

Optimal harvesting of size-structured biological populations

Olli Tahvonen

Abstract The question of harvesting size-structured biological resources is generic in resource economics but purely understood. This study is based on a well known density-dependent size-structured population model that includes an age-structured model as a special case. Harvest from each size class can be chosen independently. Mathematically the model is an any number of state and control variables discrete-time optimization problem. While earlier studies have analysed the Maximum Sustainable Yield steady states using problem-specific optimization procedures, this study applies non-linear programming and analyses the dynamic economic problem. It is shown that with two size classes, there may exist six steady state regimes. The optimal steady state is shown to be either unique or a continuum implying that earlier MSY -theorems are not entirely correct. Given a unique steady state the optimal solution converges toward a saddle point steady state or a stationary cycle. Optimal harvest timing of single individuals deviates from Faustmann-type rotation, and a higher interest rate may cause a shift to harvesting older age classes. For the general specification with any number of size classes, equations for optimal steady states and a stability result are obtained.

Keywords: Renewable resources, size-structured models, age-structured models, fisheries, forestry, optimal control

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1 Introduction

Economic analysis on biologically regenerating natural resources is heavily based on two distinct approaches. These are the optimal rotation model (Faustmann 1849, Samuelson 1976) and the dynamic biomass harvesting model (Gordon 1954, Clark 1976). The optimal rotation approach solves the question when to clear-cut a group of even-aged trees and it leads to harvest every 50 years, for example. The dynamic biomass approach describes how to optimize the rate of harvest of a biomass (e.g. fish population). Both approaches have produced extensive literature including theoretical extensions and practical applications. In spite of this success the limitation of the rotation approach is the *a priori* commitment to point-input, point-output structure and silence on whether there could be other possibilities to cope with biological density dependence, to organize the tree age class structure and the resulting timing of harvest and regeneration. The limitation of the biomass model is that it cannot answer the question on whether one should direct the harvesting activity to some age or size group and save the others.

Overcoming these limitations requires extending the description of the biologically regenerating natural resource under harvest. This can be done by specifying the population as an age- or size-structured system. One route toward such models can be based on the well-known studies by Leslie (1945) and Usher (1966), who pioneered in developing discrete-time structured population models that are currently considered basic workhorses of population ecology (Cushing 1998, Caswell 2001). In biological sciences these models are used e.g. for fish, plant, mammal and insect populations.

For clarity it is important to distinguish at least two different classes of discrete time structured optimal harvesting models. The first class is based on Leslie (1945) or Usher (1966) age- or size structured population models and on various density dependence assumptions. In these models harvest may be age class specific (perfect selectivity assumption) or models may include some specific harvesting technology and "effort" as a single control variable (Getz and Haight 1989, p. 45, 143). The second class of models has a centuries long historical background in forest sciences and forest planning (Reed 1986), Getz and Haigh 1989, p. 308-). These models consist a number of biologically separate "even-aged stands" in a larger region (e.g a country). The economic problem is to allocate the total land area over time and over the stands (with varying ages) in order to find optimal harvest and an equilibrium market price of timber. Clearly, the land allocation model is developed to analyse a very different problem compared to the single population model and not recognizing this difference may cause serious confusions (Goetz and Xabadia 2011, Xabadia and Goetz 2010, Goetz et al. 2011).

The first steps in understanding the problem of harvesting a single population were taken by Baranov (1918), Beverton and Holt (1957) and Walters (1969). Beddington and Taylor (1973) and Rorres and Fair (1975) developed a model where harvesting activity is age class-specific (the perfect selectivity assumption). While these studies apply the linear Leslie matrix model (and *ad hoc* restrictions), Reed (1980), Getz (1980) and Getz and Haight (1989) base their models on Walters (1969) and

Allen and Basasibvaki (1974), and include density dependence in recruitment. In contrast Clark (1990) studies the problem following Beverton and Holt (1957) and assumes constant exogenous recruitment. In spite of the various extensions of this model (see Getz and Haight 1989) and its use in many empirical and theoretical studies (Haight 1985, Tahvonen 2011a, Skonhøft et al. 2012), the main theoretical results are still offered by the works of Reed (1980) and Getz (1980).

Both of these studies solve the Maximum Sustainable Yield (MSY) steady state and apply a problem-specific solution method that separates the model into linear and non-linear programming problems. Their main theorem states that optimal MSY harvesting is bimodal, i.e. it involves a partial or total harvest of only one age class, or a partial harvest of one age class and a total harvest of another, older age class. Getz and Haight (1989) generalized this MSY approach to size-structured models, and proceeded to a general discussion of how the analysis could be extended by applying the discrete-time Maximum Principle. However, they did not present any further results.

In spite of its merits, the solution procedure in Reed (1980) and Getz (1980) is designed for steady-state analysis and cannot be applied for obtaining dynamic solutions. Its specific nature has perhaps additionally discouraged further developments in the analytical understanding of this problem.

This study analyses the general dynamic economic problem by applying non-linear programming and the Karush-Kuhn-Tucker (KKT) theorem. A study by Wan (1994) and further studies by Salo and Tahvonen (2002, 2003) present an example in which most theoretical properties of a structured model (land allocation forestry model) can be found by only including two classes. Applying this method for the population level model, this study shows the existence of six different steady-state regimes. These steady states are unique, except a case of a steady state continuum. This continuum is not recognized in the main theorem by Reed (1980) or Getz (1980).

The model specifies a problem in optimal harvest timing, but the solution is not within the realm of the Faustmann rotation model: it is optimal to harvest the cohorts after they have reached their maximum discounted value, and an increase in interest rate may result in harvesting of older age classes rather than younger ones. Comparing solutions with the biomass approach shows that neglecting information on population interior structure leads to suboptimal steady states and misleading "optimal extinction" results (cf. Clark 1973).

Given zero interest rate the interior steady states are shown to be local saddle points. Under some additional restrictions, the saddle point property is shown to also hold with positive interest rates. However, given "high" discounting, the optimal solution may converge toward a stationary cycle. In contrast, a boundary-type regime is independent of (small) changes in interest rate and the steady state is locally stable. Earlier literature does not present any stability results.

The analysis of two solution regimes is extended to steady-state equations with any number of age or size classes. Given the age-structured specification, it is possible to show a local stability result independently of the number of age classes. A numerical example demonstrates that the optimal harvest level within the structured

approach may equal zero, even if the initial population biomass exceeds its optimal steady state level.

2 The size- and age-structured optimization problem

Let x_{st} , $s = 1, \dots, n$, $t = 0, 1, \dots$ denote the number of individuals in size class s in the beginning of period t . A fraction $0 < \alpha_s < 1$, $s = 1, \dots, n$ moves to class $s+1$ by the end of period t and a fraction $0 \leq \beta_s < 1$, $s = 1, \dots, n$ remains in class s . The remaining fraction i.e. $0 \leq 1 - \alpha_s - \beta_s < 1$ equals natural mortality. The number of offspring x_{0t} is given as

$$x_{0t} = \sum_{s=1}^n \gamma_s x_{st}, \quad (1)$$

where $\gamma_s \geq 0$, $s = 1, \dots, n$ denotes fecundity. Offspring are vulnerable to density, and let the twice continuously differentiable function φ denote the number of offspring that survive over their first period. This function satisfies:

$$\begin{aligned} (A1) : \varphi(0) &= 0, & (A2) : 0 < \varphi'(0) &\leq 1, \\ (A3) : \varphi'' &< 0, & (A4) : \lim_{x_0 \rightarrow \infty} \varphi'(x_0) &= 0. \end{aligned}$$

Let $h_{st} \geq 0$, $s = 1, \dots, n$, $t = 0, 1, \dots$ denote the number of individuals harvested at the end of any period t . The size-structured population model is now given by (1) and

$$x_{1,t+1} = \varphi(x_{0t}) + \beta_1 x_{1t} - h_{1t}, \quad (2)$$

$$x_{s+1,t+1} = \alpha_s x_{st} + \beta_{s+1} x_{s+1,t} - h_{s+1,t} \quad s = 1, \dots, n-1. \quad (3)$$

The (valuable) size of individuals in units of weight or volume is $f_s \geq 0$, $s = 1, \dots, n$. The total harvested (valuable) biomass is $H_t \geq 0$ and

$$H_t = \sum_{s=1}^n f_s h_{st}. \quad (4)$$

The utility function U is twice continuously differentiable, increasing and concave in H . Let $b = (1+r)^{-1}$, denote the discount factor and r the interest rate. The problem is to

$$\max_{\{h_{st}, s=1, \dots, n, t=0, 1, \dots\}} \sum_{t=0}^{\infty} U(H_t) b^t, \quad (5)$$

subject to (1)-(4), the nonnegativity conditions $h_{st} \geq 0$, $x_{st} \geq 0$, $s = 1, \dots, n$, $t = 0, 1, \dots$ and the given initial size distribution x_{s0} , $s = 1, \dots, n$.

If the recruitment function φ was linear and $\varphi' = 1$, the population model (1)-(3) would be the standard size-classified model in population ecology (Caswell 2001, p. 59). Given assumptions (A1-A4), the population model is a size-classified specification with density dependence in recruitment (Caswell 2001, p. 504). A concave

increasing recruitment function is common in fishery models (Beverton and Holt 1957), but also possible for shade-tolerant trees. Assuming $\beta_s = 0$, $s = 1, \dots, n-1$, the model yields the standard density-dependent age-structured model as a special case. Note that the harvest levels h_{st} , $s = 1, \dots, n$ can be chosen independently. This is natural e.g. with trees, but sometimes it is also possible in fisheries, if specific harvesting gear types exist or different cohorts can be found from different locations.

