

# Optimal Harvesting of Age-structured Fish Populations

OLLI TAHVONEN  
University of Helsinki

**Abstract** *A generic age-structured model for optimal harvesting is formulated and analyzed. The aim is to maximize utility from the harvest, net of effort cost. Yield depends on effort, catchability, and population age structure. The recruitment function is nonlinear. The age-structured model can be viewed as a generalization of the biomass approach. Comparison with the biomass model shows that the age-structured information influences the optimal steady-state population and harvest and the qualitative features of optimal transition. Pulse fishing or interior limit cycles are possible, but the optimal solution may represent a smooth, sustainable harvest even when the model is linear in effort. Linearity assumptions do not guarantee the optimality of constant escapement. If the age distribution is dominated by young age classes, the optimal yield may be lower with higher biomass. With knife-edge selectivity, the optimal steady state may become independent of the interest rate.*

**Key words** Fisheries, bioeconomics, optimal harvesting, age-structured models, pulse fishing, Beverton-Holt population model, endogenous recruitment.

JEL Classification Codes Q22, Q57, C61.

## Introduction

Economic research on fisheries has widely applied the biomass approach to describe fish populations over time. This has led to models that are suitable for analytical methods and extensions, such as game theoretical analysis of open access and models of fishery regulation. In spite of this success, several authors have proposed that economic analysis should be extended to include the age classes of the harvested population. The issue has already been raised by Clark (1985, 1990), who wrote that the “lumped parameter” approach may be too simplistic for management purposes.<sup>1</sup> Wilen (1985, 2000) has written that the biomass approach may, at best, serve as a pedagogical tool, but that more realistic models should be based on population age structure. Hilborn and Walters (1992) write that in fisheries ecology the biomass model is seen as a poor cousin of the age-structured analysis. Townsend (1986) and Walters and Martell (2004) have raised similar issues. In

---

Olli Tahvonen is a professor of environmental economics at the Finnish Forest Research Institute, Unioninkatu 40A, 00170 Helsinki, Finland (email: [olli.tahvonen@metla.fi](mailto:olli.tahvonen@metla.fi)). His other affiliation is the Fishery and Environmental Management Group, FEM, University of Helsinki, Department of Biological and Environmental Sciences.

The study was financed by the Yrjö Jahnsson Foundation, Grant 5313, and by the Academy of Finland. The study was presented at various seminars in Australia and New Zealand during 2005-2006, at the EAERE annual meeting in Thessaloniki (2007), and at the American Agricultural Economic Association meeting in Orlando, FL (2008). I am grateful to Jim Wilen for discussions.

<sup>1</sup> The biomass model, the (dynamic) biomass approach, the lumped parameter model, and the Schaefer (1954) approach all refer to a specification where the fish stock dynamics is given by  $B_{t+1} = B_t + F(B_t) - h_t$ , where  $B_t$  is biomass,  $F$  is the growth function (e.g., logistic), and  $h_t$  is the rate of harvest. As written by Hilborn and Walters (2001), the term “biomass model” is somewhat confusing since biomass or net production is not a unique characteristic of the Schaefer model. Rather, the unique characteristic of the Schaefer model is the description of population dynamics in terms of biomass instead of numbers in age class. Thus, they use the term “dynamic biomass model” for the Schaefer approach. This paper uses “biomass model” for short.

contrast, it is surprising that in his survey Brown (2000) found that economists have not judged age-structured models to be sufficiently useful to compensate for their increased difficulties.

The existing age-structured optimization studies are typically case studies of specific fisheries. This work has shown that including the age-structure leads to a rich, versatile picture of fisheries management. However, there are several open questions as to what the general analytical features of the optimal solutions are and how the age-structure information changes the optimal solutions from those obtained by the biomass approach. The age-structured optimization model is rather complex, but it should not be impossible to achieve an understanding of its analytical properties similar to the understanding of existing models based on biomass variables.

As a step in that direction, this study formulates and analyzes a generic version of the discrete-time age-structured optimization model. Authors such as Clark (1990), Hilborn and Walters (1992), and Wilen (1985) have written that the age-structured model is analytically incomprehensible. Although this view may be too pessimistic, this paper follows the existing studies and examines the problem using numerical methods. Since a generic age-structured model can be viewed as a generalization of the biomass approach, its features and optimal solutions can be compared with those of the biomass model. Such a comparison either does not exist or is incomplete in the fishery economics literature.

Earlier studies of optimal harvesting of age-structured fish populations have been published both in fishery ecology and economics. Getz and Haight (1989) presented an extensive survey of age-structured population models and harvesting. On closer inspection, most studies they cite solve the model under more or less *ad hoc* restrictions, such as requiring that the harvest is constant over time. The reasons for presenting these “sub-optimal strategies” are that they make the model more tractable in numerical analysis and they force the solution to represent the desired smooth, sustainable harvest over time.

Quinn and Deriso (1999) emphasize optimal harvesting models in their book on fisheries ecology. A large part of their analysis is based on the biomass approach. For optimization models that include an age structure, they refer to studies on suboptimal harvesting policies. One typical example is the study by Hightower and Lenarz (1989), where the aim is to find a harvesting strategy that is linear in biomass and that maximizes the average yield over time. Another line of optimization studies (Deriso 1987) aims to develop the Beverton and Holt (1957) yield per recruit theory and has produced a collection of practically influential biological reference points (such as the  $F_{0.1}$  strategy) that from the economic point of view are *ad hoc* and similar to maximum sustainable yield (MSY).

An early study on the age-structured fishery problem maximized physical yield but applied no *ad hoc* restrictions and obtained the result that given nonselective fishing gear, the optimal solution has the feature of pulse fishing (Walters 1969). In a pioneering economic study of the Atlantic cod fishery, Hannesson (1975) obtains a similar result. Clark (1990) applies the classic Beverton and Holt (1957) model as closely as possible and writes that in its general form the problem is almost incomprehensible. Under simplifications like exogenous recruitment, Clark found that the solution almost inevitably follows the pulse fishing strategy. Kennedy (1992) finds similar pulse fishing solutions optimal for the western mackerel fishery.

Horwood and Whittle (1986) study the problem allowing nonlinear utility and cost functions. Optimal solutions are approximated by linearizing the optimality conditions in the vicinity of the steady state. Assuming that this method yields a solution, it specifies effort as a linear function of the number of fish in different age classes. For cases where an optimal linear control could not be found, the authors expect that the solution would have the properties of pulse fishing. This case is solved using a different solution method (Horwood 1987); a strategy the authors find somewhat inconvenient. Horwood (1996) applies different numerical methods, but the results are similar.

More recently the age-structured model has been used by Stage (2006), who applies an age-structured model to Namibian linefishing and finds that the main results depend on

the length of the planning horizon. He calls for more economic research on age-structured models. In a study of East Atlantic bluefin tuna fisheries, Bjorndal and Brasao (2006) apply a complex model with multiple gear types. In addition to obtaining the pulse fishing solution, they show that it would be optimal to shut down some of the existing gear types.

There is no doubt that the existing studies have provided valuable insights for the specific fisheries investigated. When it comes to a more general, theoretical understanding of the age-structured optimization model, perhaps the main result is that the optimal solution typically represents pulse fishing. This has been found somewhat inconvenient since a smooth sustainable yield and stable income are typically important goals of any successful fishery policy. Nevertheless, some studies suggest that pulse fishing disappears when the fishing gear is more selective (Walters 1969; Hannesson 1975).

It would be constructive to obtain a better understanding of how the inclusion of the age-structured information changes the qualitative properties of optimal harvesting. Two recent studies approach this question. Moxnes (2005) compares suboptimal strategies for harvesting an age-structured population and the (discrete time) biomass model solutions for the same fishery. He finds that the differences are rather minor. Tahvonen (2008) studies the outcomes of applying the feedback solutions from the biomass model for harvesting a population that is actually age structured. The results show that the biomass model may perform rather well if the initial age structure is close to equilibrium and the steady state is unique. Under multiple steady states, ignoring the age-structure may yield accidental extinctions and unexpected developments toward different steady states. Compared to the study at hand, Moxnes (2005) studies suboptimal strategies,<sup>2</sup> while Tahvonen (2008) does not attempt to present optimal solutions for the age-structured model.

This study applies the generic age-structured population model from the fisheries ecology with endogenous nonlinear recruitment (*e.g.*, Hilborn and Walters 1992). The harvest is assumed to occur in the middle of each period. This changes the model's concavity properties and makes the problem more amenable to economic analysis than the formulation typically applied, where effort is constant over each period. It is possible, for example, to study a model version that is linear in effort and harvest, as well as the possibility of "optimal extinction." The discrete time biomass model can be obtained from the age-structured model under equilibrium conditions. This connection forms a basis for comparisons and shows how the age-structured model can be viewed as a generalization of the biomass approach. The optimal solutions are computed using recently developed methods for large-scale nonlinear programming without applying linearization or any *ad hoc* constraints (Byrd, Hribar, and Nocedal 1999; Byrd, Nocedal, and Waltz 2006). These methods permit the computation of the model with complementary constraints and over a longer time horizon. This is important as it enables an understanding of the long-term stability properties of the optimal solutions.

