

Some Practical Extensions to Beverton and Holt's Relative Yield-Per-Recruit Model*

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Abstract

The relative yield-per-recruit (Y'/R) model of Beverton and Holt estimates Y'/R values based on few inputs, i.e., c = mean length at first capture/asymptotic length, ratio of natural mortality to growth (M/K) and exploitation rate ($E = F/Z$). However, when used in conjunction with high M/K values and/or a wide selection range, which frequently occur in small, short-lived tropical fishes and invertebrates, the model fails to estimate the optimum level of E for a given fishery. A number of approaches are presented to correct for this and related deficiencies.

Introduction

Following the development of an age-structured theory of fishing by Beverton and Holt (1957), these authors subsequently developed (Beverton and Holt 1964) a length-structured version of their yield-per-recruit model ideally suited for use in data-sparse, tropical setups.

The length-structured yield-per-recruit model of Beverton and Holt (1964) had only three variables (c , M/K and E : see below for definitions), against seven in the 1957 model (W_∞ , K , t_0 , t_c , t_{\max} , M , F ; see below), the gap between the two models being bridged by a set of assumptions that seemed reasonable enough, and lots of serious algebra.

Since its publication, the length-structured, "relative" yield-per-recruit model has been applied widely, notably in the tropics, and formed the base for a number of useful generalizations in fishery management (see e.g., Gulland 1971; Sinoda et al. 1979; Pauly 1984).

Sometimes, unwary users have interpreted results in ways not intended by the authors, the most common misinterpretation being that predicted yields *per recruit*

(Y/R) are perceived as *yield* predictions (Y), without regard to recruitment. Also the decline in catch per effort concomitant with increased yield per recruit is often not considered.

In this paper, a number of concepts and equations are presented which help in interpreting results obtained using Beverton and Holt's length-structured yield-per-recruit model. These concepts and equations parallel those developed for use with the age-structured version(s) of yield-per-recruit models such as

$$\frac{Y}{R} = F \cdot e^{-Mr_2} \cdot \frac{1 - e^{-Zr_3}}{Z} \left[\frac{3e^{-Kr_1}(1 - e^{-(Z+K)r_3})}{Z+K} - \frac{3e^{-2Kr_1}(1 - e^{-(Z+2K)r_3})}{Z+2K} - \frac{e^{-3Kr_1}(1 - e^{-(Z+3K)r_3})}{Z+3K} \right] \quad (1)$$

where $Z = F + M$, $r_1 = t_c - t_0$, $r_2 = t_r - t_0$ and $r_3 = t_{\max} - t_c$.

The model assumes isometric von Bertalanffy growth, natural, fishing and total mortality rates (M , F and Z , respectively) expressed by negative exponential curves and also assumes that all fish of a given cohort enter the fishing ground or become catchable by the gear or leave the fishery at the same ages through "knife-edge" recruitment (t_r), selection (t_c) and "derecruitment" (t_{\max}), respectively. These latter assumptions are reasonable with long-lived fishes, in which the biomass above t_r or t_c forms the overwhelming part of stock biomass, but not necessarily with small animals, in which, e.g., the selection range may span the entire size distribution (see below). De-recruitment, on the other hand, can usually be ignored (especially when Z is high), by setting $t_{\max} = \infty$ and simplifying equation (1) to

$$\frac{Y}{R} = F \cdot e^{-Mr_2} \cdot \frac{1}{Z} \left[\frac{3e^{-Kr_1}}{Z+K} - \frac{3e^{-2Kr_1}}{Z+2K} - \frac{e^{-3Kr_1}}{Z+3K} \right] \quad (2)$$

(Jones 1957)

From this, assuming an isometric length-weight relationship, Beverton and Holt (1964) derived the length-structured, "relative" yield-per-recruit model.

$$\frac{Y'}{R} = E(1-c)^{M/K} \cdot \left[1 - \frac{3(1-c)}{1 + \frac{(1-E)}{(M/K)}} + \frac{3(1-c)^2}{1 + \frac{2(1-E)}{(M/K)}} - \frac{(1-c)^3}{1 + \frac{3(1-E)}{(M/K)}} \right] \quad (3)$$

in which Y'/R is the relative yield per recruit, $E = F/Z$, $c = L_c/L_\infty$, where L_c is the length corresponding to t_c , where t_r is set at zero, and where L_∞ is the asymptotic length, corresponding to W_∞ in equation (1) and (2). The relationship between Y/R as expressed by equation (2) and relative yield per recruit as expressed by equation (3) is given by

$$Y/R = (Y'/R) \cdot W_\infty \cdot \exp - (M(t_r - t_0)) \quad (4)$$

Model Extension I: Derivation of a Biomass Per Recruit Index

Because unwary model users equate yield per recruit and yield, and also in order to predict relative catch per effort, biomass-per-recruit curves are often drawn as a function of F along with yield-per-recruit curves. Such biomass curves can be derived by dividing equation (2) by F .

