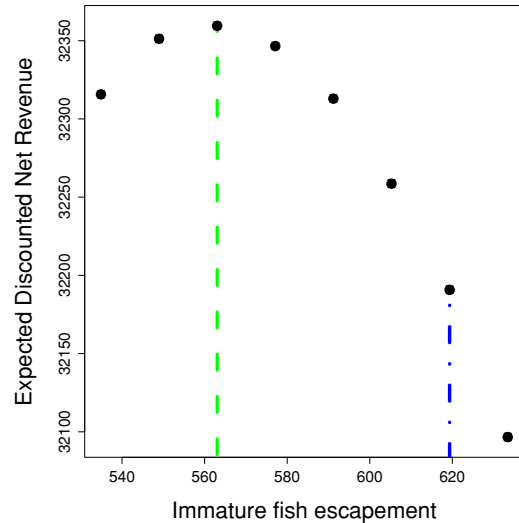


Fig. 1. Expected net revenue for eight immature fish escapement strategies, averaged over ten million simulations (confidence intervals are negligible due to the large sample size). The green dashed line is the analytic “variance corrected” optimal escapement strategy in the stochastic logistic recruitment model (563.0) and the blue dot-dashed line corresponds to the optimal escapement strategy for the corresponding deterministic model (619.3). The parameters are $a_{32} = 0.83$, $a_{21} = 2$, $r = 1.65$, $K = 2000$, $p_2 = 5$, $\delta = 0.1$ and $z_t = 0.8$ with probability 5/7 and $z_t = 1.5$ with probability 2/7.

manager chooses to fish immature biomass, he should fish more aggressively than in the deterministic case. However, if the manager harvests adults, he should do so as if the system is deterministic.

In order to verify these predictions, we simulated 20 million realizations of this system with the environmental noise distributed as a discrete probability distribution, $z_t = 0.8$ with probability 5/7 and $z_t = 1.5$ with probability 2/7, under eight immature escapement strategies including the analytic stochastic optimal escapement rule (52) and the deterministic optimal escapement rule (see Fig. 1). Note that the calculations require the population to be self sustaining at the optimal escapement value, such that $B_{2,t} - s_t^* \geq 0$ for all t , at stationary distribution. When this assumption is violated, the optimal escapement policy is still lower than in the deterministic setting, however $1/(1 + \text{var}(z_{3,t}))$ may be an overcorrection. See Fig. 2 for an example where three “bad years” can cause less immature biomass to return to the immature stage than what initially escaped three years prior, and notice that the general concept, that you fish more aggressively in the stochastic model, is still true.

4.3. The effect of the recruitment function

The logistic recruitment function allowed for a closed form analytic solution to Eq. (51). However, there is no analytically tractable solution to (51) for most density-dependent recruitment functions. We would like to know if the result that a manager should fish immatures more aggressively under environmental stochasticity is general for all density-dependent recruitment functions.

Let s^* be the optimal stationary escapement of immature fish if there is no stochasticity. In this case equilibrium spawner biomass is $\sigma^* = a_{32} s^*$. We note that if

$$\mathbb{E} [v_{\tau+1} R'(v_{\tau+1} \sigma^*)] > \frac{(1 + \delta)^3}{a_{32} a_{21}}, \tag{53}$$

then the expected biological growth rate is higher than the discount rate and one should therefore leave more fish in the ocean (i.e. increase escapement, higher than s^*). If the inequality in (53) is reversed, it is optimal to decrease escapement under environmental stochasticity. Define