When the utility function is bounded and $b < 1$, the existence of optimal solutions follows from theorem 4.6 in Stokey and Lucas (1989, p. 79). The Lagrangian and the Karush-Kuhn-Tucker (KKT) conditions are written as

$$L = \sum_{t=0}^{\infty} b^t \{ U(\sum_{s=1}^n f_s h_{st}) + \lambda_{1t} [\varphi(x_{0t}) + \beta_1 x_{1t} - h_{1t} - x_{1,t+1}] + \sum_{s=1}^{n-1} \lambda_{s+1,t} [\alpha_s x_{st} + \beta_{s+1} x_{s+1,t} - h_{s+1,t} - x_{s+1,t+1}] \}, \quad (6)$$

$$(a): \frac{\partial L}{\partial h_{st}} b^{-t} = U' f_s - \lambda_{st} \leq 0, \quad (7)$$

$$(b): h_{st} \geq 0, (c): h_{st} \frac{\partial L}{\partial h_{st}} b^{-t} = 0, \quad s = 1, \dots, n,$$

$$(a): \frac{\partial L}{\partial x_{s+1,t+1}} b^{-t} = b \lambda_{1,t+1} \varphi' \gamma_{s+1} + b \lambda_{s+1,t+1} \beta_{s+1} + b \lambda_{s+2,t+1} \alpha_{s+1} - \lambda_{s+1,t} \leq 0, \quad s = 0, \dots, n-1, \quad (8)$$

$$(b): x_{s+1,t+1} \geq 0, (c): \frac{\partial L}{\partial x_{s+1,t+1}} b^{-t} x_{s+1,t+1} = 0, \quad s = 0, \dots, n-1,$$

where $t = 0, 1, \dots$ and $\alpha_n \equiv 0$. Because the utility and recruitment functions are concave and other functions are linear, these conditions are sufficient for optimality given that the discrete analogue of the transversality condition in the Mangasarian (1966) sufficiency theorem is satisfied (Sydsaeter et al. 2008, p. 447). This holds for solutions converging to a steady state or stationary cycle. Numerical solutions will be computed by an interior point algorithm described by Byrd et al. (1999) and tested Wächter and Biegler (2006).

3 Two size classes

3.1 Steady state regimes

When $n=2$, the optimality conditions are

$$(a) : U'(H_t) f_s - \lambda_{st} \leq 0, \quad (9)$$

$$(b) : h_{st} \geq 0, (c) : h_{st} \frac{b^{-t} \partial L}{\partial h_{st}} = 0, \quad s = 1, 2,$$

$$(a) : b\lambda_{1,t+1}\varphi'(x_{0,t+1})\gamma_1 + b\lambda_{1,t+1}\beta_1 + b\lambda_{2,t+1}\alpha_1 - \lambda_{1t} \leq 0, \quad (10)$$

$$(b) : x_{1,t+1} \geq 0, (c) : x_{1,t+1} \frac{b^{-t}\partial L}{\partial x_{1,t+1}} = 0,$$

$$(a) : b\lambda_{1,t+1}\varphi'(x_{0,t+1})\gamma_2 + b\lambda_{2,t+1}\beta_2 - \lambda_{2t} \leq 0, \quad (11)$$

$$(b) : x_{2,t+1} \geq 0, (c) : x_{2,t+1} \frac{b^{-t}\partial L}{\partial x_{2,t+1}} = 0,$$

$$x_{1,t+1} = \varphi(\gamma_1 x_{1t} + \gamma_2 x_{2t}) + \beta_1 x_{1t} - h_{1t} \quad (12)$$

$$x_{2,t+1} = \alpha_1 x_{1t} + \beta_2 x_{2t} - h_{2t}. \quad (13)$$

Given a steady state the time subscripts can be cancelled. Equations (12) and (13) determine the admissible steady state levels of x_1 and x_2 and the possible solution regimes. By (12) any steady state satisfies $h_1 = \varphi - x_1(1 - \beta_1)$ implying the boundary: $h_1 = \varphi - x_1(1 - \beta_1) = 0$. At the (x_1, x_2) -plane $h_1 = 0$ defines x_2 as a convex function of x_1 (Figure 1). From (13) any steady state satisfies $h_2 = \alpha_1 x_1 - x_2(1 - \beta_2)$. Denote the boundary by $h_2 = \alpha_1 x_1 - x_2(1 - \beta_2) = 0$. A carrying capacity equilibrium with $x_1 > 0$, $x_2 > 0$ exists, if the slope of $h_1 = 0$ is below the slope of $h_2 = 0$ at the origin of the (x_1, x_2) -plane, i.e.

$$(A5) : \frac{1 - \beta_1 - \varphi'(0)\gamma_1}{\varphi'(0)\gamma_2} < \frac{\alpha_1}{1 - \beta_2}.$$

Denote this equilibrium by x_1^c, x_2^c . If $\partial h_1 / \partial x_1 = \varphi'(0)\gamma_1 - 1 + \beta_1 > 0$ the slope of $h_1 = 0$ is negative at the origin and the function intersects the x_1 -axis with some $\hat{x}_1 > 0$ (Figure 1).

At admissible steady states $h_1 \geq 0$ and $h_2 \geq 0$, i.e. the steady states exist between or on the lines $h_1 = 0$, $h_2 = 0$ but above or on the x_1 -axis. When $\hat{x}_1 > 0$ the population can survive even if all individuals entering size class 2 are harvested (at the end of every period) implying $x_2 = 0$ and $\alpha_1 x_1 = h_2$. Note that the states $0 < x_1 < \hat{x}_1$, $x_2 = 0$ require $h_1 > 0$, $h_2 > 0$. In addition to the carrying capacity level (with no harvest) Figure 1 shows the six different steady state solution regimes:

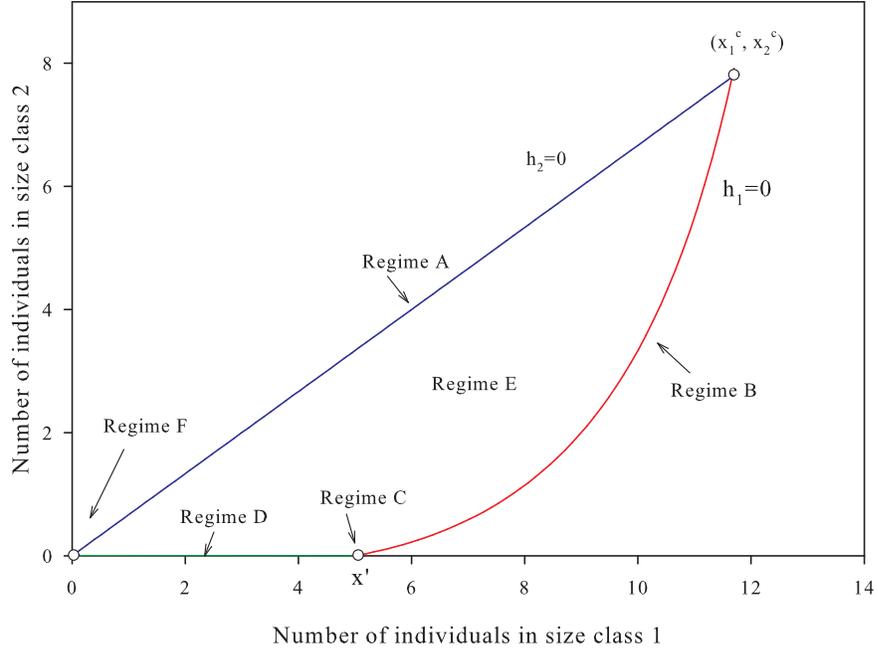


Fig. 1 Steady state regimes

$$\begin{aligned}
 A &: x_1 > 0, x_2 > 0, h_1 > 0, h_2 = 0, \\
 B &: x_1 > 0, x_2 > 0, h_1 = 0, h_2 > 0, \\
 C &: x_1 > 0, x_2 = 0, h_1 = 0, h_2 > 0, \\
 D &: x_1 > 0, x_2 = 0, h_1 > 0, h_2 > 0, \\
 E &: x_1 > 0, x_2 > 0, h_1 > 0, h_2 > 0, \\
 F &: x_1 = 0, x_2 = 0, h_1 = 0, h_2 = 0.
 \end{aligned} \tag{14}$$

Excluding regime F, the steady states satisfy $x_1 > 0$ and (10a) holds as an equality. In addition, either $h_1 = 0$ or $h_2 = 0$ or both $h_1 > 0$ and $h_2 > 0$. Define

$$\mu_1(x_1, x_2) \equiv f_1 \{1 - b [\varphi'(\gamma_1 x_1 + \gamma_2 x_2) \gamma_1 + \beta_1]\} - b \alpha_1 f_2. \tag{15}$$

Applying (9a,b,c) together with (10a) as an equality it follows that

$$\begin{aligned} (a) \mu_1 > 0 &\Rightarrow h_1 > 0, h_2 = 0, \\ (b) \mu_1 < 0 &\Rightarrow h_1 = 0, h_2 > 0, \\ (c) \mu_1 = 0 &\Rightarrow h_1 \geq 0, h_2 \geq 0, \end{aligned} \quad (16)$$

where in (16c) the case $h_1 = h_2 = 0$ is excluded. It is possible that μ_1 is positive or negative for all $x_1 \geq 0, x_2 \geq 0$ or that $\mu_1 = 0$ defines a decreasing straight line in the (x_1, x_2) -plane with slope $-\gamma_1/\gamma_2$ as shown in Figure 2a. Above the $\mu_1 = 0$ curve it holds that $\mu_1 > 0$ and $h_1 > 0$ and below the curve that $\mu_1 < 0$ and $h_2 > 0$.

Given $x_1 > 0$ and $x_2 > 0$ both (10a) and (11a) hold as equalities and imply

$$\mu_2(x_1, x_2) = (1 - b\beta_1) - b\varphi'(\gamma_1 x_1 + \gamma_2 x_2) \left(\gamma_1 + \frac{b\gamma_2 \alpha_1}{1 - b\beta_2} \right) = 0, \quad (17)$$

while for steady states with $x_1 > 0, x_2 = 0$ it must hold that

$$\mu_2 > 0. \quad (18)$$

Differentiation shows that $\mu_2(x_1, x_2) = 0$ is a straight line in (x_1, x_2) -plane with slope $-\gamma_1/\gamma_2$. Above (below) the line $\mu_2 > 0$ ($\mu_2 < 0$). Assumptions (A3-A5) imply that the locus of $\mu_2(x_1, x_2) = 0$ always exists below the population's carrying capacity level.

Any steady state with $x_1 > 0, x_2 > 0$ must satisfy (17), i.e. $\mu_2 = 0$. Given the locus of $\mu_1 = 0$ below the locus of $\mu_2 = 0$, (16a) implies that that $h_1 > 0$ and $h_2 = 0$, i.e. the optimal steady state exists in regime A and on the line $h_2 = 0$ (Figure 2a). Assume that the locus of $\mu_1 = 0$ exists above the locus of $\mu_2 = 0$ and that the latter exists above point $(\hat{x}_1, 0)$. By (16b) the optimal steady state satisfies $h_1 = 0$ and $h_2 > 0$, i.e. the optimal steady state exists in regime B and on line $h_1 = 0$ (Figure 2b).