Tables with computed relative equivalents of B/R (i.e., B'/R) are given in Beverton and Holt (1964). Since the equation they used was not given explicitly, an appropriate equation is presented here, i.e.,

$$\frac{B'}{R} = \frac{(1-E) \left[1 - \frac{3(1-c)}{1 + \frac{(1-E)}{(M/K)}} + \frac{3(1-c)^2}{1 + \frac{2(1-E)}{(M/K)}} - \frac{(1-c)^3}{1 + \frac{3(1-E)}{(M/K)}} \right]}{\left[1 - \frac{1}{1 + \frac{1}{(M/K)}} + \frac{2}{1 + \frac{2}{(M/K)}} \right]} \quad (5)$$

which has the useful property of being equal to unity when $E = 0$ and equal to 0 when $E = 1$. Conversion of this biomass index to absolute biomass per recruit can be performed, in analogy to equation (4) by the relationship

$$B/R = (B'/R) \cdot W_\infty \cdot \exp - (M(t_r - t_0)) \quad \dots 6)$$

Note that MSY is generated when relative biomass is 50% or 37% of virgin stock, at least in terms of the Schaefer (1957) and Fox (1970) models, respectively.

Model Extension II: $E_{0.1}$ Concept Analogous to $F_{0.1}$

Identification, in the context of rapid assessment, of the values of F generating Maximum Sustainable Yield ("F_{opt}") is not easy, and practitioners have therefore developed a number of rules of thumb, the most used of which is $F_{opt} = 0.5$. Another definition is $F_{opt} = F_{0.1}$, the latter term being defined as the fishing mortality at which the marginal increase of yield per recruit is 1/10 of its value at $F = 0$ (Gulland and Boerema 1973). Since the first of these rules of thumb has been shown to overestimate F_{opt} (Beddington and Cooke 1983), an equation is given below which allows estimation of $E_{0.1}$, the exploitation rate at which the marginal increase of relative yield per recruit is 1/10 of its value at $E = 0$.

The first derivative of equation (3) is

$$\frac{d(Y'/R)}{dE} = \left[(1-c)^{M/K} \cdot (Y'/R) + \frac{3E(1-c)^{1+M/K}}{M/K} \cdot A \right] \quad (7)$$

where

$$A = 2(1-c) \cdot \left(1 + \frac{2(1-E)}{M/K} \right)^{-2} - (1-c)^2 \left(1 + \frac{3(1-E)}{M/K} \right)^{-2} - \left(1 + \frac{1-E}{M/K} \right)^{-2} \quad (8)$$

which can be solved for any value of E , including $E = 0$ and $E = 1$. Using equation (7) it is simple matter to identify using an appropriate search algorithm, for a given pair of M/K and c values, the value of E generating a value of $d(Y'/R)/dE$ equal to $1/10$ of the value of $d(Y'/R)/dE$ at $E = 0$. Equation (7), obviously, can also be used to estimate the value of E at which yield per recruit is maximized, i.e., the value of E at which $d(Y'/R)/dE$ is equal to zero.

Model Extension III: Relationship Between Exploitation Rate and Mean Length of the Fish in the stock

Beverton and Holt (1956) showed that, given the same assumptions as those used in the derivation of the yield-per-recruit model,

$$Z/K = (L_{\infty} - \bar{L}) / (\bar{L} - L') \quad (8)$$

where \bar{L} is the mean length computed from L' upward, the latter being a length "not smaller than the smallest length of fish fully represented in catch samples." Note that $L_C < L'$, except in the case of knife-edge selection, where $L_C = L'$.

Equation (8) can be solved for L (J. Hoenig, pers. comm.), in which case we have

$$\bar{L} = (L_{\infty} + (L' \cdot Z/K)) / ((Z/K) + 1) \quad (9)$$

Now since $E = F/(F+M)$ and $E = 1 - (M/K)/(Z/K)$, we also have

$$\bar{L} = [L_{\infty} + \left(\frac{M/K}{1-E} \cdot L'\right)] / [(M/K)/(1-E) + 1] \quad (10)$$

for $0 \leq E < 1$. Thus, one can, when performing a relative yield-per-recruit assessment, also assess straightforwardly the reduction of mean length brought about by an increase of E .