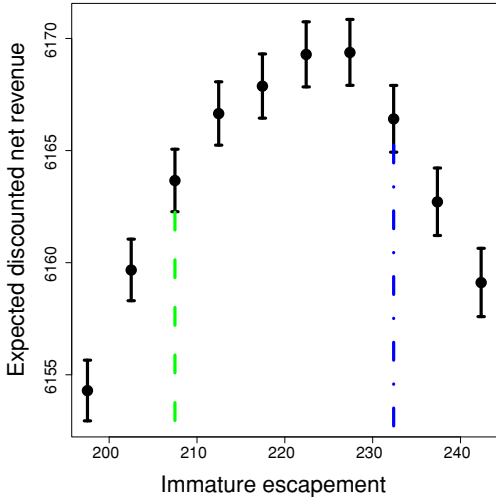


Fig. 2. Expected net revenue for eight immature fish escapement strategies, averaged over ten million simulations with 95 percent confidence intervals. $z_{1,t} = z_{2,t} = z_{3,t}$, with $z_{1,t}$ distributed uniformly on (0.4, 1.6). The green dashed line is the “variance corrected” optimal escapement strategy in the stochastic logistic recruitment model and the blue dot-dashed line corresponds to the optimal escapement strategy for the corresponding deterministic model. The parameters are $a_{32} = 0.9$, $a_{21} = 1.05$, $a_{11} = a_{22} = a_{33} = 0$, $r = 1.5$, $K = 2000$, $p_2 = 5$, $\delta = 0.1$. Note that in this case the assumptions used to derive the optimal escapement strategy do not hold because $B_{2,t} - s_t^* \geq 0$ requirement is not satisfied for all t , since $0.4^2 a_{21} R(0.4 a_{32} s^*) < s^*$ (meaning a series of bad years can send the stock below the calculated optimal escapement level). However, the general concept that you fish more aggressively in the stochastic model is still true in this example.

$$f(v) \equiv vR'(v\sigma^*). \tag{54}$$

By Jensen’s inequality, if f is strictly convex on the support of v ,

$$\mathbb{E}[f(v)] > f(\mathbb{E}[v]) = f(1) = \frac{(1 + \delta)^3}{a_{32}a_{21}}. \tag{55}$$

Similarly if f is strictly concave on the support of v , $\mathbb{E}[f(v)] < (1 + \delta)^3 / (a_{32}a_{21})$. This means that if $f'(v) > 0$, for all v , Eq. (53) is satisfied and it is more profitable to increase escapement, and if $f'(v) < 0$ it is more profitable to decrease escapement. Noting that

$$f''(v) = 2\sigma^*R''(v\sigma^*) + (\sigma^*)^2vR'''(v\sigma^*), \tag{56}$$

it is possible to calculate when fishing should be more or less aggressive for specific recruitment functions, even when such functions do not allow for tractable solutions to Eq. (51).

For logistic recruitment, (30) with $r > (1 + \delta)^3 / (a_{21}a_{32})$, we note that $f'(v) < 0$ for all $v > 0$ and $\sigma^* > 0$. This means it is more profitable to decrease the escapement of immatures, which agrees with our analytic optimal escapement rule (52).

More aggressive fishing than in the deterministic case is also optimal if recruitment follows a Ricker curve,

$$R(\sigma) = b_1\sigma e^{-b_2\sigma}, \tag{57}$$

with the parameters and random variables chosen such that

$$\frac{(1 + \delta)^3}{z_{\min}a_{21}a_{32}} < b_1 < \frac{e^2}{z_{\max}a_{21}a_{32}}, \tag{58}$$

where $z_{\min} = \min_t (z_{1,t}z_{2,t}z_{3,t})$, $z_{\max} = \max_t (z_{1,t}z_{2,t}z_{3,t})$, and $b_2 > 0$. We also restrict the domain for v_T in Eq. (49) to the set $(0, 2/b_2)$ and note that because of condition (58), this set is invariant under arbitrarily many iterations of (49) (see [35] for a proof). Note that R is concave on this restricted, invariant set.

