

# The Ultimate-Sustainable-Yield Problem in Nonlinear Age-Structured Populations\*

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## ABSTRACT

The Beverton-Holt theory of harvesting a multicohort fishery subject to constant recruitment, and the Leslie matrix harvesting model modified to include a nonlinear stock-recruitment relationship, are extended and shown to be related through the ultimate-sustainable-yield problem for an age-structured population. The well-known result that the optimal harvesting policy for the Leslie matrix model is bimodal is shown to hold for the Leslie matrix model modified to include an arbitrary stock-recruitment relationship. This conclusion extends a recent result of Reed (1979), who proved bimodality of the optimal harvesting strategy for the Leslie matrix model modified to include only compensatory stock-recruitment relationships. The paper concludes with a numerical example which demonstrates how the ultimate sustainable yield can be used as a standard of comparison for any sustainable-yield harvesting policy.

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## 1. INTRODUCTION

The problem of harvesting age-structured populations has recently received considerable attention [1, 3–5, 10, 14–18]. In all the above papers, however, with the exception of that by Clark [3], the population is modeled by a Leslie matrix [11, 12] or extended Leslie matrix model, and it is harvested by removing a certain proportion of individuals in each age group, either at the beginning of each time interval (harvesting before reproduction) or at the end of each time interval (harvesting after reproduction). Clark uses Beverton-Holt theory [2] to develop strategies for harvesting multiple cohort fisheries, but this theory suffers from the drawback that it assumes that recruitment is independent of population density.

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In the present paper the problem is considered of obtaining the ultimate sustainable yield from an age-structured population. Our approach generalizes both the Beverton-Holt theory in fisheries management as expounded by Clark [3] and the Leslie matrix model extended to include density-dependent stock-recruitment, as proposed by Reed [15]. In particular the results of Clark are extended to include a nonlinear density-dependent stock-recruitment relationship, while the results of Reed are extended to allow harvesting to take place at points in the interior of the basic iteration interval of the model. Furthermore, whereas Reed's result is derived from compensatory stock-recruitment curves only, the results in this paper are derived for arbitrary stock-recruitment curves.

The analysis results in a harvesting policy that can be regarded as providing the "ultimate" yield that the population can sustain over an arbitrarily long interval of time. This "ultimate sustainable yield" policy resembles the bimodal harvesting policies of Beddington and Taylor [1], Rorres and Fair [17], and Reed [15] (i.e., each cohort is reduced to some optimal level and then totally harvested at some subsequent age), but differs in that an optimal harvesting time is determined for each cohort.

Since the ultimate-sustainable-yield harvesting strategy depends on the implementation of impulse control in the Beverton-Holt model, this strategy cannot be physically realized and the ultimate sustainable yield cannot be attained. This yield does, however, provide a standard against which the performance of any sustainable-yield harvesting policy can be compared.

After the theory has been developed, a numerical example is presented using data derived from the purse-seine anchovy (*Engraulis capensis*) fishery situated off the Western Cape Coast of South Africa.

## 2. FORMULATION OF THE MODEL

Assume that each year can be divided into two seasons: a harvesting season of length  $0 < \bar{t} < 1$  (units of time measured in years) and a spawning season of length  $1 - \bar{t}$ . Let the  $i$ th component of the vector  $\mathbf{x}(t) \in R^n$  denote the number of individuals in the  $i$ th age class,  $i = 1, \dots, n$ , at time  $t$ . The  $i$ th age class consists of individuals of age  $i - 1$  years,  $i = 1, \dots, n - 1$ , while the  $n$ th age class consists of individuals of age  $n - 1$  years and more.

At the beginning of the  $(k + 1)$ th year,  $k = 0, 1, 2, \dots$ , a cohort of zero-year-old individuals  $(x_1(k))$  enters the population after having been spawned during the previous spawning season. Assume that the relationship between the new recruits  $x_1(k)$  and the biomass of the parent stock, denoted by  $p$ , at the beginning of the previous spawning season is given by an appropriate stock-recruitment function  $f(p) : [0, \infty) \rightarrow [0, \infty)$ . Clearly

$$p(t) = \sum_{i=1}^n c_i(t) w_i(t) x_i(t), \quad (1)$$

where  $c_i(t)$  is the proportion of individuals in the  $i$ th age class that are sexually mature at time  $t$ , and  $w_i(t)$  is the average biomass of an individual in the  $i$ th age class at time  $t$ .