Model Extension IV: Compensating for the Effects of a Wide Selection Range

In large, long-lived fish such as cod or plaice, the selection process usually takes place over a relatively narrow range of sizes, such that the assumption of "knife-edge" selection is acceptable. In some small animals such as shrimps caught by trawls, the selection range may cover most size classes represented in the population. In such cases, yield-per-recruit computations involving the assumption of knife-edge selection may involve a large bias. A simple method is developed here to show the extent of and to help overcome this bias.

Selection curves provide a probability of capture (P_i) for catch-length class (i) between L_{\min} , the smallest, and L_{\max} , the maximum length represented in the available catch samples. In the unmodified model, it is assumed that $P_i = 0$ when $L < L_C$ and $P_i = 1$ when $L > L_C$ (hence also $L' = L_C$). The implicit assumption here is that, if selection is not knife-edged, the yield from the fish caught below L_C will compensate for the yield losses due to the fact that not all fish larger than L_C are caught.

Although some compensation may occur, the assumption of knife-edge selection does generate a large bias, especially for high values of E , as can be shown by reformulating Beverton and Holt's method for computation of yield per recruit for different E values over the lifespan of a fish (section "f" in Beverton and Holt 1964) such that E is assumed constant, but P variable. This gives

$$Y'/R = \sum_{L_{\min}}^{L_{\infty}} P_i ((Y'/R)_i \cdot G_{i-1}) - ((Y'/R)_{i+1} \cdot G_i) \quad (11)$$

in which $(Y'/R)_i$ and $(Y'/R)_{i+1}$ refer to relative yield per recruit as computed from the lower limit of length class (i), P_i refers to the probability of capture between L_i and L_{i+1} (see Table 1), while G_i is defined by

$$G_i = \prod_{j=1}^i r_j \quad \dots (12)$$

and where r_i is a factor expressing the proportion of recruits of length L_i which survive, grow and reach length L_{i+1} , which is computed, for $0 < E < 1$, from

$$r_i = \frac{(1 - c_i)^{(M/K) (E/(1-E)) P_i}}{(1 - c_{i-1})^{(M/K) (E/(1-E)) P_i}}; \quad r_{L_{\min}-1} = 1; \quad r_{L_{\infty}} = 0$$

which is analogous to Beverton and Holt's "reduction factor", but considers P as a variable and has the exponent $(M/K)(E/(1-E))$ instead of F/K .

Replacing the (Y'/R) terms in equation (11) by (B'/R) as given by equation (5) is straightforward and will lead to estimates of biomass per recruit independent of the knife-edge assumption.

Table 1 gives probabilities of capture for selection gives with increasingly large ranges, from knife-edge selection in case 1 to a selection range spanning most of the range between 0 and L_∞ in case 3. In Fig. 1A, departure from knife-edge selection has a profound impact on yield-per-recruit estimation, particularly at high values of E ; similar results are obtained for relative biomass per recruit (Fig. 1B).

Model Extension V: and Empirical Equation to Predict M/K

Beverton and Holt (1964) presented their relative yield-per-recruit model in the form of yield tables at a time when microcomputers and programmable calculators did not exist. That they were able to include in their table a realistic range of M/K values is due to a previous review of the growth and mortality of fish (Beverton and Holt 1959), in which they showed that M/K varies less between stocks than either K or M alone. Pauly (1980) used their data and a number of other data sets to demonstrate the existence in fish of strong partial correlations between M on the one hand and L_∞ and mean environmental temperature on the other. Here, the data compiled in Pauly (1980) (see Pauly 1985 for correction of 4 outliers), were used to show that M/K in fishes is affected by the temperatures of their habitat, i.e.,

$$\log_e (M/K) = -0.22 + 0.30 \log_e T$$

(14)

where T is the mean water temperature, in $^{\circ}\text{C}$ ($r = 0.308$, 173 d.f., $P < 0.001$; s.e. of slope = 0.07; range 3-30 $^{\circ}\text{C}$).

Equation (14) implies that the values of M/K commonly used for stock assessment in temperate waters (say 100) should be used in the tropics (say 300) only after multiplication by a factor of about 1.4.