Since for Ricker recruitment $R'(\sigma) < 0$ for all $\sigma > 1/b_2$, by the rule $R'(\sigma^*) = \alpha$, σ^* will always be less than $1/b_2$. Therefore, as long as the support of v does not contain values large enough such that

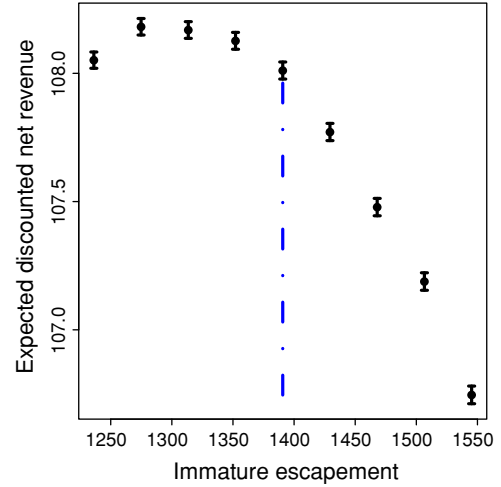


Fig. 3. Expected discounted net revenue for 9 immature escapements for a stochastic fishery with Ricker recruitment with 95 % confidence intervals, averaged over one million simulations. The dashed line is the optimal escapement strategy for the corresponding deterministic model (1390.7), calculated by solving s^* as in Case (2), numerically, using the function optimize in R. The parameters are $a_{32} = 1.2$, $a_{21} = 1.1$, $b_1 = 2$, $b_2 = 0.0002$, $p_2 = 3.43$, $p_3 = 1.66$, $\delta = 0.08$ and $z_t = 0.8$ with probability 5/7 and $z_t = 1.5$ with probability 2/7.

$v\sigma^* > 1/b_2$, it will be more profitable to decrease escapement. We simulated expected discounted net revenue when harvesting immatures in a stochastic fishery with a Ricker spawner–recruit relationship, and the example agrees with our result (Fig. 3).

Similarly, it can be shown that for the monotone recruitment function $R(\sigma) = b_1 \log(1 + b_2\sigma)$, it is also always profitable to decrease escapement. However, this is not true for all monotone recruitment functions. For Beverton–Holt recruitment, (33), both more aggressive and more conservative fishing can be optimal depending on the parameters. In this case, $f'(v) > 0$ for all v if $b_2\sigma^* \min(v) > 2$, and $f'(v) < 0$ for all v if $b_2\sigma^* \max(v) < 2$. Substituting in

$$\sigma^* = \frac{1}{b_2} [\sqrt{\rho^3 b_1 a_{21} a_{32}} - 1], \tag{59}$$

means that it is more profitable to increase immature escapement if $\sqrt{\rho^3 b_1 a_{21} a_{32}} > 1 + 2 / \min(v)$ and decrease escapement if $\sqrt{\rho^3 b_1 a_{21} a_{32}} < 1 + 2 / \max(v)$.

The above example highlights how optimal immature escapement, under environmental stochasticity depends on the third derivative of R . Since the second derivative of R will be negative for all compensatory and over-compensatory recruitment functions near σ^* , it is always more profitable to fish more aggressively when R'' is negative. However, increasing escapement can be more profitable if $R'''(\sigma^*)$ is positive, especially if σ^* is large (see Table 1).

4.4. Justification of single-stage harvest

In the stochastic case, we only calculated the optimal escapement strategy assuming exclusive harvest of either adults or immatures. This was a mathematical simplification. However, exclusive harvest will be optimal in the stochastic system in some circumstances.

Consider the stochastic stage-structured population model (40), with the addition of immature harvest, as in the deterministic optimization problem. Below, we prove that under environmental stochasticity, it is less profitable, in expectation, to increase immature harvest from zero, given any self-sustaining adult escapement strategy, as long as the condition for exclusive adult harvest in the deterministic model is met.

Table 1

The effect of environmental stochasticity on the optimal escapement of immature fish for different spawner–recruitment relationships when the variance of the environmental noise is small.

