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# Sigmoid Selection and the Beverton and Holt Yield Equation*

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## Abstract

The analytic or yield-per-recruit model of R.H. Beverton and S.J. Holt has gained wide utility in both temperate and tropical situations since its introduction in the 1950s. The model is currently applied to fish stocks with widely different growth and mortality coefficients and longevities, with the usual assumption of knife-edge selection. We examine the effect of replacing the conventional knife-edge assumption with sigmoid selection. An expression incorporating sigmoid selection is presented with relative yield per recruit expressed as a function of E (= F/Z), C (= $L_{50}/L_\infty$), M/K and selection range, defined by $\Delta C = (L_{75} - L_{50})/L_\infty$. The relative differences between the yield isopleths using knife-edge selection and those obtained using sigmoid selection are evaluated using various plausible values of M/K, C and selection range. The results indicate considerable bias generated by the knife-edge assumption in yield-per-recruit analysis applied to short-lived, tropical species (i.e., low $L_\infty$) where the selection range usually covers a large fraction of the population size distribution.

## Introduction

The analytic or yield-per-recruit model of Beverton and Holt (1957) is one of the traditional approaches to the analysis of yield from exploited fish populations. Based on the "additions and removals" theory advanced by earlier investigators (i.e., Baranov 1918; Russell 1931), it incorporates age structure of the population as

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the key element in the determination of harvestable yield. The model takes yield (Y) as a function of the products of fishing mortality rate ($F_t$), numbers ($N_t$) and mean weight ($W_t$) at age summed over all exploited ages (t), i.e.,

$$Y = \int_{t_c}^{t_{max}} F_t N_t W_t dt \qquad \ldots 1)$$

where $t_c$ and $t_{max}$ are the age at first capture and maximum exploited age, respectively. Beverton and Holt (1957) examined a number of functional forms for the fishery processes in equation (1) and these are documented in their book.

Put simply, they incorporated the following functional forms into their yield equation: (i) the weight growth ($W_t$) function is described by the von Bertalanffy growth equation, expressed in terms of length and converted to weight units assuming a cubic relationship (i.e., isometric growth); (ii) the numbers function ($N_t$) is described as a negative exponential death process; and (iii) $F_t$ is a constant value through all exploited ages. Also, the model is conventionally applied on a per-recruit basis (due to uncertainties in the determination of absolute recruitment R) with $t_{max}$ infinitely large (i.e., $t_{max} = \infty$) and $t_c$ a constant (i.e., knife-edge selection). Given these considerations, the age-structured yield-per-recruit (Y/R) equation of Beverton and Holt (1957) can be expressed in the form

$$\frac{Y}{R} = FW_\infty \left[ \frac{1}{Z} - \frac{3e^{-kr_1}}{Z+K} + \frac{3e^{-2kr_1}}{Z+2K} - \frac{e^{-3kr_1}}{Z+3K} \right] \qquad \ldots 2)$$

where Z (= F + M), F and M are the instantaneous rates of total, fishing and natural mortality, respectively; $r_1 = t_c - t_o$; and $W_\infty$, K and $t_o$ are the parameters of the von Bertalanffy growth equation.

Variation from the basic functional forms used by Beverton and Holt (1957) in their original formulation are described in the works of Ricker (1975), Gulland (1969, 1983) and Pauly (1984) among others. The modifications vary from attempts at computational and/or

analytic efficiency (e.g., Jones 1957; Tanaka 1958; Beverton and Holt 1966) to attempts at more properly depicting biological/fishery processes as they are in relation to yield (e.g., Paulik and Gales 1964; Andersen and Ursin 1977; Pauly 1984). Among these modifications, the length-structured, 3-parameter "relative" yield per recruit (Y'/R) equation of Beverton and Holt (1966) has gained wide utility. It is in the form

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

where $E = F/Z$; $C = L_c/L_\infty$, $L_c$ being the length corresponding to $t_c$ and $L_\infty$ the asymptotic length corresponding to $W_\infty$ in equation (2); and the rest as previously defined. Aside from its simplicity (making it applicable in data-sparse situations), it facilitates appreciation of the fishery processes involved. For instance, E expresses the proportion (in numbers) of a given cohort which will be caught throughout its fished lifespan. The parameter C defines the 50% retention length as a fraction of $L_\infty$; its complement (1-C), therefore, defines the proportion of the potential growth span remaining after entry into the exploited phase. The M/K ratio (less variable than the parameters M or K alone), in effect gives an idea of the relative natural change in numbers and size with age/time.