## The Optimization Problem

This study is based on an established age-structured population model from the fishery ecology literature (Hilborn and Walters 1992; Getz and Haight 1989). In these models, harvest may be specified to occur instantaneously at any moment within each period (Pope 1972; Quinn and Deriso 1999; Walters and Martell 2004) or simultaneously with natural mortality at a constant rate (Beverton and Holt 1957). In the model applied here, fishing is assumed to occur instantaneously at the middle of each period, instead of the usual assumption in age-structured optimization models, which strictly follow the Bev-

---

<sup>2</sup> It is required that yield is a piece-wise linear increasing function of population biomass.

erton and Holt (1957) formulation.<sup>3</sup> The specification that is obtained can be studied in a form that is linear in effort and yield. Thus this model and its properties can be compared with the well-known discrete time biomass model and the constant escapement (or bang-bang) solution (*cf.* Reed 1979). In addition, it is possible to analyze “optimal extinction” or the non-existence of optimal sustainable harvesting. This problem is ruled out by contraction in studies that follow the Beverton and Holt formulation.

Let  $x_{st}$ ,  $s = 1, \dots, n$ ,  $t = 0, 1, \dots$  denote the number of fish of age class  $s$  at the beginning of period  $t$ . The number of eggs (or newborns) is denoted by  $x_{0t}$ . Let  $f_s$ ,  $s = 1, \dots, n$  denote the fecundity parameters. The number of eggs is given as:

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

Thus, spawning occurs in the beginning of each period. Only a fraction of the eggs will survive as recruits. Given that  $\varphi$  denotes a recruitment function, the next period number of recruits is given as:

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

Let  $m$  denote the rate of natural mortality within each period, and assume that it is equal for all age classes.<sup>4</sup> If fishing mortality is zero, a fraction  $e^{-m}$  of an age class will survive for the next period. After half a year, the fraction that is alive equals  $e^{-m/2}$ . Assuming that fishing occurs in the middle of each period, the development of the number of fish in each age class, excluding age class 1 and  $n$  can be written as:

$$x_{s+1,t+1} = e^{-m/2}(e^{-m/2}x_{st} - h_{st}), \quad s = 1, \dots, n-2, \quad t = 0, 1, \dots, \quad (3)$$

where  $h_{st}$ ,  $s = 1, \dots, n-2$ ,  $t = 0, 1, \dots$  denote the number of fish harvested. Next, the development of the age class  $n$  (and all the older age classes) is given as:

$$x_{n,t+1} = e^{-m/2}(e^{-m/2}x_{n-1,t} - h_{n-1,t}) + e^{-m/2}(e^{-m/2}x_{nt} - h_{st}), \quad t = 0, 1, \dots \quad (4)$$

Age-structured fishery models and virtual population analysis (Gulland 1983) are heavily based on the Schaefer (1954) production function.<sup>5</sup> However, as written, for example by Clark (1985), this production function is rather restrictive; more generally the age-class specific harvest may be written as:  $h_{st} = Q_s(E_t, e^{-m/2}x_{st})$ ,  $s = 1, \dots, n$ ,  $t = 0, 1, \dots$ , where  $E_t$  is effort and  $Q_s$  is the production function that is increasing in effort and in the number of fish (at the moment of harvest). Note that under this specification different age classes cannot be harvested independently; *i.e.*, effort is nonselective. Obviously, the number of harvested fish cannot exceed the number that exists in the given age class at the moment of harvesting; *i.e.*,  $h_{st} \leq e^{-m/2}x_{st}$ ,  $s = 1, \dots, n$ ,  $t = 0, 1, \dots$ . A straightforward application of these restrictions would imply an *ad hoc* constraint on effort. However, the number of fish in any age class restricts the number of fish caught, but not the number of vessel weeks at

<sup>3</sup>Recall that in discrete time economic models the state is normally given in the beginning of each period and the control (*e.g.*, consumption) at the end of each period. Previous optimization studies have applied the original Beverton and Holt (1957) (or Baranov 1918) specification, where effort is constant over each period (Walters 1969; Hannesson 1975; Stage 2006; Horwood and Whittle 1986). It is not straightforward to view this specification as being more general than the other alternatives. The instantaneous harvest specification can be made more accurate by dividing the fishing season (normally a year) into shorter periods.

<sup>4</sup>Equal natural mortality over the age classes is typical in age-structured data. An extension of this would not cause any problems in optimization models.

<sup>5</sup>The Schaefer (1954) production function is relevant for demersal trawl-fisheries, but more generally, rather problematic.

sea. Taking this fact into account requires an additional set of restrictions of the form  $h_{st} = e^{-m/2}x_{st}$ , if  $Q_s(E_t, x_{st}) \geq x_{st}$ ,  $s = 1, \dots, n$ ,  $t = 0, 1, \dots$ . These restrictions can be formulated as the following complementary constraints:

$$h_{st} - Q_s(E_t, e^{-m/2}x_{st}) + y_{st}^1 = 0, \quad s = 1, \dots, n, \quad t = 0, 1, \dots, \quad (5)$$

$$h_{st} - e^{-m/2}x_{st} + y_{st}^2 = 0, \quad s = 1, \dots, n, \quad t = 0, 1, \dots, \quad (6)$$

$$y_{st}^1 \geq 0, \quad y_{st}^2 \geq 0, \quad y_{st}^1 y_{st}^2 = 0, \quad s = 1, \dots, n, \quad t = 0, 1, \dots, \quad (7)$$

where:

$$y_{st}^i, \quad i = 1, 2, \quad s = 1, \dots, n, \quad t = 0, 1, \dots$$

are complementary or slack variables.

The weight of fish increases with age class and the weight of age-class,  $s$ , fish is given by  $w_s$ ,  $s = 1, \dots, n$ . The total (physical) yield,  $Y_t^P$ , is obtained by summing the yield over the age classes and equals:

$$Y_t^P = \sum_{s=1}^n w_s h_{st}, \quad t = 0, 1, \dots \quad (8)$$

Consequently, the total biomass,  $B_t$ , of the population is:

$$B_t = \sum_{s=1}^n w_s x_{st}, \quad t = 0, 1, \dots \quad (9)$$

In addition to specification (8), it is possible to take into account that the price of fish may depend on fish age and size. For some species, price may increase with size due to easier mechanical treatment of harvested fish. For other species, price may decrease with size and age due to deterioration of the quality of the reproductive age classes and to increasing residue contamination, for example. Assuming that price depends on fish age or size, the total revenues from an annual harvest are given by:

$$Y_t^R = \sum_{s=1}^n p_s w_s h_{st}, \quad t = 0, 1, \dots, \quad (10)$$

where  $Y_t^R$  denotes revenues and  $p_s$ ,  $s = 1, \dots, n$  the price for each age (or size) class of fish.

Assume that  $U$  is an increasing and concave utility function and that  $C$  is an increasing and convex cost function for effort. Given that  $V$  is the economic value of the population and  $b = 1/(1+r)$  is the discount factor ( $r$  is the rate of interest), the objective function of the optimal harvesting problem is:

$$V(\mathbf{x}_0) = \max_{\{E_t, t=0,1,\dots\}} \sum_{t=0}^{\infty} b^t [U(Y_t^i) - C(E_t)], \quad (11)$$

where  $V$  is the value function,  $\mathbf{x}_0$  is the vector for the initial age class distribution, and  $Y_t^i$ ,  $i = P, R$  may denote the physical yield or economic revenues, respectively. The problem of the optimal harvesting of the age-structured population can now be defined as the problem of choosing a time path for effort,  $E_t$ , in order to maximize the net present value of economic surplus subject to restrictions (1)–(8) and to the following initial and boundary conditions:

$$x_{s0}, \quad s = 1, \dots, n, \quad \text{given and} \quad (12)$$

$$E_t \geq 0, t = 0, 1, \dots \quad (13)$$

### Optimization Procedure and Data on Population Growth

The model defined by equations (1)–(13) may be viewed as a large-scale nonlinear programming problem with complementary (or equilibrium) constraints. For numerical solutions, this study employs Knitro optimization software that includes state-of-the-art interior (or barrier) and active-set methods (Byrd, Hribar, and Nocedal 1999; Byrd, Nocedal, and Waltz 2006). When the interior point method is applied, the solver may use either the iterative conjugate gradient approach or it may factor the Karush-Kuhn-Tucker (primal-dual) matrix directly. The system has been evaluated extensively and it is suitable for smooth problems but does not require convexity (Wächter and Biegler 2006). In addition, it applies specialized methods for complementary constraints (Lopez-Calva, Leyffer, and Nocedal 2007). It is possible to choose the initial guesses by using a randomized multi-start procedure when seeking the globally optimal solution.

For the purposes of numerical analysis, this study utilizes data that has been collected and estimated in fishery stock assessment research. However, these parameter values represent a baseline case only and they are varied in the numerical analysis. Table 1 presents data for the Atlantic menhaden fishery from a study by Hightower and Grossman (1985) (see also Getz and Haight 1989). This population is described by eight age classes. Natural mortality is 0.25 and equal for all age classes. For recruitment, Hightower and Grossman (1985) apply the Ricker (1954) recruitment function:

$$x_{t+1} = x_0 \alpha e^{-\beta x_0 t} \quad (14)$$

where  $\alpha = 0.0205$  and  $\beta = 0.0024$ . Note that the catchability coefficients do not increase monotonically with fish age and size. This is not at all exceptional and reflects the fishing technology (Gulland 1983; Millar and Fryer 1999).

**Table 1**  
Age-class Data for the Atlantic Menhaden Fishery

Age (yr.)	Weight (g)	Fecundity (g)	Catchability
1	102.77	0	0.0577
2	260.21	110.25	0.1805
3	411.73	227.37	0.1579
4	530.31	302.70	0.1540
5	614.28	354.63	0.1430
6	670.60	410.44	0.1820
7	707.23	491.98	0.1703
8+	730.63	469.60	0.1703

Source: Hightower and Grossman (1985).