Model Extension VI: An Alternative for Plotting Yield Isopleth Diagrams for High Values of M/K

In the tropics, and/or when dealing with small animals, use of the relative yield-per-recruit model often implies use of high M/K values (<2 see above).

In such cases, however, yield per recruit have maxima occurring at values of E (> 0.5) and often corresponding to extremely high values of fishing mortality. When L_C/L_∞ is near 0.5, yield isopleth diagrams based on equation (3) then usually consist of 4 quadrants (A-D) with properties as given in Table 2.

Discussion

The various extensions of the length structured yield-per-recruit model presented here should help make its applications to tropical fish and invertebrates considerably easier, and lead to results that will be less biased and straightforward to interpret. These extensions also illustrate how "classical models" rather than being rejected out of hand can be adapted to better fit situations for which they may not have been originally intended.

The listing of a BASIC program implementing the equations presented in this paper is available on request from the authors.

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Table 1. Probabilities of capture for a simulation of effects on relative yield per recruit of increasing the selection range (for $L_{\infty} = 10$, $M/K = 2$).

Length class	1.0-1.9	2.0-2.9	3.0-3.9	4.0-4.9	5.0-5.9	6.0-6.9	7.0-7.9	8.0-8.9
Case 1 ^a	0	0	0	0	1	1		
Case 2	0	0	0.1	0.3	0.7	0.9	1	
Case 3	0	0.1	0.2	0.4	0.6	0.8	0.9	

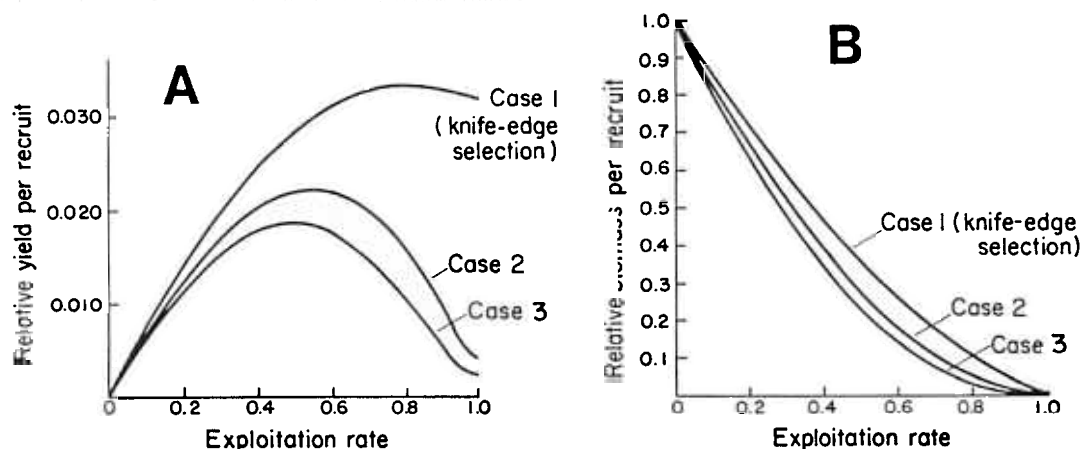


Fig. 1. Effect of an increasingly wide selection range on relative yield per recruit (A) and relative biomass per recruit (B) as assessed through application of equation (11) to the data in Table 1. Note that the knife-edge assumption leads to overestimates of yields and of optimum effort; based on Table 1.

Table 2. Properties of the 4 quadrants of relative isopleth diagrams, when $M/K > 2$, critical size ratio (L_c/L_{∞}) = 0.5 and critical exploitation rate $E = 0.5$.

Quadrant location	Fishing regime ^a	Assessment	Possible interventions ^b
A $c = 0.5$ to 1 $E = 0$ to 0.5	large fish are caught at low effort levels	underfishing	let effort increase strongly or do nothing ^c
B $c = 0$ to 0.5 $E = 0$ to 0.5	small fish are caught at low effort levels	eumetric fishing developing fishery	do nothing, but note that mesh sizes will have to be increased as effort increases
C $c = 0$ to 0.5 $E = 0.5$ to 1	large fish are caught at high effort level	eumetric fishing developed fishery	effort must be stabilized and possibly reduced ^b
D $c = 0$ to 0.5 $E = 0.5$ to 1	small fish are caught at high effort levels	overfishing	increase mesh size and decrease effort

^aIn terms of yield per recruit only.

^bConsidering that open-access fisheries will become overcapitalized if not properly managed.

^cBecause the fishery is probably generating maximum economic yield.