Since its introduction in the 1950s, the yield-per-recruit model of R.H. Beverton and S.J. Holt has been widely used (in both temperate and tropical situations) to help provide biological advice in the management of fisheries. At present, it is applied to fish stocks with widely different growth and mortality coefficients and longevities. It can be noted, however, that in large, long-lived fish (e.g., haddock or plaice to which the model was originally applied), selection usually covers a small proportion of the lifespan of the fish. Thus, the value of the $N_t$ and $W_t$ functions would have changed very little such that the assumption $F_t = 0$ for $t < t_c$ and $F_t = F$ for $t \geq t_c$ holds true (i.e., compensation occurs). In small animals (typical of many short-lived, tropical fish species), however, the selection process may cover a large fraction of the population size distribution. In such cases, the use of equations (2) and (3) involving the knife-edge assumption may result

in considerable bias (Garcia and LeReste 1981; Pauly and Soriano 1986). In addition to the selection range, it is not conceptually difficult to imagine from equation (1) and the shape of the sigmoid selection curve (see Gulland 1983; Pauly 1984) that the extent of the bias is affected by the relative position along C (between 0 and 1) of the selection ogive. This is because part of the ogive becomes increasingly truncated as C varies from 0.50.

The present contribution, which represents an attempt to expand on the earlier work of Pauly and Soriano (1986), examines the effect of replacing the conventional knife-edge assumption with sigmoid selection.

## Materials and Methods

The equation given by Pauly and Soriano (1986) can be simplified to the form

$$Y'/R = \sum_{c=0}^{1.0} P_c \{[(Y'/R)_c \cdot G_c] - [(Y'/R)_{c+DC} \cdot G_{c+DC}]\} \quad \ldots 4)$$

where $(Y'/R)_c$ and $(Y'/R)_{c+DC}$ refer to relative yield-per-recruit using equation (3), DC is the C-interval used in evaluating equation (4), $P_c$ the probability of capture between C and C+DC, and $G_c$ defined by

$$G_c = \prod_{i=o}^{c} r_i \quad \ldots 5)$$

where $r_c$ is the "reduction factor" of Beverton and Holt (1966, p. 7) expressing the proportion of recruits at c which get caught before reaching C + DC. GC is computed (for $0<E<1$) from

$$r_i = \frac{(1-C)^{(M/K)\,(E/(1-E))P_{C-DC}}}{(1-(C-DC))^{(M/K)\,(C/(1-E))P_{C-DC}}} \quad \ldots 6)$$

where $r_o = 1$ and $r_1 = 0$.

The probability of capture as a function of length ($P_L$) is often written in the form (Gulland 1969; Pope et al. 1975; Pauly 1984; Sparre 1985):

$$P_L = 1/(1+e^{(S_1 - S_2 L)});\ L_{50} = S_1/S_2;\ L_{75} = (S_1 + \ln 3)/S_2 \qquad \ldots 7)$$

where $S_1$ and $S_2$ are selection parameters (obtained conventionally through covered cod-end selection experiments); $L_{50}$ and $L_{75}$ corresponding to 0.50 and 0.75 probability of capture, respectively. Algebraically, equation (7) can be expressed in the form

$$P_L = 1/\left[1 + 3^{\left(\frac{L_{50} - L}{L_{75} - L_{50}}\right)}\right];\ L_{75} > L_{50} \qquad \ldots 8)$$

and since $C = L/L_\infty$, for $0 \leq L \leq L_\infty$, equation (8) can be written as

$$P_c = 1/\left[1 + 3^{\left(\frac{C_{50} - C}{C_{75} - C_{50}}\right)}\right] = 1/(1 + 3^{(C_{50} - c)/\Delta C}) \qquad \ldots 9)$$

where $\Delta C$ expresses 1/2 of the selection range as a ratio of $L_\infty$, and $C_{50}$ a measure of the relative position of the selection ogive along C (i.e., between 0 and 1). Thus, equation (4) can be evaluated using equations (3), (5), (6) and (9) with M/K, E, $C_{50}$ and $\Delta C$ as variables.