### Steady-state Analysis and Comparisons with the Biomass Model

For populations with an age-class structure, the biomass model represents an equilibrium solution for the age-structured model (Getz 1980). Lawson and Hilborn (1985) write

that “whenever the surplus production model is desired, the best way to calculate the parameters may be to use the age-structured model.” For this purpose let  $x_{s\infty}$ ,  $s = 1, \dots, n$  denote the equilibrium number of individuals, and take effort as a constant. Assuming the Schaefer (1954) production functions  $h_{st} = q_s x_{st} E_t$ ,  $s = 1, \dots, n$ , where  $q_s$ ,  $s = 1, \dots, n$  are catchability coefficients, it is possible to write equations (3)–(4) as:

$$\begin{aligned} x_{s+1,\infty} &= x_{s\infty} \mu_s, \quad s = 1, \dots, n-1, \text{ where} \\ \mu_s &= e^{-m} (1 - q_s E), \quad s = 1, \dots, n-2, \end{aligned} \tag{15}$$

$$\mu_{n-1} = e^{-m} (1 - q_{n-1} E) / (1 - e^{-m} + e^{-m} q_n E). \tag{16}$$

Note that in equilibrium, the complementary constraints (5)–(7) are satisfied in a form  $y_s^1 = 0$ ,  $y_s^2 \geq 0$  for  $s = 1, \dots, n$  implying that  $h_s = q_s x_s E$ . Next, using equations (15)–(16), it is possible to write the equilibrium age-class structure for  $s = 2, \dots, n$  in terms of  $x_{1\infty}$ :

$$x_{s\infty} = \Phi_s x_{1\infty}, \quad s = 2, \dots, n, \text{ where} \tag{17}$$

$$\Phi_s = \prod_{i=1}^{s-1} \mu_i, \quad s = 2, \dots, n. \tag{18}$$

The equilibrium number of newborns (or eggs) can now be written as:

$$x_{0\infty} = x_{1\infty} \sum_{s=1}^n f_s \Phi_s, \tag{19}$$

where  $\Phi_1 \equiv 1$ . Given the Ricker (1954) recruitment function and the definition  $\sum_{s=1}^n f_s \Phi_s \equiv R$ , it is possible to write the remaining equation as:

$$x_{1\infty} = x_{1\infty} R \alpha e^{-\beta x_{1\infty} R}, \tag{20}$$

which can be solved for  $x_{1\infty}$ :

$$x_{1\infty} = \frac{LN(R\alpha)}{R\beta}. \tag{21}$$

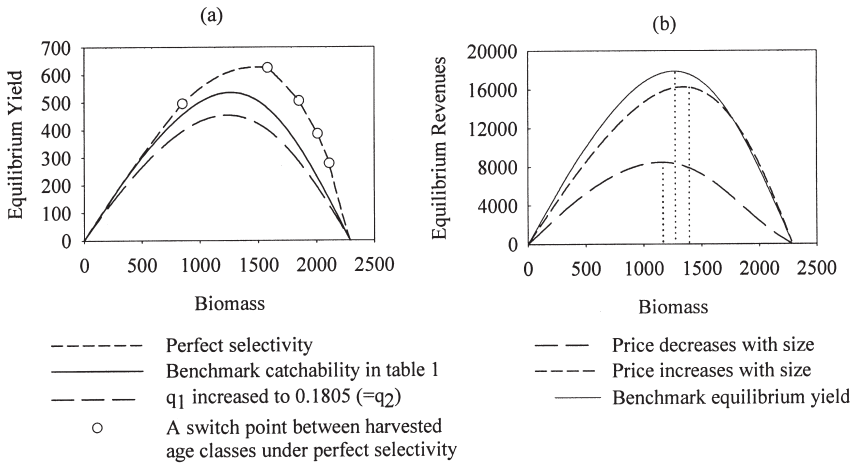
Next, applying equations (17)–(18) and the result in (21) yields the equilibrium number of fish over the age classes, and equations (8)–(9) the total harvest and biomass, respectively. Thus, it is possible to vary the level of biomass and solve for the equilibrium effort and sustainable yield. The relationship between biomass and yield represents the biomass model that corresponds with the age-structured data. Equation (21) shows that a strictly positive equilibrium exists only if  $R\alpha > 1$ . Using the data from table 1 yields  $R\alpha \approx 22$  for  $E = 0$ . It can be shown that an equilibrium of the age-class model is locally stable if  $|R \partial \phi(x_{0\infty}) / \partial x_{0\infty}| < 1$  (Getz and Haight 1980). This condition is satisfied for the data in table 1.

Figures 1a and b show analysis of the biomass-yield relationships based on the data in table 1. In figure 1a, the solid line is the equilibrium yield as a function of biomass. The carrying capacity is about 2,316 thousand tons and the MSY is about 536 thousand tons. As became clear in the derivation of equations (15) to (21), this function is an outcome of both the biological properties of the fish population and of the fishing technology included in the production functions and catchability coefficients. To demonstrate this, the

lowest function in figure 1a shows the equilibrium yield if the catchability coefficient of age class 1 is increased to equal the coefficient of age class 2. As shown, this decreases sustainable yield over all biomass levels. The highest function in figure 1a shows the equilibrium yield if a perfectly selective technology could be used. Maximizing the equilibrium yield at a given biomass level typically requires harvesting fish from only one or two age classes. The circles show biomass levels where the optimal harvesting regime switches between the age classes. For example, below biomass level 840 it is optimal to harvest age classes 1 and 2, and above biomass level 2,110 the optimal harvest is targeted to age classes 7 and 8.

Similarly, as harvesting technology determines the physical sustainable yield, the price variation over the age or size of fish may determine the level of sustainable revenues. In figure 1b, the higher dashed line shows sustainable revenues (catchability coefficients from table 1) if the price of fish increases with age and size ( $p_s = 22.8 + 2.8 \times s$ ). The lower dashed line shows the case where the market price decreases with age and size ( $p_s = 22.8 - 2.8 \times s$ ). As shown, the maximum sustainable revenues depend on the price structure and may be realized above or below the biomass level that maximizes the physical sustainable yield (solid line).

Figures 2a and b show comparisons of optimal steady states between the discrete time biomass and the age-structured models assuming zero harvesting cost. The fact that in the age-structured model sustainable yield depends on harvesting technology readily implies that, even in the simplest case with no harvesting cost, the economically optimal steady state is not determined by purely biological factors and the interest rate. This should be compared to the biomass approach where the development of biomass can be given as  $B_{t+1} = B_t + F(B_t) - h_t$ , where  $F$  is the natural growth function for biomass and  $h$  is harvest. In the absence of harvesting cost, the optimal steady state is determined by the conditions  $dF(B)/dB = r$  and  $F(B) = h$ . Clearly, interpreting  $F$  as a purely biological function is problematic (*cf.* Clark 1990, p. 9), since it cannot be defined without assumptions about the harvesting technology.<sup>6</sup>



**Figures 1a,b. Effects of Fishing Technology and Fish Price on Equilibrium Yield and Revenues**

- a) Dependence of equilibrium yield on harvesting technology.
- b) Dependence of equilibrium revenues on fish price.

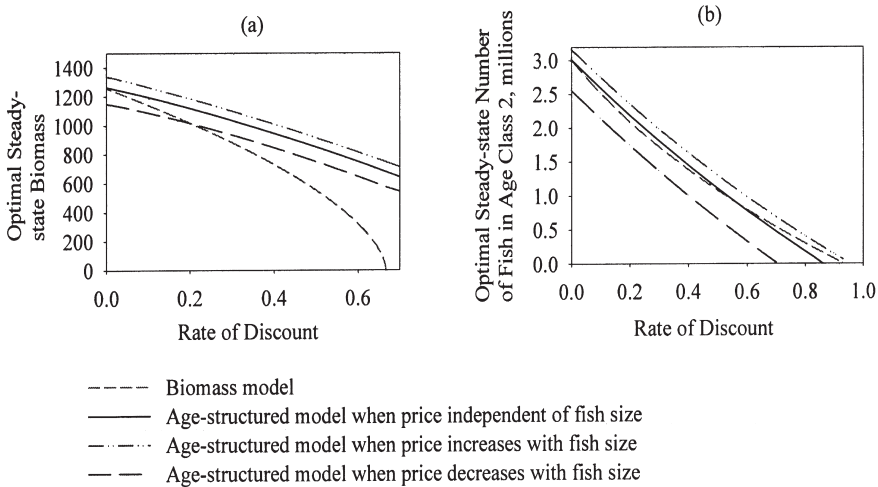
<sup>6</sup> For age-structured populations, the fact that fishing technology is a factor that determines the equilibrium biomass-yield function cannot be circumvented when the biomass model is directly estimated from empirical data on the harvested population (on estimation, see Haddon 2001).



Figure 2a presents results for the model given all eight age classes. As shown, the steady states for the biomass and the age-structured models coincide only when the discount rate is zero and price is independent of age and size. With a fixed price, the optimal steady state biomass is lower for the biomass model, and for this model the steady state does not exist when  $r \geq 0.86$ . In comparison with the age-structured model, the optimal steady state biomass at this critical interest rate is about 700 thousand tons, and depletion of the population becomes optimal only with a higher interest rate. In addition, figure 2a shows how the dependence of price on age and size changes the optimal steady state in the age-structured model.

Figure 2b shows a similar computation for a reduced model with only the two youngest age classes; *i.e.*, assuming that  $n = 2$  in the table 1 data. The steady state is now given in terms of the number of fish in age class 2. The essential difference with the full eight age-classes model is that now the age-structured model yields higher steady states with a low interest rate but lower steady states with a higher interest rate compared to the biomass model.