If $\hat{x}_1 > 0$, the optimal steady state may also exist in regimes C or D. Given $\mu_1(\hat{x}_1, 0) < 0$ and $\mu_2(\hat{x}_1, 0) > 0$, conditions (16b) and (18) imply that the optimal steady state satisfies $h_1 = 0, h_2 > 0, x_1 = \hat{x}_1 > 0$ and $x_2 = 0$. This is regime C in Figure 2c. The other possibility is that $\mu_1(\hat{x}_1, 0) > 0$ and $\mu_2(\hat{x}_1, 0) > 0$, i.e. regime D (Figure 1d) and $h_1 > 0, h_2 > 0$. If the locus of $\mu_1 = 0$ coincides with the locus of $\mu_2 = 0$, the steady states exist in regime E, which is a continuum between curves $h_2 = 0$ and $h_1 = 0$ (Figure 2e). The findings so far can be summarized as

Proposition 1 *Given (A1-A5) and*

If $\mu_2(0, 0) < 0, \mu_1(x_1, x_2)|_{\mu_2(x_1, x_2)=0} > 0$, A is optimal.

If $\mu_2(\hat{x}_1, 0) < 0, \mu_1(x_1, x_2)|_{\mu_2(x_1, x_2)=0} < 0$, B is optimal.

If $\hat{x}_1 > 0, \mu_2(\hat{x}_1, 0) > 0, \mu_1(\hat{x}_1, 0) \leq 0$, C is optimal.

If $\hat{x}_1 > 0, \mu_1(\hat{x}_1, 0) > 0, \mu_1(0, 0) < 0, \mu_2(x_1, x_2)|_{\mu_1(x_1, x_2)=0} > 0$, D is optimal.

If $\mu_2(0, 0) < 0, \mu_1(x_1, x_2)|_{\mu_2(x_1, x_2)=0} = 0$, E is optimal.

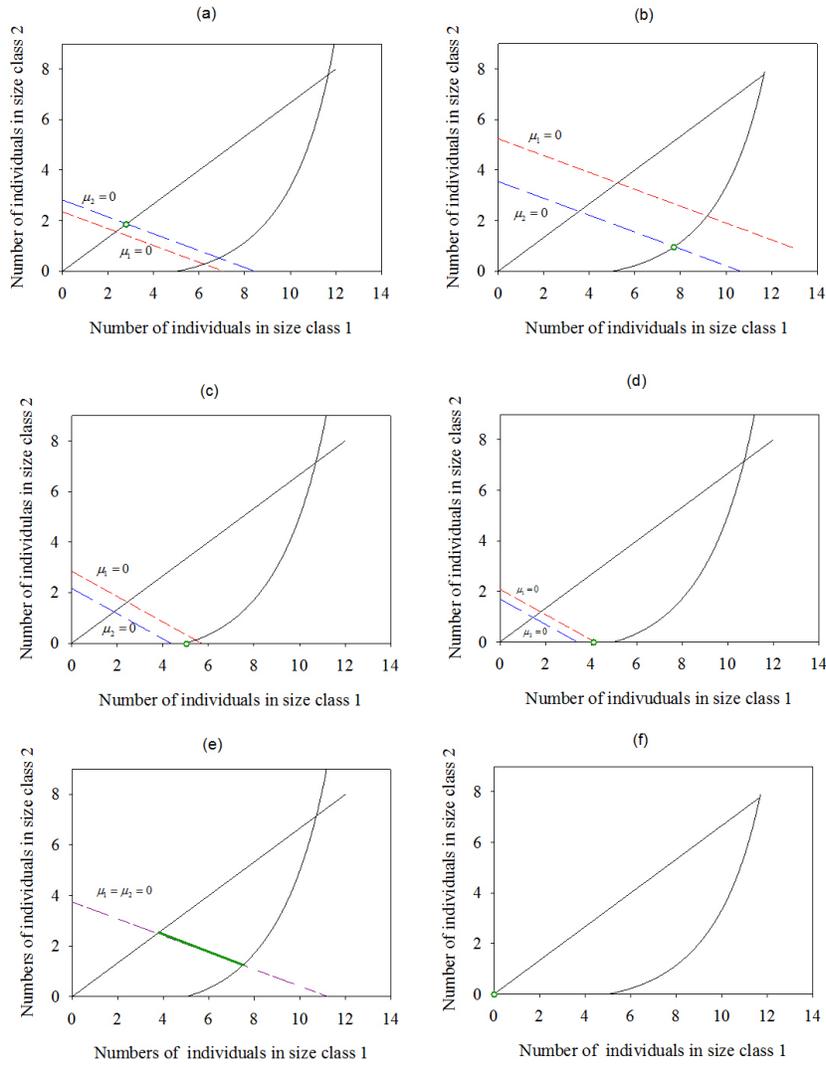


Fig. 2 Optimality of steady state regimes

3.2 Interpretations

Regime A ($x_1 > 0$, $x_2 > 0$, $h_1 > 0$, $h_2 = 0$) satisfies (from 10-13)

$$\begin{aligned}
 (a) : & \frac{f_1 [\varphi'(x_0) \gamma_1 - (1 - \beta_1)] + \alpha_1 f_2}{f_1} < r, \\
 (b) : & \varphi'(x_0) \left(\gamma_1 + \frac{b\alpha\gamma_2}{1-b\beta_2} \right) - (1 - \beta_1) = r, \\
 (c) : & h_1 = \varphi(x_0) - x_1 (1 - \beta_1),
 \end{aligned} \tag{19}$$

where $x_0 = \gamma_1 x_1 + \gamma_2 \alpha x_1 / (1 - \beta_2)$. The derivative of the LHS of (19b) w.r.t. x_1 is negative, i.e. the steady state, is unique. Given the level of x_1 , equation (19c) determines h_1 . The LHS of (19a) is the marginal rate of return when decreasing h_1 in order to harvest one unit of x_2 . It is lower than the interest rate, i.e. it is optimal to harvest class 1 instead of class 2. In addition to the return in terms of h_2 ($\alpha_1 f_2$), decreasing h_1 increases h_1 of the next period by increasing the recruitment net of the fraction that dies or moves to class 2. Equation (19c) defines a sustainable harvest and is concave in x_1 and zero with $x_1 = 0$ or x_1 sufficiently large. Maximizing h_1 using (19c) results in the LHS of (19b) if $b = 1$. Increasing x_1 marginally increases the net output of x_1 by increasing the recruitment net of the fraction not remaining in class 1, i.e. by $\varphi' \gamma_1 - (1 - \beta_1)$. In addition, an increase in x_1 causes an increase in x_2 , which after a delay, increases the level of x_1 and h_1 . Delays in term $\frac{b\alpha\gamma_2}{1-b\beta_2}$ in the LHS of (19b) are discounted (over infinite periods). Thus by (19b) the rate of interest equals the present value of the marginal surplus production of the size-structured population. Differentiation of (19b) shows that the levels of x_0, x_1, x_2 and h_1 decrease with the discount rate.

The inequality sign in (19a) is reversed in regime B, and it is thus worth saving all individuals in class 1 and only harvesting class 2. The unique x_1 and x_2 levels are given by $x_1 = \varphi(x_0) + \beta_1 x_1$ and (19b), and the harvest by $h_2 = \alpha x_1 - x_2 (1 - \beta_2)$. When regime C is optimal, the LHS of (19a) is higher and the LHS of (19b) is lower than the interest rate and $x_0 = \gamma_1 \hat{x}_1$. Although it is optimal to save all individuals in class 1 and harvest them from class 2, the discounted marginal surplus production is too low for retaining class 2 for reproduction. Finally, in regime D the latter condition still holds, but the marginal rate of return of harvesting all individuals from class 2 is too low, and it is therefore optimal to harvest a fraction of class 1. Optimal x_1 is given by the equality of the LHS of (19a) and the discount rate and the harvests by $x_1 = \varphi(x_0) + \beta_1 x_1 - h_1$ and $h_2 = \alpha_1 x_1$.

When the optimal steady state is in regime C, decreasing the discount factor decreases the LHS of (19a) and (19b), implying that an increase in interest rate may cause a switch from regime C to regime D. Decreasing the discount factor in regime D decreases the steady state level of x_1 , implying lower x_1, h_1 and h_2 . These comparative static results are intuitive: if an increase in interest rate has an effect, it causes a lower steady-state population size and the harvesting of individuals from (size or age) class 1 rather than class 2.

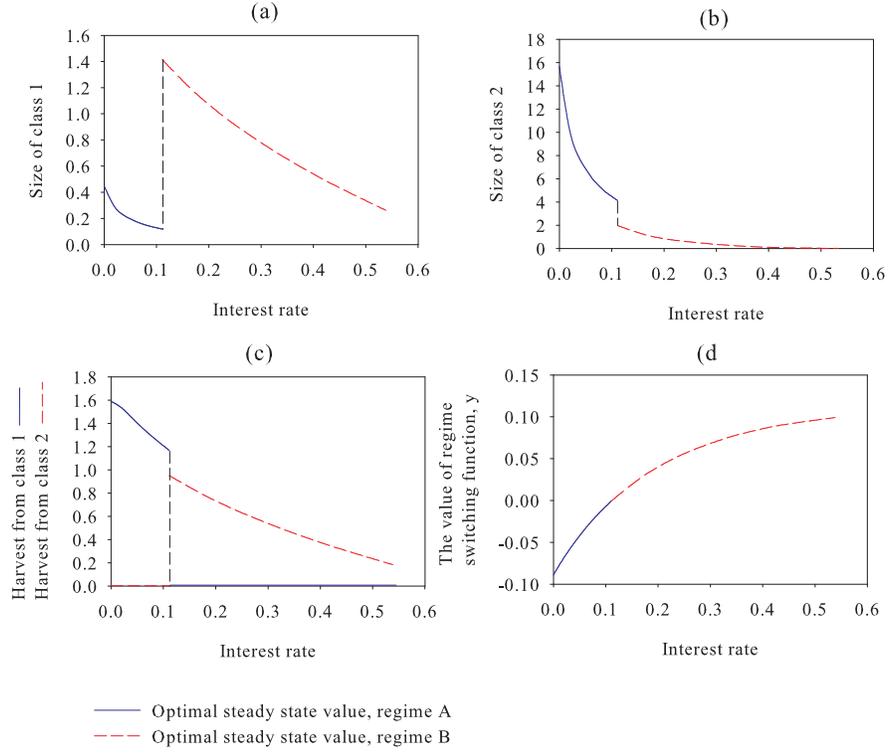


Fig. 3 Optimal steady state and the case where higher interest rate implies a switch of harvest from class 1 to class 2 Note : $\varphi = x_0/(1+0.4x_0)$, $\gamma_1 = 1$, $\gamma_2 = 0.6$, $\alpha = 0.7$, $\beta_1 = 0.1$, $\beta_2 = 0.98$, $f_1 = 1$, $f_2 = 1.1$.