Assume that the  $i$ th age class is subjected to a time-independent natural mortality rate  $\alpha_i$  (for a treatment of the case of a time-dependent period  $\alpha_i(t)$ , see [9]) and that during the harvesting season a time-dependent harvesting intensity  $u_i(t)$ ,  $i = 1, \dots, n$ , is applied. Then the following model, representing an extension of the Beverton-Holt theory, is presented in [6]:

*Harvesting season:*

$$\begin{aligned} t \in [k, k + \bar{t}], \quad k = 0, 1, 2, \dots, \\ \dot{x}_i = -(\alpha_i + u_i(t))x_i, \quad i = 1, \dots, n; \end{aligned} \tag{2}$$

*Spawning season:*

$$\begin{aligned} x_1(k + 1) &= f(p(k + \bar{t})), \\ x_{i+1}(k + 1) &= e^{-\alpha_i(1-\bar{t})}x_i(k + \bar{t}), \quad i = 1, \dots, n - 2, \\ x_n(k + 1) &= e^{-\alpha_{n-1}(1-\bar{t})}x_{n-1}(k + \bar{t}) + e^{-\alpha_n(1-\bar{t})}x_n(k + \bar{t}). \end{aligned} \tag{3}$$

Inherent in (2) is the assumption that each age class can be selectively harvested at harvesting intensities that have as yet no specific constraints on their form or magnitude. This is unrealistic, of course, owing to constraints imposed by the structure of the fishery and also physical and economic constraints which limit the type of harvesting strategies that can be implemented.

One modification to (2) is to assume that during any given harvesting season only a scalar harvesting intensity  $v$  can be applied to each age class and that each age class responds to this harvesting intensity through a catchability coefficient  $q_i$  which reflects the nature of the fishing gear (e.g. mesh size) and the availability of the age class to the fishery. In this case (2) becomes

$$\dot{x}_i = -(\alpha_i + q_i v)x_i, \quad i = 1, \dots, n. \tag{4}$$

We are interested in examining sustainable yield solutions to the model (2), (3). These solutions will arise when a periodic harvesting policy  $\hat{u}(\cdot)$  satisfying

$$\hat{u}_i(k + t) = \hat{u}_i(t), \quad t \in [0, \bar{t}], \quad k = 1, 2, 3, \dots, \tag{5}$$

is applied to an initial condition  $\mathbf{x}(0) = \hat{\mathbf{x}}$  (if one exists) for which the resulting solution is in a dynamic equilibrium, i.e.

$$\mathbf{x}(k) = \hat{\mathbf{x}}, \quad k = 1, 2, 3, \dots \tag{6}$$

If (2) is integrated over the first time interval with  $\mathbf{u}(\cdot) = \hat{\mathbf{u}}(\cdot)$  and  $\mathbf{x}(0) = \hat{\mathbf{x}}$ , then (2) and (3) together with (6) (for  $k=1$ ) can be combined to yield an equation

$$\hat{\mathbf{x}} = F(\hat{\mathbf{x}}, \hat{\mathbf{u}}(\cdot)), \quad (7)$$

which, under suitable conditions, can be solved to provide an equilibrium solution  $\hat{\mathbf{x}}$  in terms of a given  $\hat{\mathbf{u}}(\cdot)$ . This has been done in [8] for the case where  $\hat{\mathbf{u}}(\cdot)$  has the form resulting in (4), and  $f(p)$  is one of the stock-recruitment relationships

$$\text{Beverton-Holt} \quad f(p) = \frac{\beta p}{\gamma + p}, \quad (8)$$

$$\text{Ricker} \quad f(p) = \frac{\beta}{\gamma} p e^{1-p/\gamma}, \quad (9)$$

$$\text{Depensation} \quad f(p) = \frac{\beta p^2}{\gamma^2 + p^2}, \quad (10)$$

where  $\beta$  and  $\gamma$  are positive parameters.