A complete interpretation of the factors that cause the deviation between the steady states requires an analytical derivation of the steady-state equations for the age-structured model. This may well be possible, but it is somewhat tedious due to the structure determined by the nonselective harvesting technology. However, it is clear that in the age-structured model the marginal rate of return is determined via a time-delay structure through all age classes. The biomass approach does not capture these effects, implying that the steady states only coincide accidentally. In addition, the classic results on the existence of optimal sustainable harvesting policy (Clark 1973) do not carry over to the age-structured framework.



**Figures 2a,b. Comparison of Optimal Steady States of the Biomass and Age-structured Models with Zero Harvesting Cost**

(a) Steady states when the model includes all the eight age classes.

(b) Steady state number of age class two fish when the model includes two age classes.

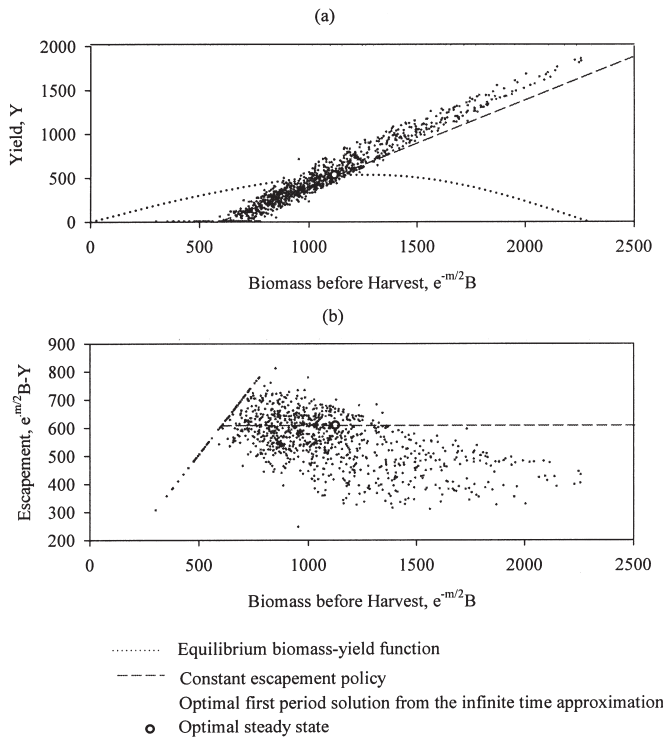
### Dynamic Analysis

#### Linear Specification

Let the utility and cost functions take the forms  $U(Y_t^P) = Y_t^P$  and  $C(Et) = cE$ . Figure 3 is based on an example where  $b=0.97$  and  $c = 10$ . In addition, assume the Schaefer production functions; i.e.,  $Q_s(E_t, e^{-m/2}x_{st}) = q_s E_t e^{-m/2}x_{st}$ ,  $s = 1, \dots, n$ . This implies that the problem is linear with respect to effort and total yield.<sup>7</sup> Thus, the properties of the optimal solution can be compared with the well-known optimal constant escapement policy that is obtained under similar assumptions for the biomass model (Spence 1973; Reed 1979).

In figures 3a and b, the optimal solution is studied by randomly choosing 200 initial age distributions and plotting the initial biomass and the first period optimal solution for aggregate yield and escapement. The optimal steady state is denoted by a circle at the point  $e^{-m/2}B_0 = 1,124$ ,  $Y_0 = 536$ . In figure 3a, the dotted line shows the equilibrium yield as a function of biomass (cf. figure 1a). The steady-state biomass is below the MSY biomass because the unit cost of effort is relatively low. Figure 3a shows that optimal total yield is not a function of biomass since it depends on how the biomass is distributed over the age classes.

Figure 3b shows the optimal escapement; i.e.,  $e^{-m/2} B_0 - Y_0$ . If the initial biomass is small enough, the optimal yield is zero and optimal escapement equals the biomass



**Figures 3a,b.** Effects of Age Class Distribution on Optimal Escapement and Yield

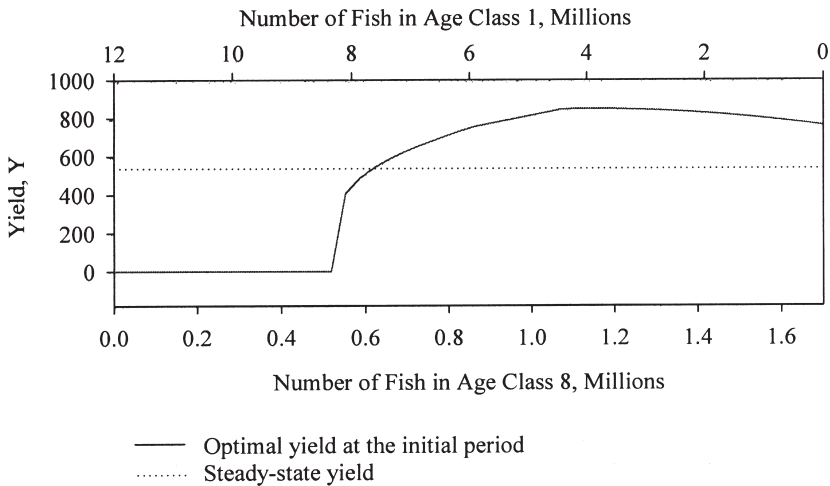
Notes: Linear model with respect to effort and yield; Parameter values, see text.

<sup>7</sup> Note that due to complementary constraints, a potential nonlinearity exists if the solution does not remain in regime  $y_{st}^1 = 0$ ,  $s = 1, \dots, n$ ,  $t = 0, \dots$

before harvest. This solution may be optimal up to  $e^{-m/2} B_0 \approx 800$  depending on how the initial biomass is distributed over the age classes. When the initial biomass is higher, the optimal escapement tends to decrease. This agrees with figure 3a, where the optimal total yield tends to increase faster than the total biomass. This reflects the fact that both higher catchability coefficients for the three oldest age classes and the Schaefer production function imply a higher optimal catch when the population is large, even at the expense of a somewhat smaller catch in the next period.

For comparison, the optimal constant escapement strategy is depicted in figures 3a and b by dashed lines. Since the optimal yield depends on the age class distribution and increases faster than the biomass, the constant escapement strategy deviates quite clearly from the true optimal solution. Note that at the biomass level of 800 thousand tons the optimal escapement may equal 800 thousand tons (*i.e.*, the optimal yield is zero), while at the biomass level of 2,300 the optimal escapement level may be much lower, equal to about 400 thousand tons.

A general feature of these solutions is the dependence of the optimal aggregate yield on the age-class structure. Figure 3c shows an analysis where the number of fish in age classes 2–8 are 1% of their optimal steady-state levels, and  $x_{10}$  and  $x_{80}$  are varied to keep the total biomass at the optimal steady-state level ( $B_0 = 1,275$ ), as in figures 3a and b. The x-axes show the level of  $x_{80}$  and  $x_{10}$ , and the y-axes the level of optimal aggregate yield at the first period of an infinite horizon solution. Thus, when the biomass is concentrated on the youngest age class, the optimal total yield is zero, although the total biomass equals its steady-state level. This reflects the fact that it is optimal to prevent growth overfishing. When the age distribution is shifted toward the older age class, the optimal aggregate yield increases and reaches a level of 848 thousand tons. However, when the biomass is further shifted toward the oldest age class, the optimal aggregate yield decreases slightly. The intuition is that it is optimal to save more of the older age class that, in this case, is responsible for the reproduction of the population; *i.e.*, to prevent recruitment overfishing.<sup>8</sup> This can be contrasted with the biomass model where the optimal yield is a monotonically increasing function of biomass.



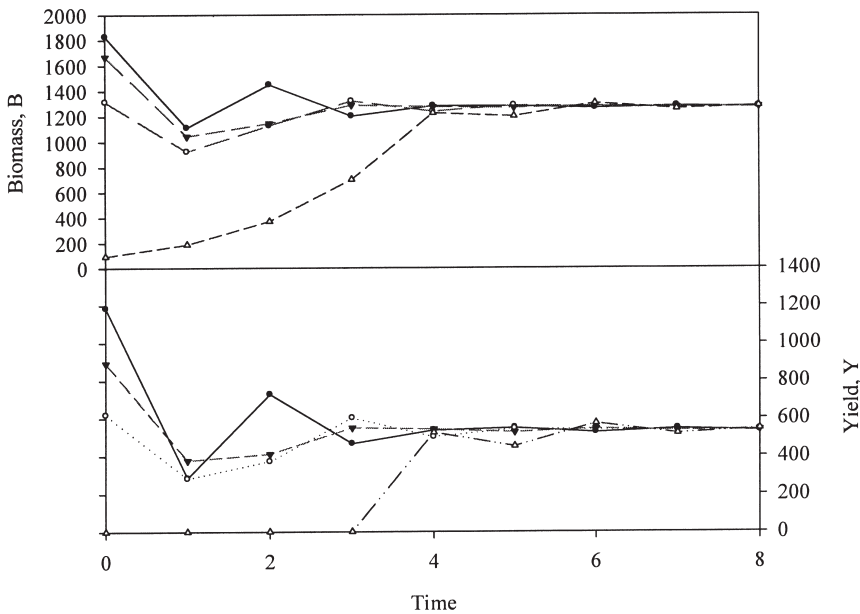
**Figure 3c.** The Effect of Age Class Distribution on Optimal Yield

Notes: Biomass is kept fixed at the steady-state level and age structure is varied from a distribution where youngest age class dominates towards a distribution where oldest age class dominates, parameter values as in figures 3a,b.

<sup>8</sup> In growth overfishing, fish are caught when they are considered to be too small and young. In recruitment overfishing, the spawning stock is harvested down to a level that is too low.