Equation (19b) holds for regimes *A* and *B*. It yields x_0 as an increasing function of b , i.e. $x_0 = x_0(b)$, $x'_0(b) > 0$. Thus, the lower the interest rate, the lower is the steady state number of recruits in these regimes. Equation (19a) and its derivative w.r.t. b can be written as

$$\begin{aligned}
 y &\equiv f_1 [b\varphi'(x_0)\gamma_1 + b\beta_1 - 1] + bf_2\alpha, \\
 \partial y/\partial b &= f_1 (\varphi'\gamma_1 + b\varphi''x'_0\gamma_1 + \beta_1) + f_2\alpha \\
 &= \frac{f_1\gamma_1 [\alpha\gamma_2 (b^2\beta_1\beta_2 - 1) - \beta_1\gamma_1 (b\beta_2 - 1)^2]}{[\alpha b\gamma_2 - \gamma_1 (b\beta_2 - 1)]^2} + \alpha f_2 + \beta_1 f_1,
 \end{aligned}$$

where the last line is obtained by (19b). If $\gamma_1 = 0$ or low, $\partial y/\partial b > 0$ implies that increasing the interest rate (decreasing the discount factor) may result in a switch from regime *B* to regime *A*, but not *vice versa*. Thus, in these cases a higher interest rate implies harvesting from class 1, where individuals are younger and/or smaller. However, when $\gamma_1 > 0$, the sign of $\partial y/\partial b$ is indeterminate. If it is negative, a decrease in the discount factor may cause a switch from regime *A* to regime *B*, i.e. a switch to harvesting older or larger individuals under a higher interest rate. An example is shown in Figure 3. When the interest rate is below $r = 0.111$, the LHS of (19a) is negative, regime *A* and harvesting only from class 1 are optimal. Increasing the interest rate above this level implies that (19a) becomes positive, i.e. regime *B* is optimal and harvesting is only optimal from class 2.

The intuition is that when higher interest rate decreases the number of offspring ($x'_0(b) > 0$), the marginal rate of return from saving class 1 individuals to class 2 increases and this effect may dominate the “normal” effects of higher discount rate.

The next question concerns the possible non-existence of steady states with strictly positive population size and harvesting:

Proposition 2 *Regime F ($x_i = h_i = 0$, $i = 1, 2$) is the optimal steady state if and only if $\mu_2(0, 0) \geq 0$ and i) $1 - \beta_1 - \varphi'(0)\gamma_1 > 0$ or ii) $\mu_1(0, 0) \geq 0$. Proof: Appendix 1.*

Condition $\mu_2(0, 0) \geq 0$ is equivalent to the LHS of (19b) being lower than the interest rate, even when both x_1 and x_2 are zero. Thus, $x_2 > 0$ cannot be optimal. Yet this is not sufficient for $x_1 = 0$ and regime *F* to be optimal. It must either hold that regimes $x_1 > 0$, $x_2 = 0$ are not admissible ($\hat{x}_1 = 0$), or if admissible, they must not be optimal. The former case follows if $1 - \beta_1 - \varphi'(0)\gamma_1 > 0$, and the latter if $\mu_1(0, 0) \geq 0$, i.e. if the LHS of (19a) is always lower than the interest rate. Note that in the case where regime *D* is always non-optimal (e.g. if $f_1 = 0$), the solution will remain in regime *C* even if $r \rightarrow \infty$.

The size-structured population model can be used to develop an equilibrium biomass model. Assume that the population biomass is given as $X = f_1x_1 + f_2x_2$. It is not possible to optimize harvesting between age classes within the biomass framework. Firstly assume that only size class 2 is harvested, implying $h_2 = \alpha x_1 - x_2(1 - \beta_2)$ and $\varphi(\gamma_1x_1 + \gamma_2x_2) - x_1(1 - \beta_1) = 0$. The last equation and the biomass equation can be used to obtain both x_1 and x_2 as functions of population biomass X . The remaining function for h_2 yields harvest as a function of population biomass. Similarly, if only size class 1 is harvested $h_1 = \varphi(\gamma_1x_1 + \gamma_2x_2) - x_1(1 - \beta_1)$ and $\alpha x_1 - x_2(1 - \beta_2) = 0$, it is once again possible to obtain the equilibrium harvest h_1 as a function of population biomass X . Denote these equilibrium harvests as $h_s = F_s(X)$, $s = 1, 2$. The optimal steady state condition within the biomass model is $F'_s(X) = r$, $s = 1, 2$. Figures 4a,b show numerical examples of these steady states and the optimal steady states obtained by the size-structured model. The maximum sustainable harvest is obtained by harvesting size class 2 only (Figure 4a). Thus, the steady states of the size-class and biomass models are equal when $r = 0$ and

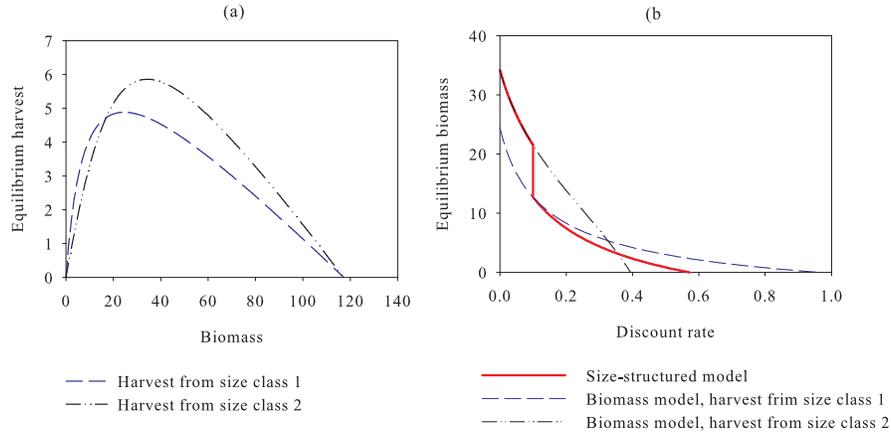


Fig. 4 Comparison of steady states between the size-structured and the biomass model Note : $\varphi = 0.9 \gamma_2 x_2 / (1 + 0.1 \gamma_2 x_2)$, $\gamma_1 = 0$, $\gamma_2 = 2$, $\alpha = 0.4$, $\beta_1 = 0.5$, $\beta_2 = 0.4$, $f_1 = 1$, $f_2 = 1.5$.

$h_1 = 0$, $h_2 > 0$ in the biomass model (Figure 4b). When $0 < r \leq 0.1$, the equilibrium biomass in the size-class model is slightly lower than in the biomass model. When $r = 0.1$, the equilibrium continuum is optimal in the size-class model (regime *E*) and when $0.1 < r < 0.577$, it is optimal to harvest only from size class 1 (regime *A*). As shown, the biomass model based on $h_1 = 0$, $h_2 > 0$ yields "optimal extinction" when $r > 0.39$ while the critical discount rate in the size-structured model is 0.578. The comparison of the two models becomes different if $h_1 > 0$, $h_2 = 0$ in the biomass model. In this case the biomass model yields a lower MSY steady state, but the biomass becomes higher when $r > 0.1$. In addition, the "optimal extinction discount rate" in the biomass model is now higher compared to the size-structured model.

3.3 Discussion

In their main theorems Reed (1980) and Getz (1980) state that assuming the maximization of sustainable yield, either a single age class or two age classes are harvested. In the latter case, the harvest is partial for the younger class and total for the older class. Reed's theorem (1980) explicitly states that in the former case where only one age class is harvested, the harvest may be partial or total. Here only a single age class is harvested in regimes *A*, *B* and *C*, with the harvest being partial in regimes *A* and *B* and total in regime *C*. Regime *D* is a case where two classes are harvested, the younger one partially and the older one totally. However, in addition to these regimes, regime *E* has two partially-harvested classes. This is not covered in the theorems by Getz (1980) and Reed (1980). They study MSY steady states

and the age-structured model, i.e. the special case $b = 1$, $\beta_1 = \beta_2 = 0$. However, this difference is not essential, and it is possible to obtain regime E as an optimal solution in an age-structured model with zero interest rate. For example, if

$$\begin{aligned}\varphi &= Ax_0 / (1 + Bx_0), \quad A = 1, \quad B = 1/5, \\ \gamma_1 &= 1, \gamma_2 = 2, \quad \alpha = 7/10, \quad f_2 = 5f_1/4, \quad b = 1,\end{aligned}$$

both $\mu_1 = 0$ and $\mu_2 = 0$ imply $x_2 = \sqrt{10} - 5/2 - x_1/10$, i.e. regime E is optimal.

Clark (1976) analyses the famous dynamic pool or cohort model by Beverton and Holt (1957). Their model coincides with the age-structured special case studied here assuming interest rate is zero, recruitment is an exogenous constant and the analysis is restricted to steady states. Clark presents the result that given non-selective harvesting gear, pulse fishing is optimal, instead of continuous harvesting as suggested by Beverton and Holt (1957). The period length between pulses is solved by an optimal rotation solution for the Faustmann (1849) formula. In his review, Wilen (1985) suggests this to be incorrect, because nothing similar to the land area constraint exists in the given problem and thus the problem must be viewed as a Fisherian "single-shot" model. However, the argument by Wilen (1985) appears to be incorrect: the assumption of non-selective fishing gear has exactly the same effect as the land area constraint in the rotation model (Tahvonen 2011b).

Similar question related to the connection with the Faustmann model can be asked here. Assuming exogenous and constant recruitment (and the age class structure), equation (19a) can be written as $f_1 - bf_2\alpha_1 \geq 0$. This is simply the optimality condition for harvesting age class 1 in a discrete-time two-period Fisherian "single shot" optimal timing problem. Given endogenous recruitment, (19a) can be written as $f_1(1 - b\varphi'\gamma_1) - bf_2\alpha_1 \geq 0$. As adding endogenous recruitment decreases the LHS of this equation (increases the LHS of 19a), it implies that cohorts should be harvested after they reach their maximum (discounted) biomass. This result is a consequence of the fact that saving individuals to be harvested from older age classes increases recruitment. Theorem 2 in Reed (1980) states the same result with zero interest rate. The land area constraint in the Faustmann model implies that cohorts should be harvested sooner than at the age of maximum (discounted) biomass. Together this shows that the model studied here does not include any Faustmann-type rotation structure.

Reed (1980) expects that introducing discounting would decrease the age of the harvested cohort. Our result shows that due to endogenous recruitment this need not be the case (Figures 3a-d).