Recruitment function	Functional form	Parameter constraints	Effect of stochasticity on immature escapement
Discrete logistic	$R(\sigma) = r\sigma(1 - \sigma/k)$	$r > \frac{(1+\delta)^3}{a_{21}a_{32}}$, $k > 0$	Decrease escapement by the multiplicative factor $1/(1 + var[z_{3,t}])$
Ricker	$R(\sigma) = b_1\sigma e^{-b_2\sigma}$	$\frac{(1+\delta)^3}{a_{21}a_{32}} < b_1 < \frac{e^2}{a_{21}a_{32}}$, $b_2 > 0$	Decrease escapement
Beverton–Holt	$R(\sigma) = b_1\sigma/(1 + b_2\sigma)$	$b_1 > \frac{(1+\delta)^3}{a_{21}a_{32}}$, $b_2 > 0$	Decrease escapement if $\sigma^* < 2/b_2$, increase escapement if $\sigma^* > 2/b_2$
Log	$R(\sigma) = b_1 \log(1 + b_2\sigma)$	$b_1 > \frac{(1+\delta)^3}{a_{21}a_{32}}$, $b_2 > 0$	Decrease escapement

Proposition 1. When letting σ units of adult biomass escape harvest, assuming σ is self-sustaining, if $\rho(a_{22}p_2 + a_{32}p_3) > p_2$, then in comparison to harvesting $h_t = B_{3,t} - \sigma$ adults and $\eta_t = 0$ immatures, harvesting an additional small amount of immature biomass $\eta_t > 0$, decreases expected discounted net revenue.

Proof. Assume a self-sustaining adult escapement strategy, σ , and let J be expected net revenue of harvesting $B_{2,t} - s$ adult biomass and η_t immature biomass, for each year t ,

$$J = \mathbb{E} \left\{ \sum_{t=0}^{\infty} \rho^t (p_2 \eta_t + p_2 [B_{3,t} - \sigma]) \right\}. \tag{60}$$

We show that if $\rho(a_{22}p_2 + a_{32}p_3) > p_2$, then $\partial J / \partial \eta_t < 0$, for all η_t such that σ adult escapement is self-sustaining.

$$\begin{aligned} \frac{\partial J}{\partial \eta_t} &= \mathbb{E} \left\{ \rho^\tau p_2 - \rho^{\tau+1} \eta_t z_{3,\tau+1} \left(1 + \sum_{i=1}^{\infty} \prod_{j=0}^{i-1} z_{2,\tau-j} \rho^j a_{22}^i \right) \right\} \\ &= \rho^\tau \left(p_2 - \frac{\rho p_3 a_{32}}{1 - \rho a_{22}} \right), \end{aligned} \tag{61}$$

which is less than zero if $\rho(a_{22}p_2 + a_{32}p_3) > p_2$. \square

Consider the stochastic age-structured population model (48) with the addition of adult harvest. In this case, a manager should not harvest any adults for small fluctuations in adult biomass above optimal adult escapement (the expected adult biomass that results from letting $a_{32}s^*$ immature biomass escape). However, when fluctuations are large, in good years, there is potentially a benefit to harvesting some excess adult biomass prior to recruitment. This can be summarized as a proposition.

Proposition 2. When letting s units of immature biomass escape harvest, assuming s is self-sustaining, if $\rho^2 p_2 a_{21} R'(\max(z_{3,t}) a_{32} s) > p_3$, then in comparison to harvesting $\eta_t = B_{2,t} - s$ immatures and $h_t = 0$ adults, harvesting any additional adults $h_t > 0$, decreases expected discounted net revenue.

Proof. Assume an immature escapement strategy, s , is deployed and let J be expected net revenue,

$$J = \mathbb{E} \left\{ \sum_{t=0}^{\infty} \rho^t (p_3 h_t + p_2 [B_{2,t} - s]) \right\}. \tag{62}$$

We show that if $\rho^2 p_2 a_{21} R'(\max(z_{3,t}) a_{32} s) > p_3$, then $\partial J / \partial h_t < 0$, at $h_t = 0$, for any arbitrary time t .

$$\begin{aligned} \frac{\partial J}{\partial h_t} &= \mathbb{E} \left\{ \rho^\tau p_3 - \rho^{\tau+2} p_2 z_{2,\tau+2} z_{1,\tau+1} a_{21} R'(z_{3,\tau} a_{32} s - h_t) \right\} \\ &\leq \rho^\tau [p_3 - \rho^2 p_2 a_{21} R'(\max(z_{3,t}) a_{32} s - h_t)]. \end{aligned} \tag{63}$$