The relative difference in yield-per-recruit values, $\Delta Y'/R$ (%) using knife-edge selection versus sigmoid selection, was evaluated in this study via

$$\Delta Y'/R\ (\%) = \frac{Y'/R - Y''/R}{Y'/R} \times 100 \qquad \ldots 10)$$

where Y'/R is computed from equation (3) and Y''/R from equation (4). The $\Delta Y'/R$ (%) values were examined for trends by varying M/K (= 1.0, 2.0 and 3.0), E (between 0 and 0.90), $C_{50}$ (= 0.10, 0.50 and 0.90) and $\Delta C$ (between 0, i.e., knife-edge selection and 0.80). The choice of M/K values used is based on the frequency distribution of M/K ratios given in Pauly (1980) who gives a comprehensive compilation of available estimates to the late 1970s. While the $\Delta Y'R$ (%) values are of certain interest, it is the change in the yield-per-recruit response surface in the E, C plane (particularly the location of the eumetric fishing lines) that are of utmost importance. Hence, an attempt to evaluate the change in position of the eumetric lines in the E, C plane with increasing $\Delta C$ was made using equations (3) and (4). As a last step, a

search of literature values of ΔC was conducted. These are tabulated to illustrate the extent of bias that the knife-edge assumption may generate for typical exploited genera/species in temperate and tropical latitudes.

## Results

Fig. 1 illustrates the frequency distribution of M/K ratios tabulated by Pauly (1980). It shows that the M/K ratios utilized in the study (i.e., 1.0, 2.0 and 3.0) cover the range of values for most exploited species (at least those for which independent M estimates were available together with K). Additionally, as will become apparent below, the M/K values used are sufficient to illustrate the trends in the bias introduced by the knife-edge assumption with changing M/K ratio.

The ΔY'/R (%) values computed using equation (10) are illustrated in Fig. 2. These are given for $C_{50}$ equal to 0.10, 0.50 and 0.90, E varying between 0 and 0.9, and ΔC from 0 to as much as 0.80 (with variable step values) for the M/K ratios mentioned above. Positive values of ΔY'/R (%) indicate that Y'/R>Y''/R, while negative

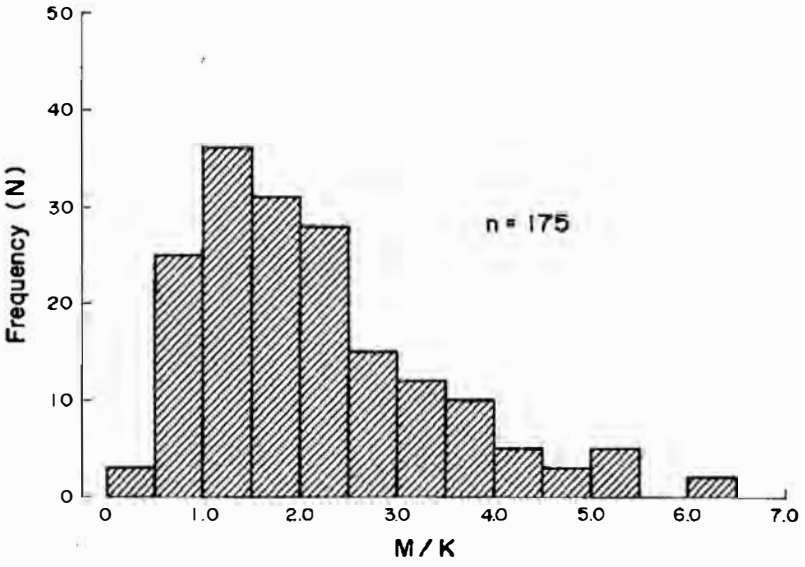


Fig. 1. Frequency distribution of M/K ratios compiled by Pauly (1980) which includes fish stocks from a wide variety of habitats (i.e., tropical to polar, marine to freshwater).