Figure 4 shows how the optimal solutions proceed over time. In the four examples, the optimal solutions approach the same steady state. This feature also holds for all of the 200 examples in figures 3a and b. Thus, these steady states may be globally stable. Another feature of the optimal solutions is that they may overshoot the steady state several times, again demonstrating the fact that the optimal solution is more complex than the constant escapement policy. However, it is worth noting that even in the case of linear specification, the optimal solution approaches a steady state with smooth sustainable harvest instead of pulse fishing (*cf.* Walters 1969; Hannesson 1975).

The constant escapement strategy is discussed both in fishery economics and ecology literature (Spence 1973; Reed 1979; Clark 1990; Hilborn and Walters 1992; Walters and Martell 2004; Jennings, Kaiser, and Reynolds 2007). It has been said to have practical relevance due to its simplicity and has been proposed in the context of both the age-structured and the discrete-time biomass approaches. The results shown in figures 3a, 3b, and 4 nevertheless show that the policy is not optimal for age-structured populations.



**Figure 4.** Optimal Solutions with Different Initial States

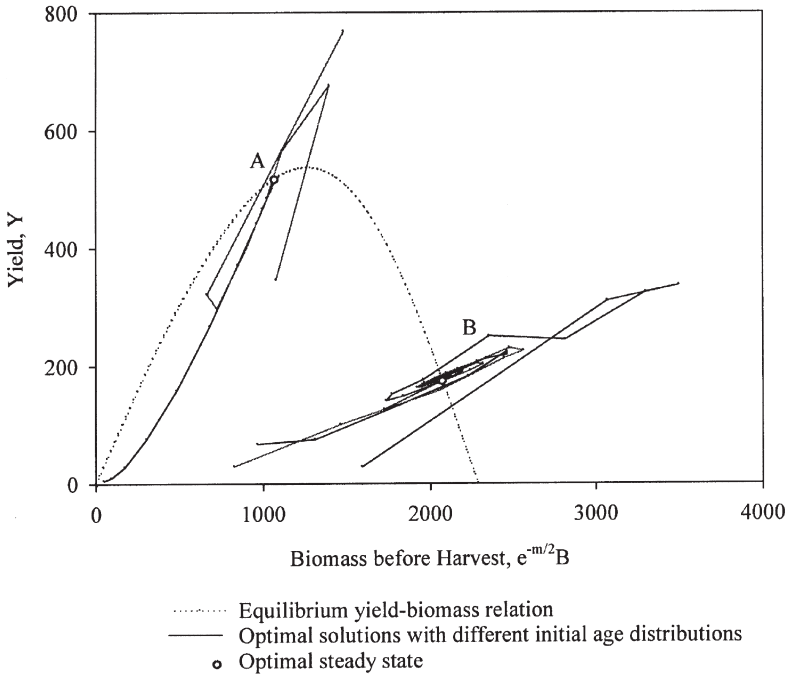
Notes: Linear specification with respect to effort and yield parameter values as in figure 3a,b.

### Nonlinear Specification

To examine the solution under nonlinearities, assume  $U(Y_t) = (10Y_t)^{0.6}$ ,  $C(E_t) = 0$ ,  $b = 0.8$ , and the Schaefer production function, where the catchability coefficients are from table 1. These parameter values imply a steady state where  $B_\infty \approx 1,078$ ,  $Y_\infty = 519$  (steady state A in figure 5a).<sup>9</sup> The dotted line shows the equilibrium biomass-yield relationship. Since

<sup>9</sup> The discount factor  $b = 0.8$  implies an annual interest rate is 25%. This high interest rate level is chosen only to reveal theoretical properties of the optimal solution. Recall that in analytical work model properties may be studied when  $r \rightarrow \infty$ .

fishing costs are zero and the discount rate is positive, the optimal steady state exists below the MSY biomass. Figure 5a shows three examples of optimal solutions that converge toward this steady state. The other solutions in figure 5a follow from an example where  $U(Y_t) = (10Y_t)^{0.6}$ ,  $C(E_t) = 60E_t^2$ ,  $b = 0.97$ , with the production functions the same as before. In this case, the discount rate is low and fishing is costly which, together with the Schaefer production function, imply that the steady-state biomass is higher and the yield is lower than the MSY levels; *i.e.*,  $B_\infty \approx 2,071$ ,  $Y_\infty \approx 178$  (steady state B in figure 5a). Figure 5a shows four examples of optimal solutions that converge toward the steady state. As in the case of linear specification (figures 3a, 3b, and 4), it is likely that under both parameter values the steady states are globally stable (in the saddle point sense).



**Figure 5a.** Optimal Solutions under Nonlinear Utility

Notes: Steady state 1: High interest rate, zero harvesting cost. Steady state 2: Low interest rate, high harvesting cost. Parameter values: see text.

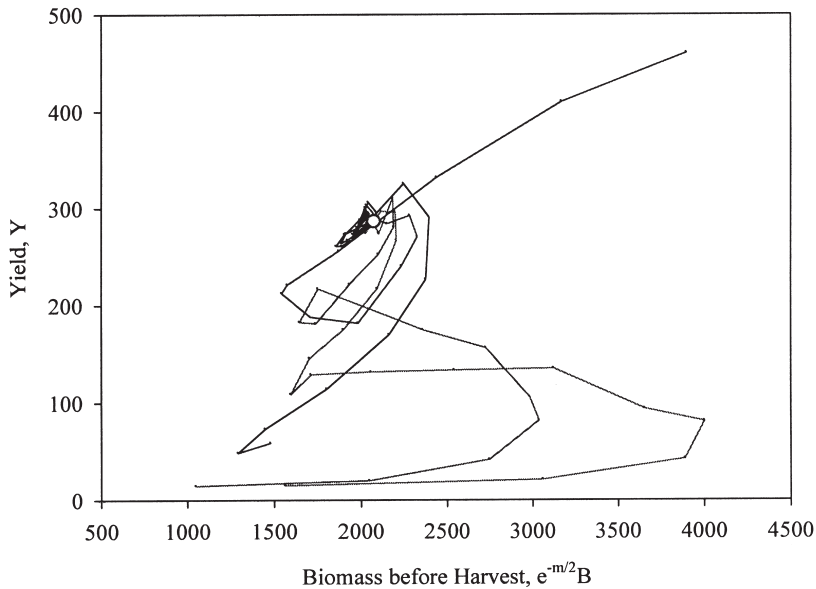
A key feature of the optimal solution is that optimal yield is not a function of the biomass, but a function of the number of fish in each age class. In spite of this, it is possible to view the examples in figure 5a as if the optimal yield is higher when the biomass is higher. This relationship may be weaker if, for example, the production functions deviate from the Schaefer formulation. The four examples in figure 5b are based on the production function:

$$Q_s(E_t, e^{-m/2}x_{st}) = q_s E_t^{0.9} (e^{-m/2}x_{st})^{0.1}.$$

This specification may be suitable for pelagic schooling species and with gear saturation (Quinn and Deriso 1999). Note that the dependence of catch on the number of fish is weaker than in the case of the Schaefer production function. The other parameter values are the same as in the example with the higher steady-state biomass in figure 5a. Figure 5b shows that with gear saturation or pelagic schooling, the total yield depends more

strongly on the age distribution of the population than in the case of the Schaefer production function. The solutions with low initial yield have an initial age structure where older age classes are close to zero, implying that optimal yield may be low although the population biomass may equal or exceed the steady-state level.

Figure 6 shows how the age-class structure develops over time. The parameter values are as in figure 5b. After 30 periods, the age structure is close to steady-state distribution. The steady-state age-class structure is a consequence of natural mortality and the fishing technology specified in production functions and catchability coefficients. It would, however, be possible to add several different fishing technologies into the model with the implication that harvest can be targeted more efficiently to specific age classes (*cf.* Bjorndal and Brasao 2006).



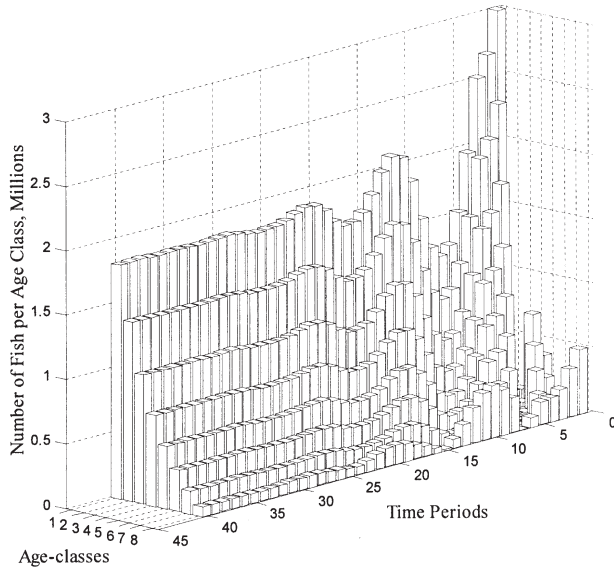
○ Optimal steady state

**Figure 5b.** Optimal Solutions under Nonlinear Utility and Generalized Production Function

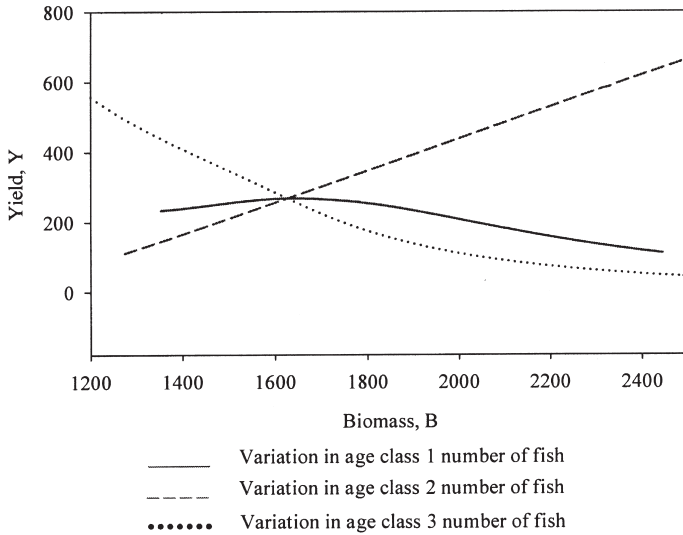
Notes: Parameter values, see text.