The stability of the equilibrium solution  $\hat{\mathbf{x}}$  depends of course on the form of the stock-recruitment function  $f$  and the parameter values of the model. A full discussion of this point can be found in [15].

Consider the biomass yield  $Y$  obtained over any given harvesting season by harvesting the population at intensity  $\hat{\mathbf{u}}(\cdot)$  and at a corresponding equilibrium level  $\hat{\mathbf{x}}$ . Then if  $w_i(t)$  is the biomass function introduced above for the  $i$ th age class [see discussion below (1)], the seasonal biomass yield is

$$Y(\hat{\mathbf{u}}(\cdot)) = \int_0^{\bar{t}} \sum_{i=1}^n w_i(t) \hat{u}_i(t) \hat{x}_i(t) dt, \quad (11)$$

where  $\hat{x}_i(t)$  is the solution to (2) when  $u_i(t) = u_i(\hat{t})$  and  $x_i(0) = \hat{x}_i$ .

In [6] it was shown that  $Y(\hat{\mathbf{u}}(\cdot))$  defined by (11) achieves its maximum value when  $\hat{\mathbf{u}}(\cdot)$  belongs to the class of impulse controls characterized by the vectors  $(\mathbf{t}^*, \hat{\mathbf{z}})$ , where the elements  $t_i^*$  of  $\mathbf{t}^* \in R^n$  denote the optimum time on  $[0, \bar{t}]$  at which the amount of biomass  $z_i$  (the  $i$ th element of  $\mathbf{z} \in R^n$ ) should be removed. If  $b_i(t)$  is the total biomass of the  $i$ th age class in the absence of harvesting, i.e. on  $[0, \bar{t}]$

$$b_i(t) = w_i(t) x_i(0) e^{-\alpha_i t}, \quad (12)$$

then  $t_i^*$  is determined by

$$t_i^* = \arg \max b_i(t), \quad t \in [0, \bar{t}], \quad i = 1, \dots, n, \quad (13)$$

while the optimal  $\hat{\mathbf{z}}$  remains to be determined. This latter problem will be given full consideration below.

Differentiating (12) with respect to  $t$ , we have

$$\dot{b}_i = w_i(t)x_i(0)e^{-\alpha_i t} \left( \frac{\dot{w}_i(t)}{w_i(t)} - \alpha_i \right). \tag{14}$$

Since the biomass functions  $w_i(t)$  are derived from a biomass growth function  $w(t)$  by means of the relationship

$$w_i(t) = w(t - k + i - 1), \quad i = 1, \dots, n \quad t \in [k, k + 1), \tag{15}$$

then under the physically reasonable assumptions that  $w(t)$  is increasing and bounded and that the proportional rate of increase in  $w(t)$  is a decreasing function of time, i.e.

$$0 \leq w(t) \leq \bar{w}, \quad \dot{w}(t) > 0, \quad \frac{d}{dt} \left[ \frac{\dot{w}(t)}{w(t)} \right] < 0, \tag{16}$$

the condition (13) yields

$$\begin{aligned} t_i^* &= 0 && \text{if } \dot{w}_i(0)/w_i(0) \leq \alpha_i \\ t_i^* &= \bar{t} && \text{if } w_i(\bar{t})/w_i(\bar{t}) \geq \alpha_i; \end{aligned} \tag{17}$$

or if  $\dot{w}_i(\bar{t})/w_i(\bar{t}) < \alpha_i < \dot{w}_i(0)/w_i(0)$ , then  $t_i^*$  is the solution to

$$\dot{w}_i(t_i^*)/w_i(t_i^*) = \alpha_i. \tag{18}$$

Under impulse control  $(z, t^*)$  the model (2), (3) can be shown (following [6]) to reduce to the system