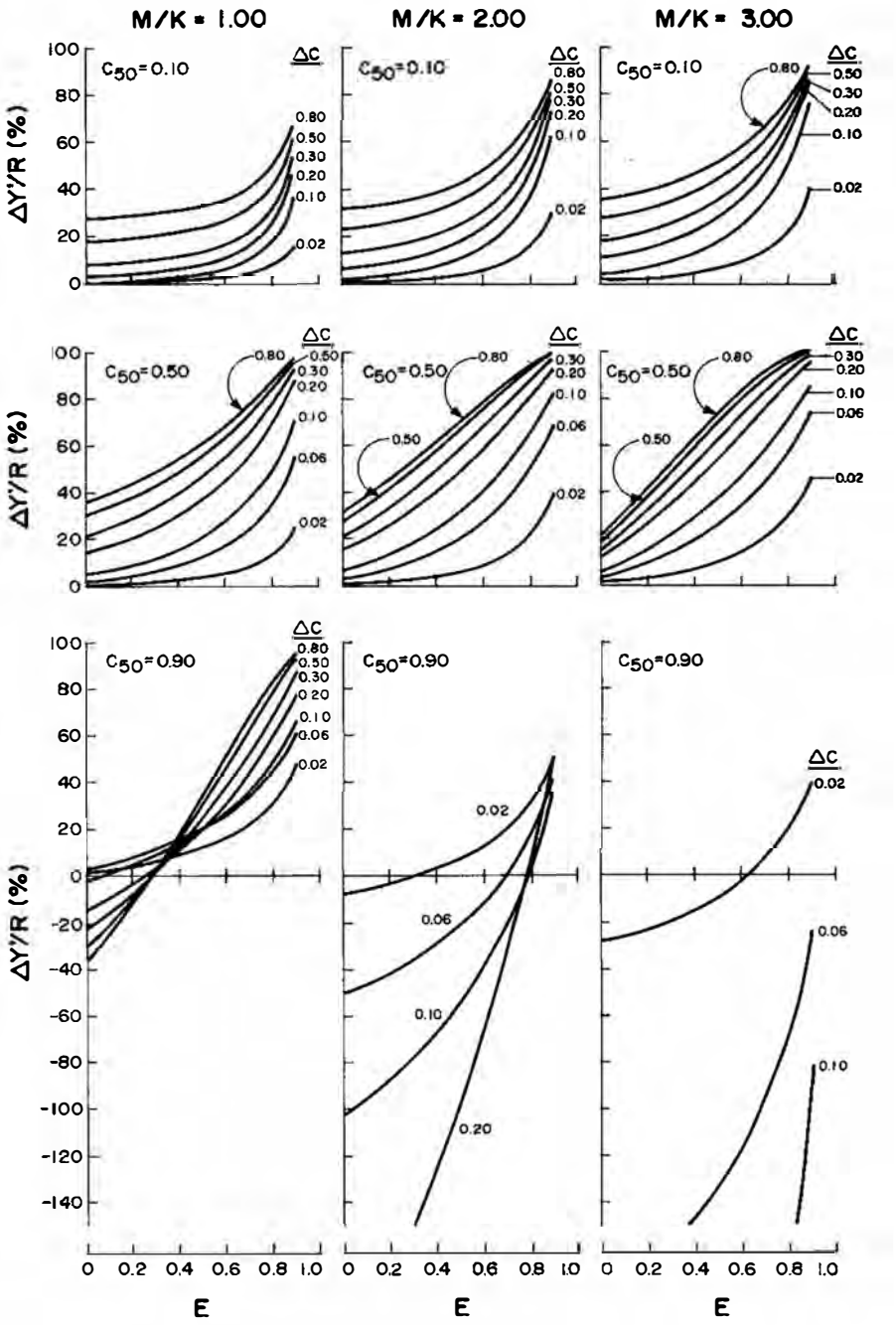


**Fig. 2. Relative differences in yield-per-recruit (ΔY'/R) based on computations involving knife-edge selection and sigmoid selection for different values of M/K, $C_{50}$, E and ΔC (see text).**