### *Optimal Yield and Number of Recruits*

Horwood and Whittle (1986) solve their model by linearizing the necessary conditions at a steady state, with the implication that the optimal aggregate yield becomes a linear function of fish in various age classes. They note that in their numerical example, optimal aggregate yield decreases with the number of fish in the youngest age class. This result is closely related with the computation results shown in figure 3c and can be studied further. Figure 7 is based on an example where  $f_1 = f_2 = 0$ ,  $U = (10Y_1)^{0.7}$ ,  $b = 0.97$ ,  $C = E$ , and production functions are from Schaefer (1954). The x-axis shows the aggregate biomass when the number of fish in age class 1, 2, or 3 is varied and other age classes are kept fixed at their steady-state levels. The y-axis shows the optimal aggregate yield for the first period. As shown, the aggregate yield initially increases and later decreases as a function of the recruit biomass. Next, it can be observed that the optimal yield is a monotonically decreasing and convex function of the fish biomass in the second age class. For age classes 3 and older, the optimal yield increases with the size of the given age class.



**Figure 6.** The Development of Age Classes over Time



**Figure 7.** Optimal Yield and Size Variations in Different Age Classes

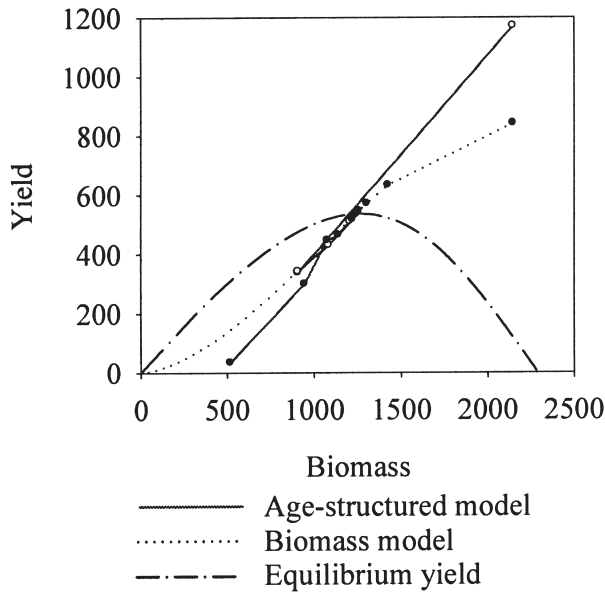
The result that the optimal yield may decrease with the aggregate biomass if the increase is in the youngest age classes is in contrast to the biomass model where the optimal yield is always a non-decreasing function of biomass. The age-structured approach recognizes that the population age structure contains valuable information on future harvesting possibilities and that it is economically optimal to take this information into account in harvesting decisions. Thus, it is optimal to postpone effort and harvest the large cohort later when its weight and economic value are higher. Figure 7 also shows that the lin-

earization procedure applied by Horwood and Whittle (1986) may lose some essential properties of the optimal solution.

### *Effects of Some Bioeconomic Parameters*

In the table 1 data all age classes are vulnerable to fishing. However, it is possible that fishing gear has a knife-edge selectivity property, meaning that some youngest age classes are not harvested. Another possibility is that fecundity is zero for youngest age classes, or that the fishing gear is nonselective and the youngest age classes are commercially worthless. Such changes have rather strong implications for the properties of the model.

Figure 8 shows the baseline case where, in addition to the parameter values in table 1, it is assumed that the production functions follow the Schaefer specification and  $U(Y_t) = (10Y_t)^{0.7}$ ,  $b = 0.97$ ,  $C(E_t) = 0$ . Two optimal solutions (solid lines A and B) are shown in an aggregate biomass-yield state space. For comparison, the dotted lines show the feedback control for the biomass model.

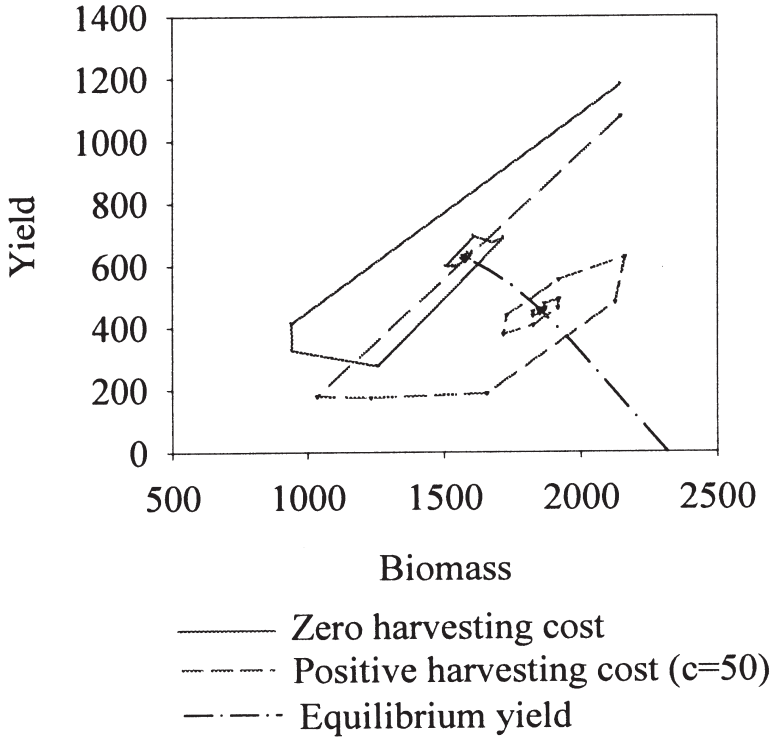


**Figure 8.** Comparison of Biomass and Age-structured Models

In figure 9 it is assumed that fishing gear has the knife-edge selectivity property. Under such fishing technology, the model's properties change drastically. If harvest affects only the six oldest age classes and the discount rate is high enough, in the resulting equilibrium, age class 3 is completely harvested every period and older age classes do not exist. Obviously, it is not possible to reach lower biomass levels independently of the discount rate. Note that the equilibrium biomass-yield function exists only for biomass levels containing fish from age class 3 and older. In figure 9, this lowest attainable biomass level is somewhat below 1,500 thousand tons. The solution that reaches this biomass level after several over-shootings has the same parameter values as the benchmark case in figure 8 (the solution with a higher initial biomass) excluding that  $q_1 = q_2 = 0$ . The other solution in figure 9 follows if harvesting costs are positive but linear ( $c = 50$ ). The case of knife-



edge selectivity is highly relevant in fishery regulation, but it is unclear how the biomass approach could describe fisheries applying such technologies. More complications would arise if a possibility to choose from several fishing technologies were added to the model.



**Figure 9.** Optimal Solutions under Knife Edge Selectivity

Note:  $q_1 = q_2 = 0$ .

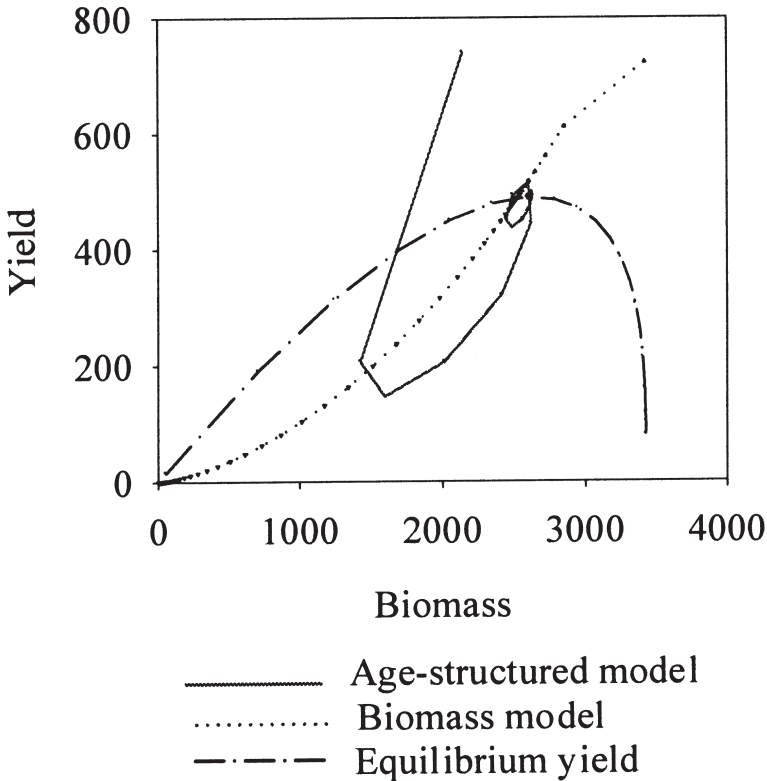
Figures 10a and b describe a case where fecundity is zero for age classes  $s = 1, \dots, 4$ . In this case, the equilibrium biomass-yield function exists over the normal range, but its shape differs from the benchmark case (figure 8). Again, the optimal solution for the age-structured model contains over-shootings, while the solutions for the biomass model are monotonic paths toward the steady state with a slightly lower biomass level. Figure 10b compares the optimal solutions under high interest rates. Zero fecundity for the young age classes decreases the slope of the equilibrium biomass-yield function for low biomass levels, implying that the existence of optimal steady states becomes more critical. In the example, an interest rate equal to  $r = 0.287$  is high enough to imply that according to the biomass model, it is optimal to deplete the population. However, as shown, an optimal sustainable harvesting solution exists for the age-structured model. Clearly such an interest rate is high, but nevertheless the example demonstrates a crucial difference between the biomass and the age-structured model.