$$\begin{aligned} x_1(k+1) &= f \left( \sum_{i=1}^n \bar{c}_i \bar{w}_i(x_i(k)e^{-\alpha_i \bar{t}} - z_i e^{-\alpha_i(\bar{t}-t_i^*)}) \right), \\ x_{i+1}(k+1) &= x_i(k)e^{-\alpha_i} - z_i e^{-\alpha_i(1-t_i^*)}, \quad i = 1, \dots, n-2, \\ x_n(k+1) &= x_{n-1}(k)e^{-\alpha_{n-1}} + x_n(k)e^{-\alpha_n} - z_{n-1}e^{-\alpha_{n-1}(1-t_{n-1}^*)} - z_n e^{-\alpha_n(1-t_n^*)}, \end{aligned} \tag{19}$$

where the  $\bar{c}_i = c_i(k + \bar{t})$ ,  $\bar{w}_i = \bar{w}_i(k + \bar{t})$ , and the elements  $z_i$  must clearly satisfy

$$0 \leq z_i \leq x_i(k)e^{-\alpha_i t_i^*}, \quad i = 1, \dots, n. \tag{20}$$

The system (19) can be recognized as a harvested Leslie matrix model extended as in [15] to include a nonlinear stock-recruitment function  $f(p)$ .

At equilibrium, i.e. using (6), the system (19) can be rearranged so that all elements of  $\hat{x}$  are expressed in terms of  $\hat{z}$  and  $\hat{x}_1$ , thus obtaining

$$\begin{aligned} \hat{x}_1 &= f\left(p_0 \hat{x}_1 - \sum_{i=1}^n p_i \hat{z}_i\right), \\ \hat{x}_{i+1} &= \prod_{j=1}^i e^{-\alpha_j} \hat{x}_1 - \sum_{r=1}^i \prod_{j=r}^i e^{-\alpha_j} e^{\alpha_r t_r^*} \hat{z}_r, \quad i = 1, \dots, n-2, \\ \hat{x}_n &= \frac{1}{1 - e^{-\alpha_n}} \left[ \prod_{j=1}^{n-1} e^{-\alpha_j} \hat{x}_1 - \sum_{r=1}^{n-1} \prod_{j=r}^{n-1} e^{-\alpha_j} e^{\alpha_r t_r^*} \hat{z}_r - e^{-\alpha_n(1-t_n^*)} \hat{z}_n \right], \end{aligned} \tag{21}$$

where

$$\begin{aligned} p_0 &= c_1 e^{-\alpha_1 \bar{t}} + \sum_{i=2}^{n-1} c_i e^{-\alpha_i \bar{t}} \prod_{j=1}^{i-1} e^{-\alpha_j} + \frac{c_n e^{-\alpha_n \bar{t}}}{1 - e^{-\alpha_n}} \prod_{j=1}^{n-1} e^{-\alpha_j}, \\ p_i &= \left[ c_i e^{-\alpha_i \bar{t}} + \sum_{r=i+1}^{n-1} c_r e^{-\alpha_r \bar{t}} \prod_{j=i}^{r-1} e^{-\alpha_j} + \frac{c_n e^{-\alpha_n \bar{t}}}{1 - e^{-\alpha_n}} \prod_{j=i}^{n-1} e^{-\alpha_j} \right] e^{\alpha_i t_i^*}, \\ & \qquad \qquad \qquad i = 1, \dots, n-2, \end{aligned} \tag{22}$$

$$p_i = \left[ c_i e^{-\alpha_i \bar{t}} + \frac{c_n e^{-\alpha_n \bar{t}} e^{-\alpha_i}}{1 - e^{-\alpha_n}} \right] e^{\alpha_i t_i^*}, \quad i = n-1, n.$$

Furthermore it has been shown [6] that under impulse control  $(t^*, \hat{z})$  (11) reduces to

$$Y_{t^*}(\hat{z}) = \sum_{i=1}^n w_i(t_i^*) \hat{z}_i. \tag{23}$$

If  $\hat{z}$  and  $\hat{x}$  are inserted in (20), i.e.