4 Stability of steady states

The steady state stability analysis calls for an analysis of the four non-linear difference equations (conditions (9)-(13)). However, some special cases where the opti-

mal solution can be found in closed form exist. Denote the steady state harvests in regimes A and B by h_1 and h_2 respectively.

Proposition 3 *Given (A1-A5), $\mu_2(\hat{x}_1, 0) < 0$, $\gamma_1 = \gamma_2$, $\alpha + \beta_1 = \beta_2$ and $\mu_2(x_{10}, x_{20}) = 0$, the optimal solution is a) $h_{1t} = h_1$, $h_{2t} = 0$, $t = 0, 1, \dots$, if $\mu_1(x_{10}, x_{20}) > 0$, and b) $h_{2t} = h_2$, $h_{1t} = 0$, $t = 0, 1, \dots$, if $\mu_1(x_{10}, x_{20}) < 0$.*

Proof: Case a): Recall that the slope of $\mu_2(x_1, x_2) = 0$ in the (x_1, x_2) -plane is $-\gamma_2/\gamma_1$. Denote this linear function by $x_2 = \eta - x_1$, where η is a constant and positive by $\mu_2(\hat{x}_1, 0) < 0$. When $\mu_1(x_{10}, x_{20}) > 0$, the steady state satisfies $x_1 = \varphi + \beta_1 x_1 - h_1$, $x_2 = \alpha x_1 + \beta_2 x_2$ and $x_2 = \eta - x_1$. This yields $h_1 = \varphi - \eta(1 - \beta_2)$. Given $\mu_2(x_{10}, x_{20}) = 0$, it follows that $x_{1,t+1} = \varphi(\eta) + \beta_1 x_{1t} - [\varphi(\eta) - \eta(1 - \beta_2)]$, and $x_{2,t+1} = \alpha x_{1t} + \beta_2 x_{2t}$ for $t = 0$. Thus $x_{11} + x_{21} = \eta$ and then by induction $x_{1,t+1} + x_{2,t+1} = \eta$ for $t = 1, 2, \dots$. In addition, $x_{1t} \rightarrow \varphi(\eta)(1 - \beta_2)/(1 - \beta_1)$ and $x_{2t} \rightarrow \alpha\eta(1 - \beta_1)$, as $t \rightarrow \infty$ since $0 < \beta_1 < 1$. The constants $\lambda_1 = U'f_1$ and $\lambda_2 = f_1 U'[1 - b\varphi'(\eta) - b\beta_1]/(b\alpha)$ solve (9)-(11) by $\mu_2(x_{10}, x_{20}) = 0$ and $\mu_1(x_{10}, x_{20}) > 0$, implying that the solution is optimal. Case b) is analogous with case a). ■

In the case of Proposition 3, the size classes are symmetric in the sense that fecundities and natural mortalities coincide, although the usable size of harvested individuals may differ. The symmetry property, together with specific initial states, implies that harvest and recruitment levels are constant over time. Numerical examples of these solutions are given in Figures 5a and b, by the solid straight lines.

When applying conditions (9)-(13) more generally for interior solutions, solutions in regime A are determined by the system:

$$x_{1,t+1} = \varphi(\gamma_1 x_{1t} + \gamma_2 x_{2t}) + \beta_1 x_{1t} - h_1(\lambda_{1t}), \quad (20a)$$

$$x_{2,t+1} = \alpha_1 x_{1t} + \beta_2 x_{2t}, \quad (20b)$$

$$\lambda_{1,t+1} = \frac{\lambda_{2t} \alpha_1 - \lambda_{1t} \beta_2}{b\varphi'(x_{1,t+1}, x_{2,t+1}, \lambda_{1,t+1})(\alpha_1 \gamma_2 - \beta_2 \gamma_1) - b\beta_1 \beta_2}, \quad (20c)$$

$$\lambda_{2,t+1} = \frac{\varphi'(x_{1,t+1}, x_{2,t+1}, \lambda_{1,t+1})(\lambda_{1t} \gamma_2 - \lambda_{2t} \gamma_1) - \lambda_{2t} \beta_1}{b\varphi'(x_{1,t+1}, x_{2,t+1}, \lambda_{1,t+1})(\alpha_1 \gamma_2 - \beta_2 \gamma_1) - b\beta_1 \beta_2}, \quad (20d)$$

$$\begin{aligned} \varphi'(x_{1,t+1}, x_{2,t+1}, \lambda_{1,t+1}) = \\ \varphi'\{\gamma_1 [\varphi(\gamma_1 x_{1t} + \gamma_2 x_{2t}) + \beta_1 x_{1t} - h_1(\lambda_{1t})] + \gamma_2 (\alpha_1 x_{1t} + \beta_2 x_{2t})\}, \end{aligned} \quad (20e)$$

$$h'_2(\lambda_{1t}) = 1/(U''f_1), \quad (20f)$$

and in regime B by (20c), (20d) and

$$x_{1,t+1} = \varphi(\gamma_1 x_{1t} + \gamma_2 x_{2t}) + \beta_1 x_{1t}, \quad (21a)$$

$$x_{2,t+1} = \alpha_1 x_{1t} + \beta_2 x_{2t} - h_{2t}(\lambda_{2t}), \quad (21b)$$

$$\begin{aligned} \varphi'(x_{1,t+1}, x_{2,t+1}, \lambda_{2,t+1}) = \\ \varphi' \{ \gamma_1 [\varphi(\gamma_1 x_{1t} + \gamma_2 x_{2t}) + \beta_1 x_{1t}] + \gamma_2 [\alpha_1 x_{1t} + \beta_2 x_{2t} - h_{2t}(\lambda_{2t})] \}, \end{aligned} \quad (21c)$$

$$h'_2(\lambda_{2t}) = 1 / (U'' f_2). \quad (21d)$$

Proposition 4 *Given the conditions of Proposition 3 and $U'' < 0$, but excluding the initial state restrictions, the optimal equilibria in regimes A and B are local saddle points, i.e. two characteristic roots have absolute values below 1 and two above 1.*

Proof: For regimes A and B, computing the Jacobian matrix and the associated characteristic equation yields the fourth order polynomial

$$\Omega_s(r) = \frac{(\beta_1 - r) [Q_s r + (1 - r)(br - 1)] (b\beta_1 r - 1)}{b^2 \beta_1},$$

where $Q_s = \lambda_s b^2 \varphi'' h'$, $s = 1, 2$. The characteristic roots are: $r_1 = \beta_1$, $r_2 = 1 / (b\beta_1)$,

$$r_{3,4} = \left(\sqrt{Q_s^2 + 2Q_s(b+1) + b^2 - 2b + 1} \pm (Q_s + b + 1) \right) / (2b), \quad s = 1, 2.$$

Obviously $0 < r_1 < 1$ and $1 < r_2$. When $Q_s = 0$, $s = 1, 2$ the value of r_{s3} ($= \sqrt{\bullet} + Q_s + b + 1$) equals b^{-1} and the value of r_{s4} ($= \sqrt{\bullet} - Q_s - b - 1$) equals 1. Since $\partial r_{s3} / \partial Q_s > 0$ and $\partial r_{s4} / \partial Q_s < 0$ and $\lim_{Q_s \rightarrow \infty} r_{s4} = 0$ for both $s = 1, 2$ the steady states are saddle points where two roots have absolute values above 1 and two roots have absolute values below 1. ■

Examples under the assumptions in Proposition 4 are shown by black dashed lines in Figure 5. The next result does not require symmetry, but is restricted to zero discounting and cases where the Jacobian matrix for system (20a-f) can be evaluated at the steady state:

Proposition 5 *Given (A1-A5), $b=1$, $U'' < 0$ and $\tau_2 \equiv (\beta_2 - 1)(\alpha_1 \gamma_2 - \beta_2 \gamma_1) + \alpha_1 \gamma_2 \beta_1 \neq 0$, the steady state in regime A is a (local) saddle point, i.e. two characteristic roots have absolute values below 1 and two above 1. Proof: Appendix 2.*

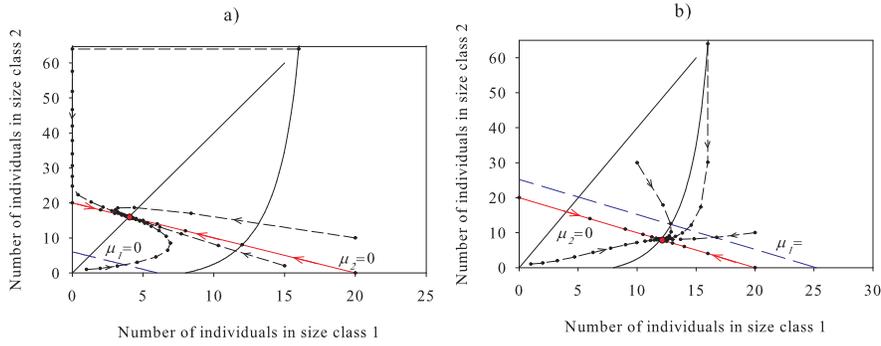


Fig. 5 Optimal solutions under the assumptions in Propositions 3 and 4. Note : $\varphi = \frac{0.9x_{0t}}{1+0.1x_{0t}}$, $x_{0t} = x_{1t} + x_{2t}$, $b = 1$, $U = H_t^{0.9}$, $\alpha_1 = 0.4$, $\beta_1 = 0.5$, $\beta_2 = 0.9$, $f_1 = 1$, $f_2 = 0.5$ in a, $f_2 = 2$ in b. Equilibrium in a : $x_1 = 4$, $x_2 = 16$, $h_1 = 4$, $h_2 = 0$ and in b $x_1 = 12$, $x_2 = 8$, $h_2 = 4$. Roots of the characteristic equation in a : $r_1 = \frac{1}{2}$, $r_2 = 2$, $r_3 = \frac{5}{3}$, $r_4 = \frac{5}{3}$

The zero discount rate assumption in Proposition 5 is far from necessary for the steady state properties stated in the proposition. However, when the discount rate is high enough, the stability properties may change and three of the roots may become unstable.