The inequality is guaranteed by the assumption that R is concave. Plugging in $h_t = 0$ yields the desired result. \square

5. Hard clam example

Historically, the hard clam fishery has been one of the most lucrative fisheries in New York state and the largest shellfish fishery on the east coast of North America [21]. We use a snap-shot of this fishery circa 1980 as an example for our model. In New York, the clams are sold in three common varieties: littlenecks (width < 36.5 mm), cherrystones (width < 41.3 mm) and chowders (width > 41.3 mm) [21]. As the clams grow, their flesh becomes tough and less desirable. Although smaller clams command the highest price, it is illegal to harvest clams with a width less than 25.4 mm in the United States [21]. We classify the clams that are too small to be legally harvested as juveniles, littleneck clams as immatures and both cherrystones and chowders as adults. Clams with a width less than 25 mm do not typically contribute to reproduction [21]. While littleneck clams can reproduce, their average fecundity is only about one third of cherrystones and chowders and hence, we ignore it as a mathematical simplification. On average it takes juveniles two years to grow larger than 25.4 mm, and another two years to become cherrystones [36]. The probability a juvenile survives is 0.16 [37] and in the absence of harvest, immature and adult survival is 0.91 [38]. The respective weights of the three sizes of clam were calculated from their shell length as reported by Anderson et al. [39] using the relationship $\text{weight}[g] = (0.671 \times \text{length}[cm])^3$ [40], yielding juvenile, immature and adult clam weights of 4.50, 57.4 and 158 g, respectively. The above assumptions yield parameters,

$$\begin{aligned} a_{11} &= (\text{survival prob.})(\text{transition prob.}) = 0.16 \times 0.5 = 0.08, \\ a_{21} &= (\text{survival prob.})(\text{transition prob.})(\text{growth}) \\ &= 0.16 \times 0.5 \times 57.4/4.5 = 1.02, \end{aligned}$$

with the rest calculated similarly, giving $a_{22} = 0.46$, $a_{31} = 0$, $a_{32} = 1.25$, and $a_{33} = 0.91$. An adult clam produces, on average, seven million eggs per spawning event, but the probability of larvae survival is very small, estimated at 0.00058 over five days [38]. Assuming larva survival continues at this rate for the ten days it takes to develop into a juvenile clam (studies reviewed in [41] ranged from eight days to two weeks) and that recruitment follows the Beverton–Holt model, then $b_1 = 2.35$. The carrying capacity of this fishery is unknown, so we set it to be equal to the largest reported historical landing (as reported in [42]), yielding $b_2 = 4.42 \times 10^{-5}$. On October 1, 1980 the price for littlenecks and cherrystones were $p_2 = 2228$ and $p_3 = 527.7$ USD per metric ton, respectively [42]. We arbitrarily set the baseline discount rate to $\delta = 0.07$.

Under this parameterization, it is more valuable to fish the immature stage class exclusively. The sensitivity of the optimal equilibrium biomass to the parameter values is shown in Fig. 4. As is standard for bioeconomic models, higher discount rates lead to lower equilibrium stock biomass. Equilibrium biomass increases with a_{ij} . If a_{22} is small, only immatures are harvested, but for large a_{22} harvest switches to adults and stock sizes increase. As a_{31} increases,