$$0 < \hat{z}_i \leq \hat{x}_i e^{-\alpha_i t_i^*}, \quad i = 1, \dots, n, \tag{24}$$

we are faced with the problem of choosing  $\hat{x}_1$  and  $\hat{z}$  to maximize (23) subject to the equations (21) and constraint inequalities (24). This latter set of constraint inequalities can, by means of (21), be shown to be equivalent to

$$\begin{aligned} \hat{x}_1 &\geq 0, \\ \sum_{r=1}^i q_r \hat{z}_r &\leq \hat{x}_1, \quad i = 1, \dots, n, \end{aligned} \tag{25}$$

where

$$\begin{aligned}
 q_1 &= e^{\alpha_1 t_1^*}, \\
 q_r &= e^{\alpha_r t_r^*} \prod_{j=1}^{r-1} e^{\alpha_j}, \quad r=2, \dots, n-1, \\
 q_n &= e^{\alpha_n t_n^*} \prod_{j=1}^{n-1} e^{\alpha_j} e^{-\alpha_n}.
 \end{aligned}
 \tag{26}$$

It should be noted that once  $\hat{x}_1$  and  $\hat{z}$  are known,  $\hat{x}_i, i=2, \dots, n$ , are generated using (21).

It is clear from (26) that  $q_i > 0, i=1, \dots, n$ , which together with the constraints  $\hat{z}_i \geq 0, i=1, \dots, n$ , implies that if the final inequality in (25) (i.e.  $i=n$ ) is satisfied, then so are the preceding  $n-1$  inequalities, which are thus redundant. Hence the problem of finding the optimal  $\hat{z}$  reduces to the following programming problem:

*IMPULSE HARVESTING PROBLEM*

$$\max_{\hat{x}_1, \hat{z}} Y_{t^*}(\hat{z}) = \sum_{i=1}^n w_i(t_i^*) \hat{z}_i$$

subject to

$$\begin{aligned}
 \hat{x}_1 &= f\left(p_0 \hat{x}_1 - \sum_{i=1}^n p_i \hat{z}_i\right), \\
 \sum_{i=1}^n q_i \hat{z}_i &\leq \hat{x}_1, \\
 \hat{z}_i &\geq 0, \quad i=1, \dots, n, \\
 \hat{x}_1 &\geq 0.
 \end{aligned}
 \tag{27}$$

This harvesting problem can be converted into a linear programming problem in one of two ways. The first of these is appropriate when the stock-recruitment function has an inverse  $f^{-1}$  on  $[0, \infty)$ , as is the case when  $f$  is strictly increasing on  $[0, \infty)$ . The Beverton-Holt curve (8) and depensation curve (10) are of this type, as are all curves in the class of normal compensatory curves. In case  $f^{-1}$  exists, (27) reduces to the following problem.

*PARAMETRIC LINEAR PROGRAMMING PROBLEM WHEN  $f^{-1}$  EXISTS*

$$\max_{\hat{x}_1, \hat{z}} \sum_{i=1}^n w_i(t_i^*) \hat{z}_i$$

subject to

$$\begin{aligned} \sum_{i=1}^n p_i \hat{z}_i &= p_0 \hat{x}_1 - f^{-1}(\hat{x}_1), \\ \sum_{i=1}^n q_i \hat{z}_i &\leq \hat{x}_1, \\ \hat{z}_i &\geq 0, \quad i = 1, \dots, n, \end{aligned} \quad (28)$$

where  $\hat{x}_1$  is a parameter that ranges over  $[0, \infty)$ .

If  $f$  does not possess an inverse on  $[0, \infty)$ , then a parameter  $\hat{p}$  can be introduced such that (27) reduces to the following problem.

*PARAMETRIC LINEAR PROGRAMMING PROBLEM FOR GENERAL  $f$*

$$\max_{\hat{p}, \hat{x}_1, \hat{z}} \sum_{i=1}^n w_i(t_i^*) \hat{z}_i$$

subject to

$$\begin{aligned} p_0 \hat{x}_1 - \sum_{i=1}^n p_i \hat{z}_i &= \hat{p}, \\ \hat{x}_1 &= f(\hat{p}), \\ \sum_{i=1}^n q_i \hat{z}_i - \hat{x}_1 &\leq 0, \\ \hat{x}_1 &\geq 0, \quad \hat{z}_i \geq 0, \quad i = 1, \dots, n, \end{aligned} \quad (29)$$

where  $\hat{p}$  is a parameter that ranges over  $[0, \infty)$ .