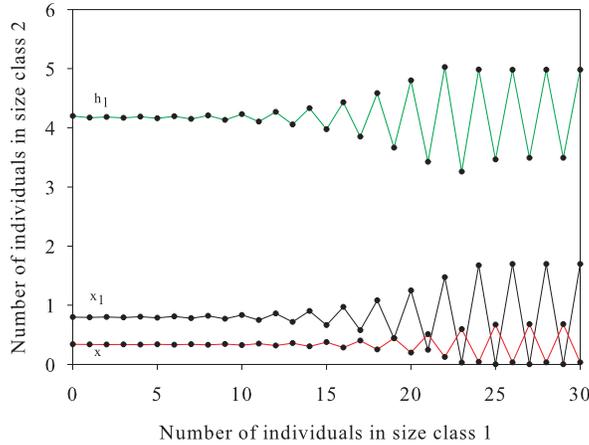


Fig. 6 Optimal stationary cycle. Note : $\varphi = \frac{0.9x_{0t}}{1+0.1x_{0t}}$, $x_{0t} = 5x_{1t} + 20x_{2t}$, $b = 0.45$, $U = H_t^{0.99}$, $\alpha_1 = 0.4$, $\beta_1 = 0.4$, $\beta_2 = 0.05$, $f_1 = 5$, $f_2 = 1$. Equilibrium : $x_1 = 0.80$, $x_2 = 0.34$, $h_1 = 4.2$, $h_2 = 0$. Roots : $r_1 = -1.70$, $r_2 = -1.31$, $r_3 = 0.01$, $r_4 = 206.55$.

The cyclical solution is depicted in Figure 6. The initial state is close to the steady state, but because of a small deviation the solution diverges and approaches a stationary cycle.

When $\tau_2 = 0$, the denominators of (20c and d) approach zero when the solution approaches the steady states. Since the Jacobian matrix becomes indeterminate at the steady state, the stability properties cannot be analysed by the linearization method. However, numerical computation suggests that optimal solutions are perfectly continuous around $\tau_2 = 0$. With the age-structured model (i.e. $\beta_1 = 0$), this special case implies that the difference equation system collapses into three equations, and the steady-state stability properties can be analysed using the ordinary linearization method:

Proposition 6 *Assume (A1)-(A5), $b=1$, $U'' < 0$ and $\beta_1 = 0$. If $\alpha_1\gamma_2 - \beta_2\gamma_1 \neq 0$, the steady state in regime A is a local saddle point and two of the characteristic roots have absolute values above 1 and two have values below 1. If $\alpha_1\gamma_2 - \beta_2\gamma_1 = 0$, optimal solutions are determined by three difference equations with a steady state, where the absolute values of two characteristic roots are below 1 and one above 1.*

Proof: When $\alpha_1\gamma_2 - \beta_2\gamma_1 \neq 0$, the structure of characteristic roots follows from Proposition 5. When $\alpha_1\gamma_2 - \beta_2\gamma_1 = 0$, optimal solutions are defined by (20e-f) and

$$x_{1,t+1} = \varphi(\gamma_1 x_{1t} + \gamma_2 x_{2t}) - h_1(\lambda_{1t}), \quad x_{2,t+1} = \alpha_1 x_{1t} + \beta_2 x_{2t},$$

$$\lambda_{1,t+1} = \frac{\lambda_{1t}}{\beta_2 + \varphi'(x_{1t}, x_{2t}, \lambda_{1t}) \gamma_1}, \quad \lambda_{2t} = \frac{\lambda_{1t} \gamma_2}{\gamma_1}.$$

The Jacobian matrix of this system evaluated at the steady state has two characteristic roots with absolute values below 1 and one above 1. ■

Propositions 5 and 6 assume zero discounting. However, ordinary saddle point properties can be shown to hold over a wide range of positive discount rates:

Proposition 7 *Given (A1-A5), $U'' < 0$, $\gamma_1 = 0$ and $\frac{1}{\beta_1 + \beta_2 + 1} \leq b < \frac{1}{\beta_1 + \beta_2}$ the steady state in regime A is a (local) saddle point, i.e. two characteristic roots have absolute values below 1 and two above 1. Proof: Appendix 2.*

Propositions 5, 6 and 7 show stability properties for the steady states of regime A. Identical propositions can also be given for the stability properties of regime B steady states, with only some minor changes in the proofs. The stability properties of regime C and D are given as:

Proposition 8 *Given (A1-A5) and $U'' < 0$, the steady state in regime C is locally stable and the steady state in regime D is a local saddle point. Proof, Appendix 4.*

Note that given the steady state solution exists in these regimes, the qualitative stability properties are independent of the discount rate. In regime C the optimal harvest is simply $h_{1t} = \alpha x_{1t}$, implying that the solution is unique despite the steady state being locally stable. Given the solution is already in this regime at the initial state, it is independent of changes in the discount rate and utility function.

Earlier studies of this model have not analysed the steady-state stability properties. Reed (1980) writes that such analysis appears to be difficult, but if initial numbers of individuals exceed the steady state levels in all age classes, a constant escapement policy where all age classes are harvested down to their steady state values "would certainly be an acceptable policy". However, even with a linear objective function such a solution is, in general, non-optimal. The reason is simply that if it is optimal to only harvest one age class at a steady state, a similar regime is optimal also in the vicinity of the steady state. Another simple example of the non-optimality of constant escapement is regime C, where the optimal solution is $h_1 = 0$, $h_2 = \alpha_1 x_{1t}$ in the vicinity of the steady state, implying that the steady state is approached asymptotically.

5 Any number of size classes

A natural extension of the two classes specification is to assume that the optimal steady state harvest is targeted to some size class m such that $1 < m$ and $m + 1 < n$, i.e. the harvest targets interior size classes. Thus, suppose: $x_s > 0$, $s = 1, \dots, m$, $x_s = 0$, $s = m + 1, \dots, n$, and either $h_s = 0$, $s = 1, \dots, m$, $h_{m+1} = \alpha_m x_m > 0$, $h_s = 0$, $s = m + 1, \dots, n$ or $h_m = \alpha_{m-1} x_{m-1} - (1 - \beta_m) x_m > 0$, $h_{m+1} = \alpha_m x_m > 0$. The former case is an extension of regime C and the latter an extension of regime D. The steady state satisfies

$$x_s = \mu_s x_{s-1}, \mu_s = \alpha_{s-1} / (1 - \beta_s), s = 2, \dots, m - 1,$$

$$x_m = \alpha_{m-1} x_{m-1} / (1 - \beta_m) - h_m / (1 - \beta_m) = \mu_m x_{m-1} - h_m / (1 - \beta_m),$$

$$x_s = l_s x_1, s = 1, \dots, m - 1, x_m = l_m x_1 - h_m / (1 - \beta_m),$$

$$x_0 = x_1 \sum_{s=1}^m \gamma_s l_s - \gamma_m h_m / (1 - \beta_m) \equiv R_0^m x_1 - \gamma_m h_m / (1 - \beta_m),$$

$$\text{where } l_s = \prod_{i=2}^s \mu_i, \quad s = 1, \dots, m, \quad l_1 = \prod_{i=2}^1 \mu_i \equiv 1 \quad \text{and} \quad R_0^m = \sum_{s=1}^m \gamma_s l_s,$$

implying that

$$x_1 = \varphi [R_0^m x_1 - \gamma_m h_m / (1 - \beta_m)] + \beta_1 x_1, \quad (22)$$

which directly yields equilibrium x_1 if $h_m = 0$. Note that R_0^m equals the expected steady state number of offspring individuals produce over their lifetime, and is called the net reproductive value (Fisher 1930, Samuelson 1977).

At the steady state $x_s > 0$, $s = 1, \dots, m$ and the KKT conditions (8) can be written as

$$\lambda_{s+1} + \lambda_s (b\beta_s - 1) / (b\alpha_s) = -\lambda_1 b\varphi' \gamma_s / (b\alpha_s), \quad s = 1, \dots, m, \quad (23)$$

where $\lambda_{m+1} = U' f_{m+1}$ and, if $h_m > 0$ in addition $\lambda_m \geq U' f_m$. Equation (23) is a linear non-autonomous difference equation for λ_s with $\lambda_{m+1} = U' f_{m+1}$ as the boundary condition. It can be solved iteratively starting from $s = m$ and proceeding toward λ_2 . This yields

$$\lambda_s = \lambda_1 \Psi_{1s} + \Psi_{2s} U' f_{m+1}, \quad s = 2, \dots, m+1, \quad (24)$$

$$\text{where } \Psi_{1s} = \sum_{j=s}^m \sigma_j \prod_{k=s}^{j-1} \eta_k, \quad \Psi_{2s} = \prod_{i=s}^m \eta_i, \quad s = 2, \dots, m+1$$

$$\sigma_j = \frac{b\varphi' \gamma_j}{1 - b\beta_j}, \quad \eta_i = \frac{b\alpha_i}{1 - b\beta_i}, \quad j, i = s, \dots, m+1.$$

Finally, solution (24) for λ_2 and (8) for $x_1 > 0$ yields

$$\lambda_1 = \frac{b\alpha_1 \Psi_{22} U' f_{m+1}}{1 - b\varphi' \gamma_1 - b\beta_1 - b\alpha_1 \Psi_{12}}. \quad (25)$$

In addition, the optimal solution must satisfy conditions (7a,b), i.e. $U' f_s \leq \lambda_s$, $s = 1, \dots, m$. Applying solutions (25) and (24) for λ_s , $s = 1, \dots, m$ yields:

$$\left(\frac{\alpha_1 \Psi_{22} \Psi_{1s}}{1 - b\varphi' \gamma_1 - b\beta_1 - b\alpha_1 \Psi_{12}} + b^{-1} \Psi_{2s} \right) \frac{f_{m+1}}{f_s} - 1 \geq r, \quad s = 1, \dots, m, \quad \text{where } \Psi_{21} = 0. \quad (26)$$

When $h_m > 0$ equation (26) for $s = m$ holds as an equality, and it with (22) determines h_m and x_m . For size classes $s = m+1, \dots, n$ it must hold that $U' f_s - \lambda_s \leq 0$ and $\partial L / \partial x_{s,t+1} \leq 0$. Setting $U' f_s = \lambda_s$, $s = m+1, \dots, n$ yields conditions (8) in the form

$$\frac{\varphi' \gamma_s b \alpha_1 \Psi_{22} f_{m+1}}{(1 - b \varphi' \gamma_1 - b \beta_1 - b \alpha_1 \Psi_{12}) f_s} + \beta_s + \frac{\alpha_s f_{s+1}}{f_s} - 1 \leq r, \quad s = m+1, \dots, n, \quad \text{where } \alpha_n \equiv 0. \quad (27)$$

6 Interpretations

Conditions (26) state that saving any individual from classes $s = 1, \dots, m$ to be harvested as a size class $m+1$ individual is an investment with a marginal rate of return higher or at least equal to the discount rate. This equation is a generalization of (19a). Assuming constant recruitment ($\varphi' = 0$) implies that the first LHS quotient of (26) is zero, and in the case of the age-structured specification ($\beta_s = 0, s = 1, \dots, n$) the condition collapses to

$$b^s f_s \prod_{s=1}^{m-1} \alpha_s \leq b^{m-1} f_{m+1} \prod_{s=1}^m \alpha_s, \quad s = 1, \dots, m, \quad (28)$$

i.e. to the discrete-time Fisherian "single shot" optimality condition. Given $\varphi' > 0$, the first LHS quotient of (26) is positive (by 25 and 7), implying that it is never optimal to harvest a cohort (at the steady state) before it reaches the maximum discounted biomass level. The size-structured case generalizes this set-up and the outcome is similar. Conditions (27) in turn state that given size classes $s = m+1, \dots, n-1$, saving an individual from size class s to be harvested as a size class $s+1$ individual is an investment with a marginal rate of return lower than the discount rate.