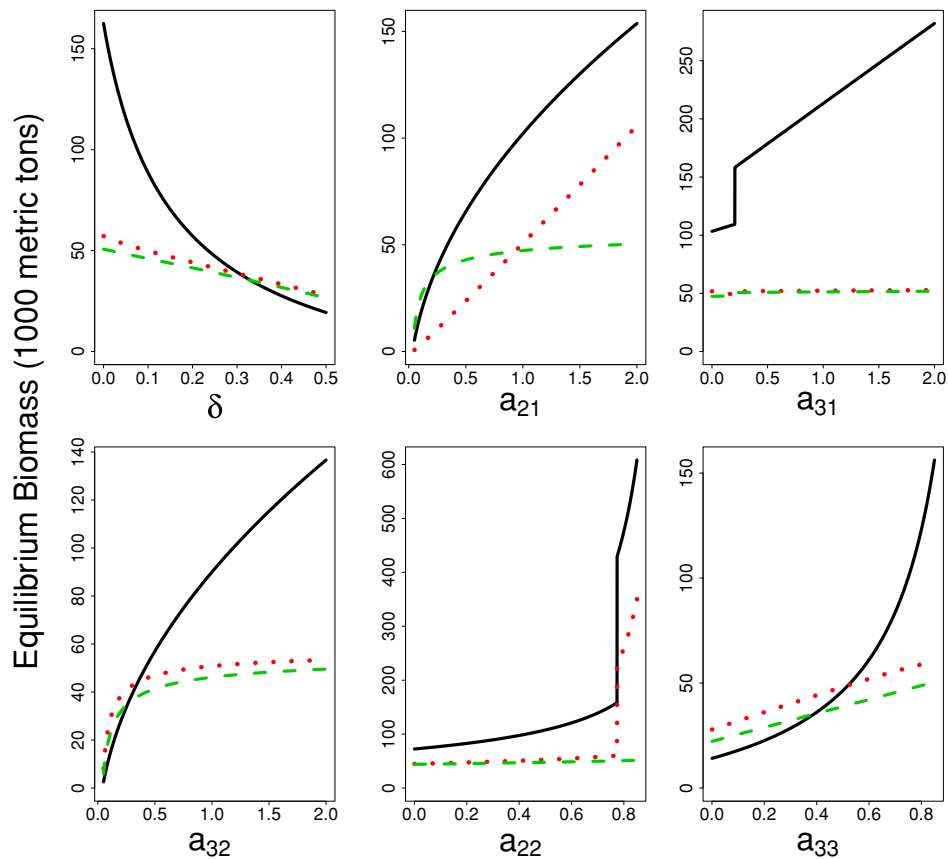


Fig. 4. Equilibrium adult (black solid line), immature (red dotted line) and juvenile (green dashed line) biomass as a function of each parameter. Recruitment is Beverton–Holt and baseline parameter values are $a_{11} = 0.08$, $a_{21} = 1.02$, $a_{22} = 0.46$, $a_{32} = 1.25$, $a_{33} = 0.91$, $\delta = 0.07$, $p_2 = 2228$, $p_3 = 527.7$, $b_1 = 2.3$, and $b_2 = 4.42 \times 10^{-5}$ and were chosen to match values reported in the literature for hard clam.

optimal harvest switches from only fishing immatures to harvesting some adults in addition to all of the immatures. This is important because it says that if the probability of transitioning from a sub-legal size clam directly into a cherrystone was underestimated, it could explain why cherrystones and chowders are harvested in practice.

Using the parameters above, we added environmental stochasticity to this example as described in (36), with $z_{1,t} = z_{2,t} = z_{3,t}$ and $z_{1,t}$ independently identically distributed such that $z_{1,t} = 0.8$ with probability $5/7$ and $z_{1,t} = 1.5$ with a probability $2/7$, and calculated expected discounted net revenue under two discount rates, a conservative rate of $\delta = 0.07$ and a myopic rate of $\delta = 0.35$ (the median fisher personal discount rate as reported in [43]). For $\delta = 0.07$, stochasticity means the best strategy is to fish more conservatively than in the deterministic scenario (see Fig. 5a), which we would expect, based on our analytic calculation for the effect of stochasticity on immature escapement under Beverton–Holt recruitment, since $\sigma^* = 103,312 > 45,227 = 2/b_2$. For $\delta = 0.35$, stochasticity means the best strategy is to fish more aggressively than in the deterministic scenario (see Fig. 5b), which we would also expect, based on our analytic calculation, since, for this discount rate, $\sigma^* = 32,892 < 45,227 = 2/b_2$.¹

If stochastic fluctuations are higher for hard clam than in this hypothetical example, Proposition (2) also suggests a possible reason for why commercial fishing operations harvest adults in practice, at least in good years.