values indicate the opposite. The following trends, among others, are apparent from the figure (with respect to the bias introduced by the knife-edge assumption) considering the M/K, $C_{50}$, E and $\Delta C$ combinations: (1) positive $\Delta$ Y'/R (%) values are obtained at low $C_{50}$'s, while increasingly negative values are obtained as $C_{50}$ increases from 0.50; (2) the magnitude of the negative values noted in (1) for high $C_{50}$'s increases with increasing $\Delta C$ and M/K; (3) the bias (i.e., variation from $\Delta$Y'/R (%) = 0) generally increases with increasing $\Delta C$ for fixed M/K, $C_{50}$ and E; (4) for fixed M/K, $\Delta C$ and E, the bias generally increases with increasing $C_{50}$; (5) for fixed $\Delta C$, E and $C_{50}$, the bias generally increased with increasing M/K ratio; and (6) for fixed M/K, $\Delta C$ and $C_{50}$, the bias generally increases with E. The general trends noted in (3) through (5) above are true with the exception of limited E and $\Delta C$ ranges at very high $C_{50}$ values. The trend noted in (6) is reversed at very high values of $C_{50}$ and $\Delta C$ except for limited E ranges and low M/K ratios.

Fig. 3 illustrates schematically how positive and negative values of $\Delta$ Y'/R (%) can be obtained using equation (10). The probability ($P_c$), relative number ($N_c/N_o$ and $N'_c/N_o$) and relative weight ($W_c/W_\infty$) functions were obtained using fixed $\Delta C$(= 0.10), M/K(= 2.0) and E(= 0.50) with the following variants and $\Delta$Y/R (%) results: (A) $C_{50}$ = 0.10, $\Delta$Y'/R (%) = 10.2; (B) $C_{50}$ = 0.50, $\Delta$Y'/R (%) = 31.3; and (c) $C_{50}$ = 0.90, $\Delta$Y'/R (%) = -53.5. In case (A), Y'/R > Y''/R, i.e.,

$$\int_0^{0.1} P_c F_c N'_c W_c dc < \int_{0.1}^{1.0} (1 - P_c)\ F_c N_c W_c dc$$

because, among others, $P_c$ is truncated below C = 0 and $W_c/W_\infty$ is very low at C <0.10 (despite the high relative numbers). Thus, overcompensation occurs using knife-edge selection. In case (C), Y''/R >Y'/R (i.e., knife-edge selection leads to undercompensation) because $P_c$ is truncated above C=1 and the relative numbers ($N_c/N_o$) are far too low despite the higher $W_c/W_\infty$ values. In case (B) where equal truncation of the $P_c$ function occurs on both sides, it is the numbers and weight functions which determine the direction of the bias. In all cases where $C_{50}$ = 0.50, the higher $W_c/W_\infty$ values above C = 0.50 (despite the lower relative numbers) lead to overcompensation using knife-edge selection, i.e., positive $\Delta$Y'/R (%) (see also Fig. 2).

The assumption of knife-edge selection leads to different magnitudes of error for fixed M/K and $\Delta C$ along the E, C plane. Thus,