It should be noted that the range of  $\hat{p}$  follows from the fact that  $\hat{p}$  is the equilibrium level of the adult spawning stock. Also, since  $f$  is a stock-recruitment curve, we have that  $f(0) = 0$ .

The fundamental theorem of linear programming (see, for example, [13]) asserts that an optimal basic feasible solution exists whenever an optimal feasible solution exists. Also, for any given value of  $\hat{p} \in [0, \infty)$  a basic feasible solution of the constraints (29) will involve at most  $\hat{x}_1$  and two elements of  $\hat{z}$  being nonzero. Thus for a given value of  $\hat{p}$  the corresponding optimal solution will be of the form

$$\hat{x}_1 \geq 0, \quad \hat{z}_j \geq 0, \quad \hat{z}_k \geq 0, \quad \hat{z}_i = 0, \quad i \neq j \text{ or } k, \quad i = 1, \dots, n.$$

It should be noted that  $\hat{x}_1 = 0$  can be optimal only when the only feasible solution is  $\hat{x}_1 = 0, \hat{z}_i = 0, i = 1, \dots, n$ , since the parameters  $q_i$  defined in (28) are all positive.

If the inequality constraint in (29) is inactive at the optimal solution, then at most one element of  $\hat{z}$  needs to be nonzero. Furthermore if the inequality constraint in (29) is tight at the optimal solution, this implies that the right-hand inequality in (24) is tight, so that the older of the two age groups that need to be harvested must then be harvested completely. Thus, generalizing Theorem 1 in [15], which pertains to models of the form (19) for which the stock-recruitment curve  $f$  belongs to the class of compensatory curves, we have the theorem below, which holds for any stock-recruitment curve.

**THEOREM**

*If the Leslie matrix sustainable-yield harvesting problem, extended to include an arbitrary stock-recruitment function, has an optimal solution, then it has an optimal solution in which either*

- (a) *a single age class is harvested, or*
- (b) *two age classes are harvested, the younger partially and the older completely.*

Consider the parametric linear programming problem (28), i.e. that where  $f^{-1}$  exists. Since this problem involves only two constraints, its dual formulation [13] is two-dimensional, which facilitates the development of a simple algorithm to search for the solution to the original impulse harvesting problem as stated in (27). This dual formulation is the following.

**DUAL PARAMETRIC LINEAR PROGRAMMING PROBLEM** ( $f^{-1}$  exists on  $[0, \infty)$ )

$$\min_{\hat{x}_1, y_1, y_2} J(\hat{x}_1) = [p_0 \hat{x}_1 - f^{-1}(\hat{x}_1)] y_1 + \hat{x}_1 y_2 \tag{30}$$

subject to

$$\begin{aligned} p_i y_1 + q_i y_2 &\geq w_i(t_i^*), & i = 1, \dots, n, \\ y_1 &\in R, & y_2 \geq 0, \\ & & \hat{x}_1 \geq 0. \end{aligned} \tag{31}$$

The constraint set (31) is bounded below by  $n + 1$  equations

$$\begin{aligned} y_2 &= 0, \\ y_2 &= -\frac{p_i}{q_i} y_1 + \frac{w_i(t_i^*)}{q_i}, & i = 1, \dots, n, \end{aligned} \tag{32}$$

among which a certain number of the last  $n$  may be redundant. Suppose the redundant equations have been discarded, leaving  $r$  equations in (32) which