¹ Note we assumed $a_{33} = 0$ in our analytic calculation for optimal immature escapement under environmental stochasticity. However, the calculation appears to provide the correct intuition in the above cases where $a_{33} > 0$.

6. Discussion

While optimal harvest strategies for age-structured populations have been widely studied in the bioeconomics literature, little is known about how environmental stochasticity affects the optimal harvest of structured populations. In this paper, we developed optimal, steady state, escapement rules for a stage-structured fish stock, where transitions between all classes were possible (except for shrinking) and used a stochastic version of the model to extend classic theoretical results on the optimal harvest of stochastic one-dimensional models [30] to structured populations.

Two discrete-time, size-structured models have been analyzed previously [22,23]. Setting fecundity of small fish equal to zero in Tahvonen's two size-class model [23], yields a similar equation for optimal offspring abundance to the equation we derived for optimal biomass escapement, $R'(\sigma^*) = \alpha$, as long as we set the skipping stages term, a_{31} , equal to zero. The only minor difference is that the discount rate is cubed in our equation and squared in Tahvonen's, which matches the 3-year vs. 2-year life cycles in the two models, respectively. This optimal amount of biomass (or abundance in Tahvonen's model) follows a rule similar to the "golden rule of bioeconomics" derived for one dimensional models, under no harvest costs, where the marginal productivity of the fish stock is equal to the discount rate [1]. The difference is that in size and stage-structured models, stock productivity and discounting interact in more complicated ways due to all the possible transitions between the various stage or size classes.

Some aspects of Tahvonen's models are more general than ours, including the possibility of a nonlinear objective function and