In his analysis on multiple cohorts/selective gear and exogenous recruitment Clark (1990, p. 301) obtains continuous time analogue of equation (28) and writes that including recruitment that depends on population level would lead to severe theoretical difficulties. The equations (26) and (27) represent solutions to such extension in discrete time.

7 On steady-state stability

In the vicinity of the steady state in regime C , the solution is defined as

$$x_{1,t+1} = \varphi(x_0) + \beta_1 x_1, \quad x_{s,t+1} = \alpha_{s-1} x_{s-1,t} + \beta_s x_s, \quad s = 1, \dots, m, \quad h_{m+1,t} = \alpha_m x_{m,t}.$$

This solution is optimal within the region of the state space where conditions (7) and (8) are satisfied, and it is not optimal to harvest other size classes besides $m+1$. Such a region can be guaranteed to exist, by assuming that $f_s, s = 1, \dots, n, s \neq m+1$ are low enough. Given this solution regime the system of state variables and conditions (7) and (8) are separate in the sense that state variable development determines the

development of the Lagrange multipliers, but no feedback from the Lagrange multipliers to optimal harvesting, i.e. to the level of $h_{m+1,t}$ exist. Thus, it is possible to study the local stability of the steady state by simply analysing system of state variables, and to extend the regime C part of Proposition 8. For simplicity the analysis is restricted to the special case of the age-structured model.

Proposition 9 *Given (A1-A7), $n \geq 2$, $\beta_s = 0$, $s = 1, \dots, n$ and that the optimal steady state is in regime C , the steady state is locally stable.*

Proof: The Jacobian matrix of system (29) is

$$J = \begin{bmatrix} \varphi' \gamma_1 & \cdots & \varphi' \gamma_{m-1} & \varphi' \gamma_m \\ \alpha_1 & \cdots & 0 & 0 \\ \vdots & \ddots & \vdots & \vdots \\ 0 & \cdots & 0 & 0 \\ 0 & \cdots & \alpha_{m-1} & 0 \end{bmatrix}.$$

The characteristic equation can be given as

$$\sum_{s=1}^m \frac{\varphi' \gamma_s \mu_s}{r^s} = 1, \quad (29)$$

assuming that $r \neq 0$. This implies by the Perron-Frobenius theorem that the absolute values of all characteristic roots remain below 1 if

$$\varphi' \sum_{s=1}^m \gamma_s \mu_s = \varphi' \Gamma_m < 1.$$

The steady state must satisfy $\varphi(x_1 \Gamma_m) - x_1 = 0$. Since φ is a concave function, the steady state must satisfy $\varphi' \Gamma_m - 1 < 0$, implying that the Perron root is positive and lower than 1 and that the steady state is locally stable. ■

The dynamic properties of this system coincide with those of an unharvested age-structured population when $n = m - 1$ and $\beta_{m-1} = 0$. This was studied by Getz and Haight (1989, p. 40), who derived the characteristic equation (30).

Figure 7a shows how increasing the discount rate transforms the optimal steady state solution from the $m = 6$ steady state to the $m = 5$ steady state via regime D , where it is optimal to simultaneously harvest from age classes 6 and 7. An example of the solution described in Proposition 9 is shown in Figure 7b. Initially individuals exist only in age class 1. With no discounting it is optimal to apply a steady state harvest only in age class 7, i.e. $x_s > 0$, $s = 1, \dots, 6$, $x_s = 0$, $s = 7, \dots, 10$. Given the linear utility function, this is the only age class that is harvested during the whole transition period.

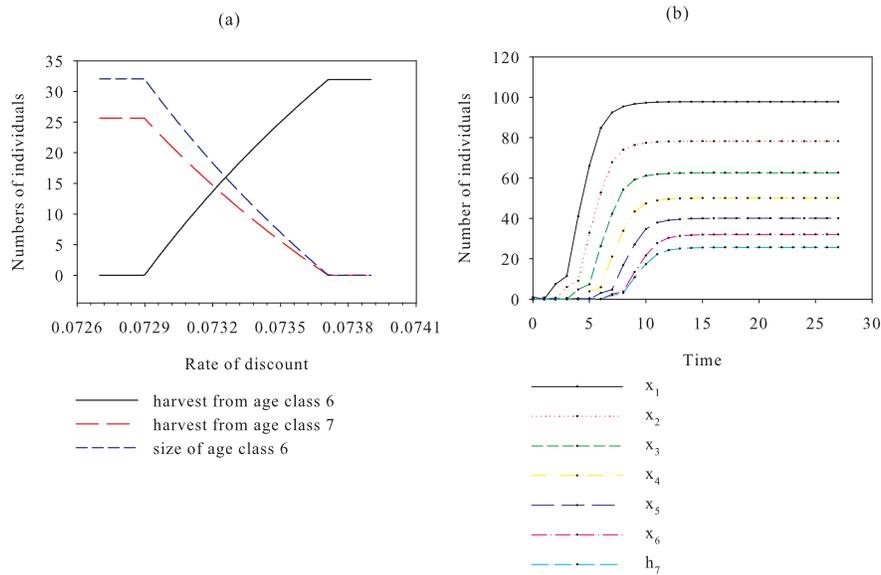


Fig. 7 A numerical example of solution approaching a steady state in regime C. Note: $\alpha_s = 0.8$, $s = 1, \dots, 10$, $f = 1, 2.7, 6.9, 16.7, 35.5, 60, 80.3, 91.7, 98.8, 100$, $\gamma = 0, 1, 2, 2, 2, 2, 2, 2, 2, 2, U = H_t$, $r = 0$, $\varphi = 10x_0 / (1 - 0.1x_0)$

Finally, Figures 8a,b show the optimal solutions for the data in Reed (1980). Given no discounting, the optimal steady state (i.e. MSY) harvest is to remove about 44% from age class 6 (as obtained in Reed 1980). Thus, the number of individuals in all age classes remains positive and the solution is an example of regime B. Figure 8a shows the optimal dynamic solution (not computed by Reed 1980). Note that although the initial biomass slightly exceeds the steady state biomass, the initial harvest level is zero because the biomass is located in age classes that are too young for harvesting. Almost half of the biomass at the steady state is in age classes 6, ..., 12. Such a solution is clearly impossible to obtain within the unstructured biomass approach. Figure 8b shows that the optimal steady state exists only if the discount rate is below 11.5%.

8 Summary

The objective of this study has been to extend the understanding of a generic discrete-time age- and size-structured optimization model where the harvest is perfectly selective. Given an increasing and concave function for recruitment, this model can be viewed as a theoretical description of harvesting shade-tolerant

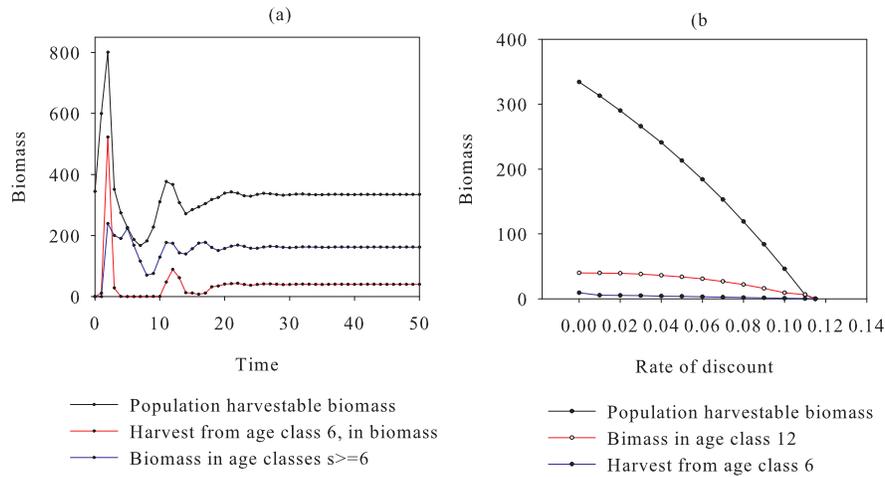


Fig. 8 Optimal dynamic solution (a) and the dependence of the steady state on discounting using the data in Reed 1980

uneven-aged tree populations. Selective harvesting may be possible in fisheries if e.g. different age classes can be found in different locations. The model was first studied assuming two age or size classes, and it was shown that six different steady-state regimes exist. One of the steady states is a continuum. It was shown that the structured model can be viewed as a generalization of the biomass model. However, neglecting information on population structure will not yield correct optimal steady states.

The classic Faustmann (1849) model answers the questions "at what age it is optimal to fell a tree"? According to the answer (and assuming no regeneration cost), it is optimal to harvest the tree before it reaches its discounted maximum value, because waiting postpones all future harvests. The model studied here can be interpreted to answer the same question. However, the model does not include the Faustmann-type (1849) rotation structure, and it is optimal to harvest the tree after it reaches the discounted maximum value because waiting increases regeneration. In the Faustmann (1849) model, increasing the discount rate decreases the age of the harvested cohort, but a higher interest rate in the study at hand may imply a switch to harvesting an older age class.

Analysing steady-state stability reveals that with a zero or "low" interest rate the optimal steady states are saddle point stable. However, it was possible to give a numerical example showing that with a "high" interest rate the optimal solution may converge toward a limit cycle. Given a linear objective, constant escapement is optimal in the generic biomass model (Reed 1979) but it is not, in general, optimal in structured models.

Finally, the optimal steady-state equations were solved without limiting the number of age or size classes. These equations (not presented in earlier studies) further reveal the structure of the optimal solution: when the harvest is moved forward in the age or size classes, the yield *per capita* may increase but natural mortality has a negative effect on the number of individuals obtained. This decrease is compensated by increased recruitment due to an increased number of reproductive individuals. Finally, these trade-offs are influenced by discounting, but differently than in optimal rotation models.