have been reordered to satisfy

$$y_2 = -\frac{p_i}{q_i}y_1 + \frac{w_i}{q_i}, \quad s = 1, \dots, r$$

where

$$\frac{p_i}{q_i} < \frac{p_{i+1}}{q_{i+1}}, \quad s = 1, \dots, r-1.$$

For given  $\hat{x}_1$  the optimal solution  $\hat{y}_1 = y_1(\hat{x}_1)$  and  $\hat{y}_2 = y_2(\hat{x}_2)$  is then found by comparing  $[p_0\hat{x}_1 - f^{-1}(\hat{x}_1)]/\hat{x}_1$  with  $p_i/q_i$ . The two nonzero harvesting strategies will then be  $\hat{z}_i$  and  $\hat{z}_{i+1}$  or  $\hat{z}_{i-1}$  depending on how the comparison is made. Let  $\hat{J}$  denote the optimal value of (30) for given  $\hat{x}_1$ . The only problem that remains is to investigate  $\hat{J}$  as a function of  $\hat{x}_1$  and locate the optimal value of  $\hat{x}_1$ . An algorithm for doing this has been devised for the Beverton-Holt stock-recruitment function (8), and details can be found in [7]. Also, Reed [15] gives an algorithm for the case of any compensation curve. In those cases where  $f$  has an inverse that can be obtained analytically in a closed form, it should be possible to devise similar algorithms to solve the impulse harvesting problem (27).

### 3. NUMERICAL EXAMPLE

The data for the numerical example pertain to the purse-seine anchovy fishery (*Engraulis capensis*) situated off the Western Cape Coast of South Africa.

We have assumed that this fishery satisfies a Beverton-Holt stock-recruitment relationship. A yield-effort curve is generated for the fishery under the present harvesting regime in which nets with a mesh size of 13 mm are utilized and the dynamics of the population satisfy (3), (4), and (8) with the parameter values given in Table 1. This yield-effort curve is compared in Fig. 1 with those obtained by first setting  $q_1 = 0$  and then setting  $q_1 = 0$  and  $q_2 = 0$ , i.e. the curves obtained when all but the first age group is harvested, and then all but the first two age groups are harvested, under the assumption that the catchability of the other age classes is not affected.

TABLE 1  
Parameter Values for the Anchovy Fishery (*Engraulis capensis*)

Number of age classes	$n = 5$
Length of harvesting season	$\bar{t} = 0.666$ years
Natural mortality parameters	$\alpha_i = 0.8, i = 1, \dots, n$
Growth function [see (15)]	$w(t) = 35(1 - 0.73e^{-0.43t})^3$ grams
Fecundity parameters [see (1)]	$c_1 = \frac{1}{2}; c_i = 1, i = 2, \dots, 5$
Stock-recruitment parameters [see (8)]	$\beta = 122 \times 10^9, \gamma = 110,000$ metric tons
Catchability coefficients [see (4)]	$q_1 = 0.24, q_2 = 0.36,$ $q_3 = 0.42, q_4 = q_5 = 1$