Figures 11a and b show the outcome if the youngest (and smallest) fish are not commercially valuable. In figure 11a, it is assumed that the three youngest age classes are commercially worthless but that the catchability and fecundity parameters are as in the baseline case (table 1). As shown in figure 11a, the optimal solution does not converge to a steady state with constant yield and biomass. Instead, the long-run optimal solution is a limit cycle where yield and biomass (and other variables) fluctuate over time (the

solid line in figure 11b). This type of solution is optimal, since after closing the fishery for some periods, the age distribution changes and a larger proportion of the catch will consist of the valuable older age classes. This solution therefore attempts to avoid growth overfishing (see footnote 8). If it is assumed that the gear has the knife-edge selectivity property and  $q_s = 0$ ,  $s = 1,2,3$ ; the cycle disappears and the solution approaches a steady state with constant yield and biomass over time.

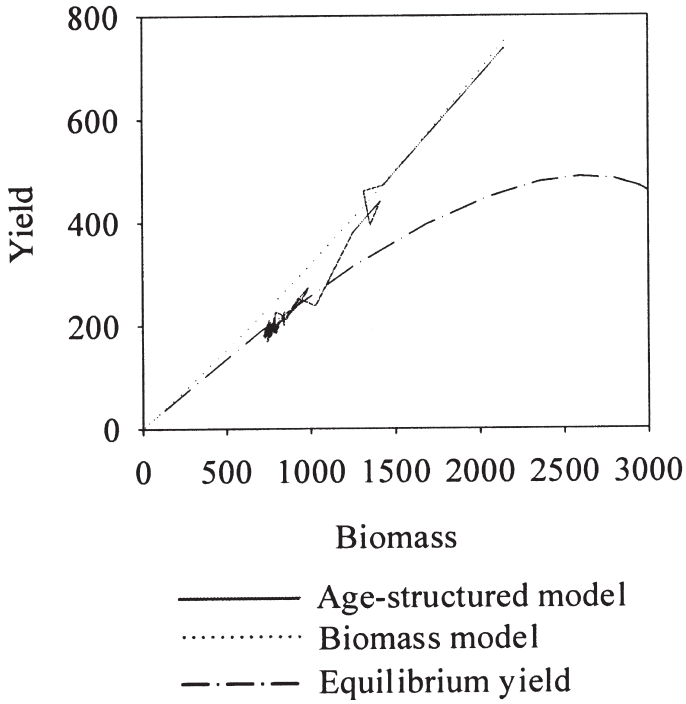
The concavity properties of the utility function also have implications for the cyclicity of the optimal solution. In figure 11b, the path that stabilizes at the yield level of 200 thousand tons is the optimal solution if the concavity parameter in the utility function is decreased from 0.7 to 0.5. Thus, the cycle disappears when the concavity of periodic outcome with respect to yield is increased. In contrast, the dotted line in figure 11b is the optimal solution when the objective function is linear with respect to yield (and effort). This solution is an example of a pure pulse fishing strategy.

Pulse fishing is a somewhat mysterious topic in fishery literature. Age-structured optimization studies have typically proposed pulse fishing as the optimal solution (Walters 1969; Hannesson 1975). Clark (1990) offers an analysis of pulse fishing in the context of the classic Beverton-Holt model with constant exogenous recruitment, zero harvesting cost, linear utility, and a somewhat *ad hoc* application of the Faustmann forest formula. In his solutions, the entire fish population is harvested at regular intervals, the length of which is solved using the Faustmann forest formula. Clark (1990) writes that in his analysis exogenous recruitment is one prerequisite for pulse fishing.

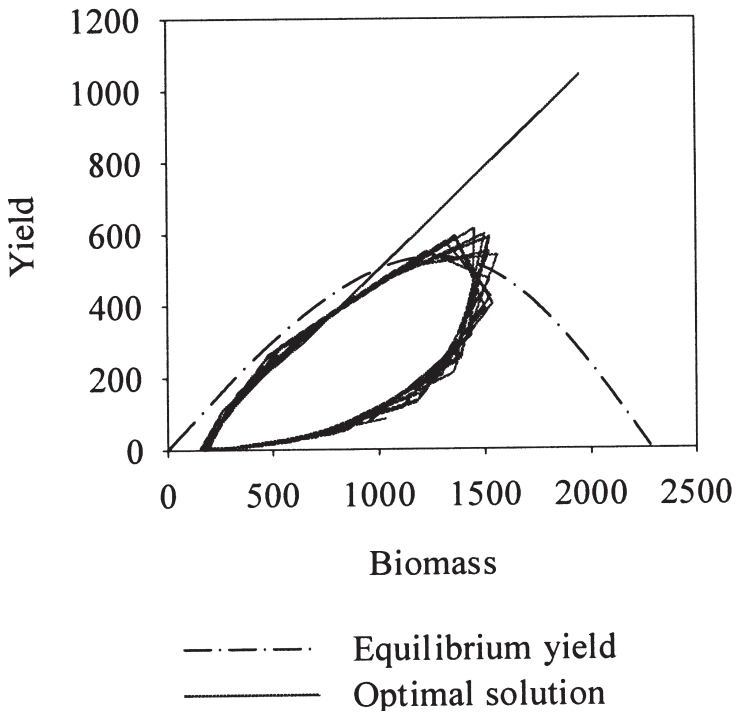


**Figure 10a.** Zero Fecundity for Young Age Classes

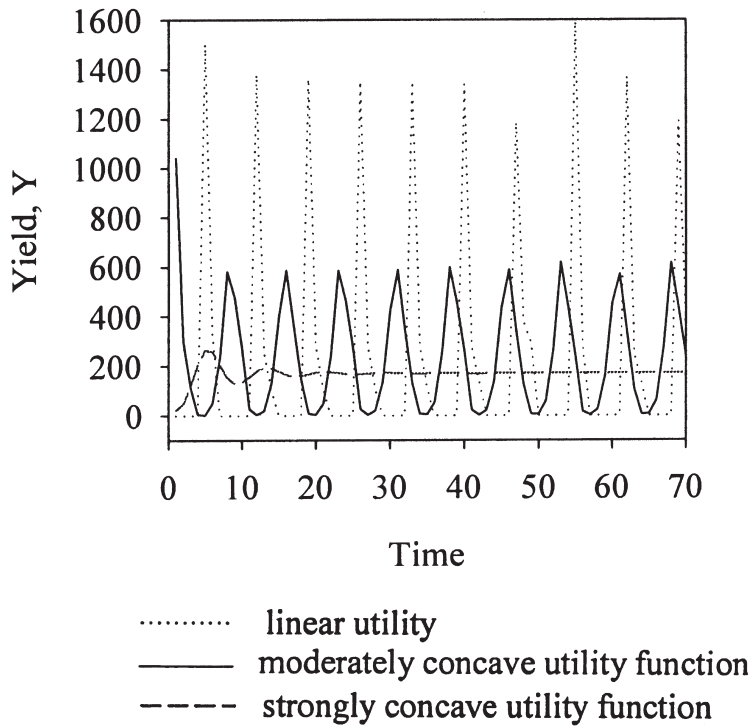
Note:  $q_s = 0$ ,  $s = 1,2,3,4$ .



**Figure 10b.** Zero Fecundity for Young Age Classes and High Rate of Interest: Extinction under the Biomass Model, Sustainable Harvest under Age-structured Model



**Figure 11a.** Optimal Limit Cycle when the Three Youngest Age Classes are Commercially Valueless



**Figure 11b.** Optimal Pulse Fishing when the Three Youngest Age Classes are Commercially Valueless

The analysis in this paper shows that pulse fishing should be understood as a boundary limit cycle. Between the pulse fishing solution and the equilibrium with smooth harvest over time, there is a continuum of interior limit cycles depending on the model parameters. The intuition is that since gear is nonselective, and the youngest age classes are not commercially valuable, the normal sustainable harvest strategy that is constant over time implies growth overfishing. This can be partly avoided if harvesting is periodically decreased to nearly zero so that older age classes form a larger proportion of the population. With linear utility and effort cost, the optimal harvest level is temporarily equal to zero between the periods with positive yield, but due to endogenous recruitment, the population level must remain strictly positive over the cycle (figure 11a).

## Summary

This study shows that there is no guarantee that any of the basic features of the biomass model will carry over to the age-structured framework. The differences between the two approaches can be summarized as follows:

1. In the biomass model, sustainable yield is based on biological properties of the natural production function; while in the age-structured approach, it is based both on biological factors and fishing technology.
2. Excluding coincidences, the optimal steady states of the two models are equal only for MSY.