Given the age class-specification and the optimal steady-state regime where only one age class is harvested and the harvest is total, it was possible to show that the steady state is locally stable, i.e. harvesting all individuals at the end of the period when they enter the (optimal harvestable) age class yields a convergence to a stable age structure. This suggests that instead of the constant escapement solution often proposed, a simple practically applicable harvesting rule may be just to harvest the individuals when they enter the age class that is the oldest at the optimal steady state.

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Appendix 1

Proof of Proposition 2. Case i): Because $1 - \beta_1 - \phi'(0)\gamma_1 > 0$ the condition (9a), i.e. $\lambda_1 [b\phi'(0)\gamma_1 + b\beta_1 - 1] + b\lambda_2\alpha_1 \leq 0$ will always be satisfied as an equality by some choice $\lambda_1 \geq U'(0)f_1$, $\lambda_2 \geq U'(0)f_2$. Eliminating λ_1 from (10a) shows that this condition is satisfied as an inequality when $\mu_2(0,0) \geq 0$. Thus, regime *F* satisfies the necessary optimality conditions and must be optimal. Case ii): Setting $\lambda_1 = U'(0)f_1$ and $\lambda_2 = U'(0)f_1 [1 - b(\phi'\gamma_1 + \beta_1)] / (b\alpha_1)$ implies by $\mu_2(0,0) \leq 0$ that (10a) is satisfied with $x_1 = x_2 = 0$. The solutions for λ_1 and λ_2 imply that (8a) is satisfied for $i = 1$ as an equality and $h_1 = 0$ and by $\mu_1(0,0) \leq 0$ for $i=2$ as an inequality with $h_2 = 0$ and (9a) as an equality, i.e. regime *F* is optimal. Thus, conditions $\mu_2(0,0) \geq 0$ and i) or ii) are sufficient for regime *F* to be optimal. If condition $\mu_2(0,0) \geq 0$ holds but neither conditions i) or ii) hold, the optimal steady state is in regime *D*) or *E*). If condition $\mu_2(0,0) \geq 0$ does not hold, the optimal solution is in regime *A*), *B*), *C*), *D*) or *E*). Thus conditions are necessary for the optimality of regime *F*. ■

Appendix 2

Proof of Proposition 5: Given (20a)-(20f) and $b=1$ the characteristic equation evaluated at the steady state is $\Omega_1(r) = r^4 + y_1r^3 + y_2r^2 + y_1r + 1$, where

$$y_1 = \left\{ \lambda_1 \phi'' h' \gamma_1 (\alpha \gamma_2 - \beta_2 \gamma_1) \tau_1^2 - \alpha^2 \gamma_2^2 \beta^2 + \gamma_1 (\beta_2^2 - 1) (2\alpha_1 \gamma_2 \beta - \gamma_1 \beta_2^2 + \gamma_1) \right\} / \tau_2,$$

$$y_2 = \left\{ \lambda_1 \phi'' h' \tau_1^2 (\gamma_2^2 \alpha_1^2 - 2\beta_2 \gamma_1 \gamma_2 \alpha_1 + \gamma_1^2 \beta_2^2 + \gamma_1^2) + 2 [\alpha_1^2 \gamma_2^2 (\beta^2 - \beta + 1)] + \alpha_1 \gamma_1 \gamma_2 (1 - \beta_2) (2\beta_1 \beta_2 + \beta_1 + 2\beta_2^2 + 1) + \gamma_1^2 (\beta_2 - 1)^2 (\beta_2^2 + \beta_2 + 1) \right\} / \tau_2,$$

where $\tau_1 = \alpha_1 \gamma_2 - \gamma_1 \beta_2 + \gamma_1$, $\tau_2 = \tau_1 \tau_3$, $\tau_3 = (\beta_2 - 1) (\alpha_1 \gamma_2 - \beta_2 \gamma_1) + \alpha_1 \gamma_2 \beta_1 \neq 0$, $\beta = \beta_1 + \beta_2$. Computing yields:

$$\Omega_1(1) = \frac{\lambda_1 \phi'' h' \tau_1^3}{\tau_2},$$

$$\Omega_1(-1) = \frac{\lambda_1 \phi'' h' \tau_1^2 (\gamma_2 \alpha_1 - \gamma_1 \beta_2 - \gamma_1)^2 + 4 [\gamma_2 \alpha_1 \beta + \gamma_1 (1 - \beta_2) (1 + \beta_2)]^2}{\tau_2}.$$

Thus, if u is a root then $1/u$ is a root. The numerators of both $\Omega(1)$ and $\Omega(-1)$ are strictly positive. Thus, when $\tau_3 < 0$, it holds that $\Omega(1) < 0$, $\Omega(-1) < 0$ and by $\Omega(0) = 1$ there exists four real roots, two with absolute values above one and two below one. Write $\Omega_1(r)r^{-2} = r^2 + w_1 r + w_2 + w_1 r^{-1} + r^{-2}$ and $|r| = 1$, $\Rightarrow r = e^{ia} = \cos(a) + i \sin(a)$ implying

$$\Omega_1(r)r^{-2} = \frac{\lambda_1 \phi'' h'}{\tau_2} \Theta_1 + 4 [\cos(a)^2 - 1] + \Theta_2 [\cos(a) - 1],$$

$$\Theta_1 = \left\{ [2\gamma_1 \tau_1^2 (\alpha_1 \gamma_2 - \beta_1 \gamma_1)] \cos(a) + \tau_1^2 (\gamma_2^2 \alpha_1^2 - 2\beta_2 \gamma_1 \gamma_2 \alpha_1 + \gamma_1^2 \beta_2^2 + \gamma_1^2) \right\},$$

$$\Theta_2 = -\frac{2}{\tau_2} [\gamma_2 \alpha_1 \beta + \gamma_1 (1 - \beta_2^2)]^2.$$

The minimum of term Θ_1 is zero and is attained when $a = \pi$ and $\gamma_2 = \gamma_1 (\beta_2 + 1) / \alpha_1$. Given these values for a and γ_1 , it follows that $\Omega_1(r)r^{-2} > 0$ by $\tau_3 > 0$. The minimum of $4 [\cos(a)^2 - 1] + \Theta_2 [\cos(a) - 1]$ is attained when $a = 0$ and is zero because $\Theta_2 \leq 8$. When $a = 0$ it holds that $\frac{\lambda_1 \phi'' h'}{\tau_2} \Theta_1 > 0$. Thus, no root lying on the unit circle can solve the polynomial implying that the steady state must be a saddle point. ■

Appendix 3

Proof of Proposition 7. The characteristic equation is $\Omega(r) = r^4 + r^3y_1 + r^2y_2 + ry_1/b + 1/b^2 = 0$, where

$$y_1 = \frac{\beta(\beta b + b - 1)}{1 - b\beta}, \quad y_2 = \frac{\lambda_1 \alpha_1^2 b^4 \varphi'' \gamma_2^2 h'^3 \beta^2 + b^2 (\beta_1^2 + 2\beta_1 \beta_2 + \beta_2^2 + 1) - 2b\beta + 1}{b^2(b\beta - 1)}.$$

This yields

$$\Omega(1) = \frac{\lambda_1 \alpha_1^2 b^2 \varphi'' \gamma_2^2 h'}{b\beta - 1}, \quad \Omega(-1) = \frac{\lambda_1 \alpha_1^2 b^3 \varphi'' \gamma_2^2 h' + 2\beta [b^2(\beta + 1)] + b\beta - 1}{b^2\beta - b}.$$

Recall that $\beta = \beta_1 + \beta_2$. Given $b < \frac{1}{\beta_1 + \beta_2}$ the denominators of both $\Omega(1)$ and $\Omega(-1)$ are negative. The numerator of $\Omega(1)$ is positive and $\Omega(1) < 0$. The numerator of $\Omega(-1)$ is positive if $\frac{1}{\beta_2 + \beta_2 + 1} \leq b$, implying together with $\Omega(0) = 1/b^2$ that under these conditions roots are real and the absolute value of two roots are below 1 and the absolute values of two roots are above 1, i.e. the steady state is a saddle point. ■

Appendix 4

Proof of Proposition 8

Regime *C* is defined by $x_{1,t+1} = \varphi(\gamma_1 x_{1t}) + \beta_1 x_{1t}$, $h_{2t} = \alpha_1 x_{1t}$. This regime exists only when $\partial \sigma_2(0,0)/\partial x_1 = 1 - \beta_1 - \varphi'(0)\gamma_1 < 0$ and at the steady state $x_1 = \hat{x}_1$ it must hold that $\partial \sigma_2(\hat{x}_1, 0)/\partial x_1 = 1 - \beta_1 - \varphi'(\hat{x}_1)\gamma_1 > 0$ implying that $\varphi'(\hat{x}_1)\gamma_1 + \beta_1 < 1$, i.e. that the steady state is locally stable.

In regime *D* $\lambda_{1t} = U' f_1$, $\lambda_{2t} = \lambda_{1t} f_2 / f_1$, $\lambda_{1,t+1} [b\varphi'\gamma_1 + b\beta_1 + b\alpha_1 f_2 / f_1] - \lambda_{1t} = 0$, $x_{1,t+1} = \varphi(\gamma_1 x_{1t}) + \beta_1 x_{1t} - h_{1t}$ and $h_{2t} = \alpha_1 x_{1t}$. This leads to the system:

$$U'(H_{1,t+1}) f_1 [b\varphi'(\gamma_1 x_{1,t+1}) \gamma_1 + b\beta_1 + b\alpha_1 f_2 / f_1] - U'(H_t) = 0,$$

$$x_{1,t+1} = \varphi(\gamma_1 x_{1t}) + \beta_1 x_{1t} - h_{1t}.$$

The characteristic equation is given as:

$$\Omega(r) = r^2 - r(\delta_1 + \varphi'\gamma_1 + \beta_1) + \delta_1(\varphi'\gamma_1 + \beta_1) + \delta_2,$$

where

$$\delta_1 = 1 + \frac{f_2 \alpha_1}{f_1} + \frac{U' b \varphi'' \gamma_1^2}{U'' f_1}, \text{ and } \delta_2 = -\frac{f_2 \alpha_1 (\varphi' \gamma_1 + \beta_1 - 1)}{f_1} - \frac{U' b \varphi'' \gamma_1^2 (\varphi' \gamma_1 + \beta_1)}{U'' f_1}.$$

Since $\Omega(0) = \varphi' \gamma_1 + \beta_1 + \frac{f_2 \alpha_1}{f_1} > 0$, and $\Omega(1) = -\frac{U' b \varphi'' \gamma_1^2}{U'' f_1} < 0$, both roots are positive and the value of one root is below 1 and the value of the other is above 1, i.e. the steady state is a saddle point. ■

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