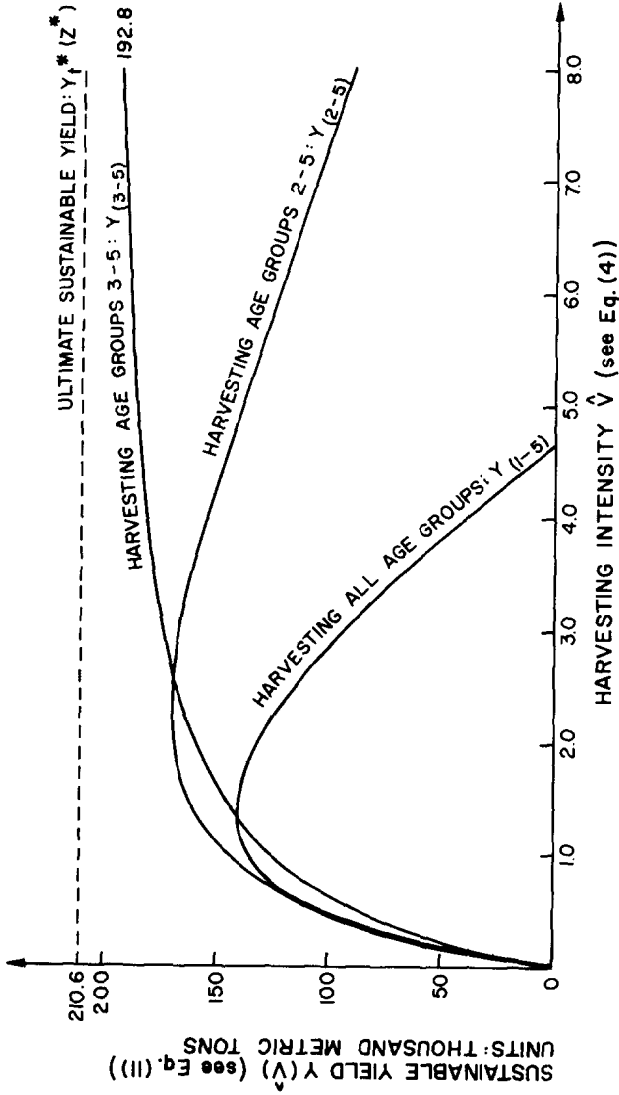


FIG. 1. Sustainable yield levels for the South African west coast anchovy fishery (*Engraulis capensis*).

The ultimate sustainable yield for this fishery was evaluated using the algorithm devised in Getz [7], the following results being obtained.

The optimum harvesting times for each age group [see (17) and (18)] were found to be

$$t_1^* = 0.666, \quad t_2^* = 0.501, \quad t_3^* = t_4^* = t_5^* = 0;$$

the optimum point at which the fishery should be maintained in equilibrium was found to be

$$x_1^* = 95.22 \times 10^9 \text{ individuals}; \quad (33)$$

and the optimum harvesting strategy was found to be

$$\begin{aligned} z_1^* = z_2^* = z_4^* = 0, \quad z_3^* = 9.84 \times 10^9 \text{ individuals}, \\ z_5^* = 4.22 \times 10^9 \text{ individuals}. \end{aligned} \quad (34)$$

It should be noted that from (21), (33), and (34) the corresponding optimal equilibrium population structure  $\mathbf{x}^*$  can be calculated, in which case  $z_5^*$  corresponds to the removal of all individuals entering the fifth age class at the beginning of the harvesting season.

The actual value of the ultimate sustainable yield for this fishery (see Table 1) was found to be [see (23) or (27)]

$$Y_{1, \bullet}(\mathbf{z}^*) = 210,634 \text{ metric tons}. \quad (35)$$

This figure provides a standard with which the various harvesting policies depicted in Fig. 1 can be compared.

At present the fishery is operated by harvesting all age classes (1–5) at the average harvesting intensity of  $\hat{v} = 2.15$ . The corresponding (theoretical) yield [see (11)] is

$$Y_{(1-5)}(2.15) = 126,305 \text{ metric tons},$$

which is only 60.0% of the ultimate sustainable yield (35). From Fig. 1 it is clear that the strategy of harvesting age groups 2–5 when  $\hat{v} = 2.15$  provides a greater yield, viz.

$$Y_{(2-5)}(2.15) = 169,236 \text{ metric tons},$$

which is 80.3% of the ultimate sustainable yield (35). For a twofold increase in effort, i.e.  $\hat{v} = 4.30$ , and harvesting only age classes 3–5, a yield of

$$Y_{(3-5)}(4.3) = 182,533 \text{ metric tons}$$

can theoretically be obtained. This already represents 86.7% of the ultimate sustainable yield, and it is clear from the  $Y_{(3-5)}$  curve in Fig. 1 that substantial increases in  $\hat{v}$  will yield only a marginal improvement in the total yield.

#### 4. CONCLUSION

The problem has been examined of obtaining a value for the ultimate sustainable yield when harvesting an age-structured population exhibiting general nonlinear stock-recruitment behavior. It was shown that the problem formulation is an extension of both the modified-Leslie-matrix approach of Reed [15] and the extended Beverton-Holt theory of Clark [3].

In particular it was shown that the bimodal harvesting strategy, which was first shown by Beddington and Taylor [1] to be optimal for the Leslie matrix harvesting problem and then shown by Reed [15] to be optimal for the Leslie matrix harvesting problem modified to include a compensatory stock-recruitment relationship, is optimal for the Leslie matrix harvesting problem modified to include any biologically feasible stock-recruitment relationship.

It was also demonstrated in the numerical example how the ultimate sustainable yield can be used as a standard against which the performance of any sustainable-yield policy can be compared in terms of yield obtained.

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