3. Conditions for the existence of optimal steady state (or optimal sustainable harvesting policy) are different for the biomass and age-structured models.
4. In the biomass framework the optimal transition paths are monotonic, but in the age-structured framework the paths (in biomass-yield state space) are typically non-monotonic and may contain damped oscillations.
5. In the biomass model, optimal yield is an increasing function of biomass, while in the age-structured framework, optimal yield is a function of the number of individuals in different age classes. If the population is dominated by young age classes, the optimal yield may decrease as a function of biomass.
6. If the optimization problem is linear in yield and effort, the discrete time biomass model yields constant escapement. This policy is not optimal for the age-structured model.
7. Under knife-edge selectivity, the equilibrium biomass-sustainable yield relationship does not exist in the usual sense and the optimal steady state may be (locally) independent of the discount rate.
8. Depending on the catchability profile, effort cost, and price determination, the age-structured model may yield limit cycles and pulse fishing as the optimal solution. Similar factors behind the pulse fishing strategy are difficult (or impossible) to analyze applying the biomass model.

Earlier studies have found that the age-structured model would almost inevitably yield the pulse fishing strategy as the optimal solution (Walters 1969; Hannesson 1975; Clark 1990). This study suggests that even when the problem is linear in yield and effort, the optimal solution may converge toward a steady state with constant harvest. To some extent, this difference may follow from the choice of this study to apply the normal approach in economic models where control is specified as an instantaneous event instead of the classic Beverton and Holt (1957) formulation where fishing is constant over each period.<sup>10</sup> However, pulse fishing is also possible and is shown to represent a boundary limit cycle. In the case of knife-edge selectivity, the biomass-sustainable yield curve does not exist in the usual sense and the optimal steady state may be (locally) independent of the discount rate. These results, and the generic model version developed, are new both to fishery economics and ecology. From the economic point of view, the study emphasizes that the population age structure includes valuable information on future harvesting possibilities that is ignored when the biomass model is applied.

Ongoing discussions suggest that including the population age structure into economic studies deserves more emphasis (Walters and Martell 2004; Moxnes 2005; Stage 2006; Tahvonen 2008). An example of an interesting problem is the endogenous choice of fishing gear with different catchability profiles (*cf.* Bjorndal and Brasao 2006). Despite complexity, it should be possible to study the age-structured model analytically without deviations from the most fruitful specifications. Analytical work will increase the understanding of why the optimal steady states differ for the two models. Studying deterministic fishery models should be understood only as stepping stones toward empirically more realistic models with stochastic recruitment and fish price. Adding multiple species or spatial structure should not produce overly complex problems for numerical analysis.

## References

Baranov, F.I. 1918. On the Question of the Biological Basis of Fisheries. Institute for Scientific Ichthyological Investigations. *Proceedings* 1:81-128.

---

<sup>10</sup> Recall that this specification is applied by several fishery ecologists as well (Pope 1972; Walters and Martell 2004; Quinn and Deriso 1999) but not in optimization studies.

- Beverton, J.R.H., and S.J. Holt. 1957. On the Dynamics of Exploited Fish Populations. Ministry of Agriculture, Fisheries and Food. *Fishery Investigation Series* 2(19).
- Bjorndal, T., and A. Brasao. 2006. The East Atlantic Bluefin Tuna Fisheries: Stock Collapse or Recovery? *Marine Resource Economics* 21:193-210.
- Brown, G.M. 2000. Renewable Natural Resource Management and Use without Prices. *Journal of Economic Literature* 38(3):875-914.
- Byrd, R.H., M.E. Hribar, and J. Nocedal. 1999. An Interior Point Algorithm for Large Scale Nonlinear Programming. *SIAM Journal on Optimization* 9(4):877-900.
- Byrd, R.H., J. Nocedal, and R.A. Waltz. 2006. KNITRO: An Integrated Package for Nonlinear Optimization. *Large-Scale Nonlinear Optimization*, G. di Pillo and M. Roma, eds., pp. 35-59. New York, NY: Springer.
- Clark, C.W. 1973. Profit Maximization and the Extinction of Animal Species. *Journal of Political Economy* 81:950-61.
- \_\_\_\_\_. 1985. *Bioeconomic Modelling of Fisheries Management*. New York, NY: John Wiley & Sons, Inc.
- \_\_\_\_\_. 1990. *Mathematical Bioeconomics: The Optimal Management of Renewable Resources*. New York, NY: John Wiley & Sons, Inc.
- Deriso, R.B. 1987. Optimal  $F_{0.1}$  Criteria and Their Relationship to Maximum Sustainable Yield. *Canadian Journal of Fisheries and Aquatic Sciences* 44:339-48.
- Getz, W.M. 1980. The Ultimate Sustainable Yield Problem in Nonlinear Age-Structured Populations. *Mathematical Biosciences* 48(3-4):269-92.
- Getz W.M., and R.G. Haight. 1989. *Population Harvesting: Demographic Models for Fish, Forest and Animal Resources*. Princeton, NJ: Princeton University Press.
- Gulland, J.A. 1983. *Fish Stock Assessment: A Manual of Basic Methods*. New York, NY: John Wiley & Sons.
- Haddon, M. 2001. *Modelling and Quantitative Methods In Fisheries*. Boca Raton, FL: Chapman & Hall/CRC.
- Hannesson, R. 1975. Fishery Dynamics: A North Atlantic Cod Fishery. *Canadian Journal of Economics* 8(2):151-73.
- Hightower, J.E., and G.D. Grossman. 1985. Comparison of Constant Effort Policies for Fish Stocks with Variable Recruitment. *Canadian Journal of Fisheries and Aquatic Sciences* 42:982-88.
- Hightower, J.E., and W.H. Lenarz. 1989. Optimal Harvesting Policies for Widow Rockfish Fishery. *American Fishery Society Symposium* 6:83-91.
- Hilborn, R., and C.J. Walters. 1992. *Quantitative Fisheries Stock Assessment: Choice, Dynamics and Uncertainty*. London: Chapman & Hall, Inc.
- Horwood, J.W. 1987. A Calculation of Optimal Fishing Mortalities. *Journal of the International Council for the Exploration of the Sea* 43:199-208.
- \_\_\_\_\_. 1996. Risk-Sensitive Optimal Harvesting and Control of Biological Populations. *Mathematical Medicine Biology* 13(1):35-71.
- Horwood, J.W., and P. Whittle. 1986. The Optimal Harvest from a Multicohort Stock. *IMA Journal of Mathematics and Applied Medicine Biology* 3:143-55.
- Jennings, S., M.J. Kaiser, and J.D. Reynolds. 2007. *Marine Fisheries Ecology*. Malden, MA: Blackwell.
- Kennedy, J. 1992. Optimal Annual Changes in Harvest from Multicohort Fish Stocks: The Case of Western Mackerel. *Marine Resource Economics* 7:95-114.
- Lawson, A.T., and R. Hilborn. 1985. Equilibrium Yields and Yield Isoleths from a General Age-Structured Model of Harvested Populations. *Canadian Journal of Fisheries and Aquatic Sciences* 42:1766-71.
- Lopez-Calva, G., S. Leyffer, and J. Nocedal. 2007. Interior Point Methods for Mathematical Programs with Complementarity Constraints. *SIAM Journal of Optimization* 17:52-77.
- Millar, R.B., and F.J. Fryer. 1999. Estimating Size-Selective Curves of Trawls, Traps, Gillnet and Hooks. *Review of Fish Biology and Fisheries* 9:89-116.

- Moxnes, E. 2005. Policy Sensitivity Analysis. Simple versus Complex Fishery Models. *Systems Dynamics Review* 21(2):123-45.
- Pope, J.G. 1972. An Investigation of the Accuracy of Virtual Population Analysis Using Cohort Analysis. *Research Bulletin of the International Commission Northwest Atlantic Fisheries* 9:65-74.
- Quinn II, T.J., and R.B. Deriso. 1999. *Quantitative Fishery Dynamics*. Oxford: Oxford University Press.
- Reed, W.J. 1979. Optimal Escapement Levels in Stochastic and Deterministic Harvesting Models. *Journal of Environmental Economics and Management* 6:350-63.
- Ricker, W.E. 1954. Stock and Recruitment. *Journal of Fishery Resource Board Canada* 11:559-623.
- Schaefer, M.B. 1954. Some Aspects of the Dynamics of Populations Important to the Management of Commercial Marine Fisheries. *Bulletin, Inter-American Tropical Tuna Commission* 1:25-56.
- Spence, M. 1973. Blue Whales and Applied Control Theory. *Technical Report No. 108*. Institute for Mathematical Studies in the Social Sciences. Stanford University, CA.
- Stage, J. 2006. Optimal Harvesting In an Age-Class Model with Age-Specific Mortalities: An Example from Namibian Linefishing. *Natural Resource Modelling* 19(4):609-31.
- Tahvonen, O. 2008. Harvesting Age-Structured Populations as a Biomass: Does it Work? *Natural Resource Modelling* 21:525-50.
- Townsend, R.E. 1986. A Critique of Models of the American Lobster Fishery. *Journal of Environmental Economics and Management* 13:277-91.
- Wächter, A., and L.T. Biegler. 2006. On the Implementation of an Interior-Point Filter Line-Search Algorithm for Large Scale Nonlinear Programming. *Mathematical Programming* 106:25-57.
- Walters, C.J. 1969. A Generalized Computer Simulation Model for Fish Population Studies. *Transactions of the American Fisheries Society* 98:505-12.
- Walters, C.J., and S.J.D. Martell. 2004. *Fisheries Ecology and Management*. Princeton, NJ: Princeton University Press.
- Wilén, J.E. 1985. Bioeconomics of Renewable Resource Use. *Handbook of Natural Resource and Energy Economics*, vol.1, A.V. Kneese and J.L. Sweeney, eds. Amsterdam: Elsevier.
- \_\_\_\_\_. 2000. Renewable Resource Economists and Policy: What Differences Have We Made? *Journal of Environmental Economics and Management* 39:306-27.