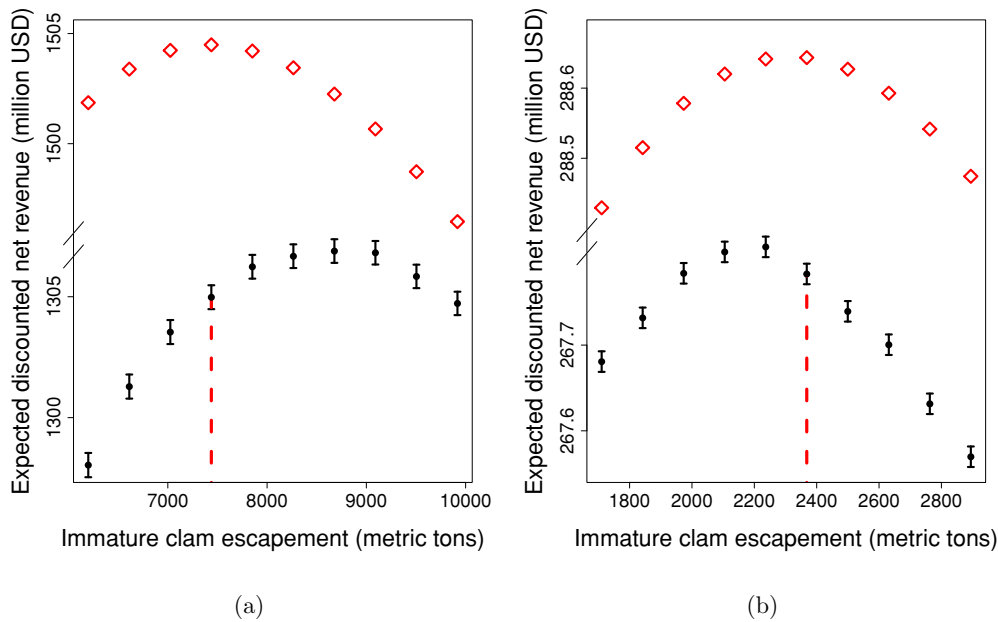


Fig. 5. Expected discounted net revenue for hard clam escapement levels in the stochastic model (black circles) and for the deterministic model (red diamonds) for two values of the discount rate (a) $\delta = 0.07$ and (b) $\delta = 0.35$. Error bars represent 95 percent confidence intervals for the mean. The dashed line is the theoretical, deterministic, optimal escapement, s^* , for the corresponding discount rate. Note that for $\delta = 0.35$, only a few time steps contribute heavily to discounted net revenue, so we had to compute the net revenue under each escapement strategy for 100 million simulations in order to get an accurate estimate of the expectations plotted in (b), whereas, only ten million simulations were required to generate (a).

reproduction by all stage-classes. These generalities combined with the assumption that harvest occurs after adult recruitment, can lead to the existence of cyclical interior solutions corresponding to partial harvests of both immature and adult stages. Tahvonen reveals this possibility by studying the stability of optimal harvest solutions. Since our primary goal was to study the effect of stochasticity we leave stability analysis in our deterministic setting as future direction.

However, other aspects of Tahvonen's model are more restrictive, such as the assumption that individuals do not skip stages and that dynamics are deterministic. Some species can undergo short periods of rapid growth with high variability among individuals, and hence skipping stages may be common for structured populations. For example, it is possible for a large juvenile clam to transition into a cherystone in one year [36]. We have shown how skipping stages can create an additional case where it is optimal to harvest all of the early stage and in addition partially harvest the late stage, even though it is less valuable.

For a linear objective function, as in one-dimensional models [30], stochasticity does not affect optimal adult escapement. However, if harvest occurs during an immature stage, we showed that random fluctuations in stock dynamics can affect the optimal escapement strategy depending on the second and third derivative of the recruitment function.

The reason why stochasticity does not affect optimal adult escapement, in this model, is that we assumed stochastic fluctuations in adult population biomass occur prior to harvest, meaning there is no stochasticity during the short period between adult harvest and reproduction. This is a standard assumption in stochastic one-dimensional biomass models [1,30], but it means that adult harvest, through a self-sustaining escapement rule, allows for a deterministic amount of biomass to reproduce. On the other hand, an immature biomass escapement rule allows for stochasticity to enter the density dependent recruitment function through fluctuations in the realizations of unharvested reproductive-adult biomass. If stochasticity were allowed to occur between adult harvest and reproduction, we would expect similar results on how stochasticity affects optimal

adult escapement to the results presented in this paper for optimal immature escapement.

In the stochastic model, we assumed the manager was either exclusively harvesting immatures or adults. Exclusive adult harvest is indeed optimal under the same condition as presented in Case (1) in the deterministic problem. However, when this condition is not met, we can only show that exclusive immature harvest is optimal for tightly bounded noise. For large fluctuations, partial harvest of adults and immatures may be optimal, and hence future analysis is required to determine the best harvest strategies.

The effect of stochasticity on optimal harvest with nonlinear utility remains an open question for stage-structured fisheries. It should be possible to do similar analysis to what we have done here if the objective function is separable. For one-dimensional models, Reed [30] showed that if utility is concave, stochasticity increases optimal escapement and if utility is convex, stochasticity decreases optimal escapement. It is important to note that concave utility in Reed's one-dimensional models and concave recruitment in our stage-structured model, when harvesting immatures, have a diametrically opposite effect on optimal escapement if the third derivative of the recruitment function is negative. Future analysis should shine light on the interplay between these two nonlinearities when determining optimal harvest in stochastic fisheries.

Acknowledgments

We thank Stephen Ellner and Collin Edwards for insight during the course of this research. Stephen Ellner also provided helpful comments on previous drafts of the manuscript. We thank two anonymous reviewers for helpful comments, one of whose suggestions greatly simplified the calculations in Section 3.

Supplementary material

Supplementary material associated with this article can be found, in the online version, at [10.1016/j.mbs.2015.08.021](https://doi.org/10.1016/j.mbs.2015.08.021)

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