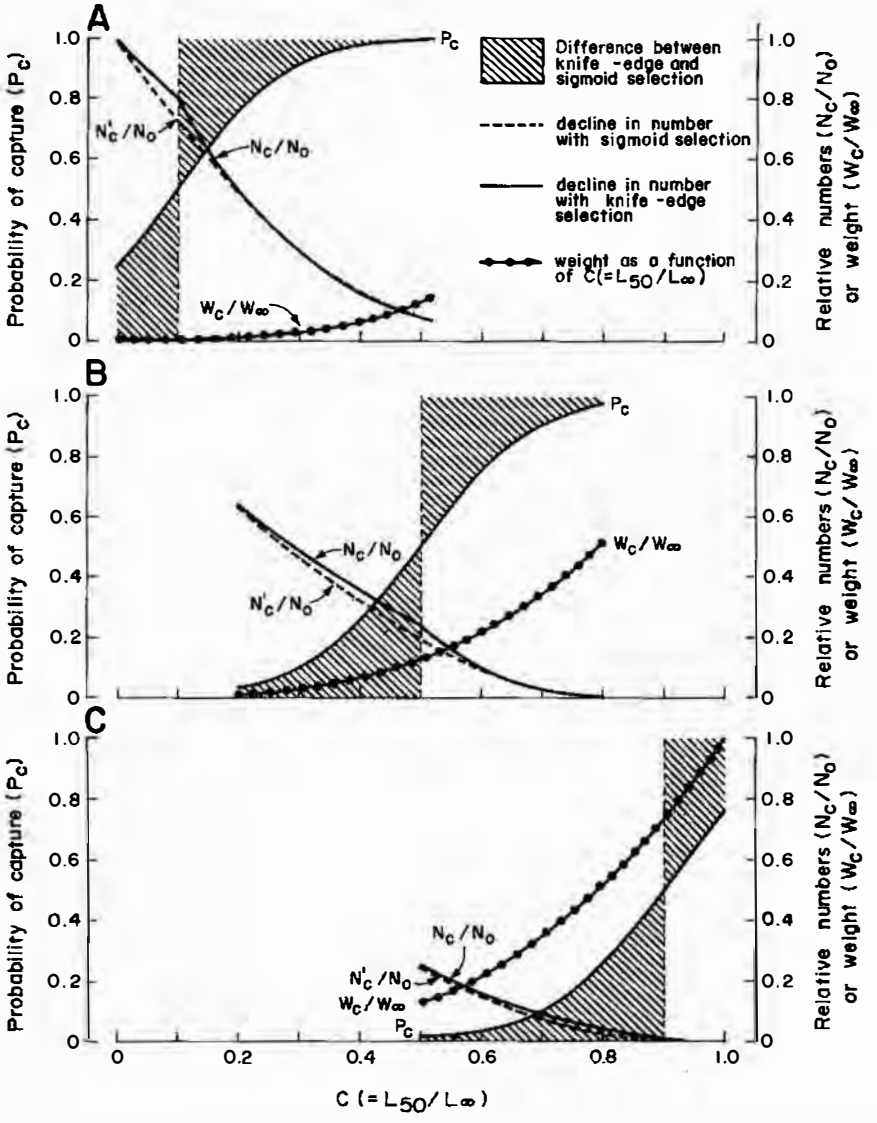


Fig. 3. Schematic representation of the interactions between the probability ($P_c$), relative numbers ($N_c/N_0$ and $N_c'/N_0$), and relative weight ($W_c/W_\infty$) functions in determining the extent and direction of bias ($\Delta Y'/R$ (%)) generated using knife-edge versus sigmoid selection in yield-per-recruit computations. The parameter values and biases generated are as follows: (A) $C_{50} = 0.01$, $\Delta Y'/R$ (%)) = 10.2; (B) $C_{50} = 0.50$, $\Delta Y'/R$ (%) = 31.3; and (C) $C_{50} = 0.90$, $\Delta Y'/R$ (%) = 53.5, with $\Delta C = 0.10$, $M/K = 2.0$ and $E = 0.50$. The $W_c/W_\infty$ function assumes a cubic length-weight relationship. See text.

the shape of the yield-per-recruit response surface and the location of the eumetric fishing lines are altered. Fig. 4 illustrates the effect of increasing $\Delta C$ from 0 (i.e., knife-edge selection, indicated by lines marked A and A') to 0.02 (B and B') and 0.10 (C and C'). The lines marked A, B and C indicate the C values (i.e., $C_{max}$) where yield-per-recruit is maximum for fixed E's, while the lines marked A', B' and C' indicate the E values (i.e., $E_{max}$) where yield-per-recruit is maximum for fixed C's. Note that the $E_{max}$ curve is displaced to the left (i.e., lower E's) with increasing $\Delta C$. The $C_{max}$ curve, on the other hand, is generally displaced downward with higher $\Delta C$, except for the upper half of the E range at high M/K ratios. Additionally, the location of the global maximum yield-per-recruit (marked by solid squares in the figures) is shifted to lower E, C combinations as $\Delta C$ increases from 0 to 0.10.

Table 1 gives a summary of $\Delta C$ and $C_{50}$ values obtained in the literature for some exploited genera/species in temperate and tropical areas. It shows that values of $\Delta C$ (together with the corresponding $C_{50}$ and M/K) for shortlived tropical species/genera are usually high enough to generate considerable bias when the assumption of knife-edge selection is made in yield-per-recruit computations. In the case of the two temperate species included in the table (i.e., *P. platessa* and *M. aeglefinus*), the $\Delta C$ values/ranges are considerably lower. However, the $\Delta C$ (and $C_{50}$) value for *M. aeglefinus* may also be large enough such that the knife-edge assumption can lead to some bias.

Table 1. Summary of $\Delta C$ and $C_{50}$ values obtained at different mesh sizes for some exploited tropical and temperate genera/species (based on a compilation by Sambilay et al., unpublished data, and selected data in Beverton and Holt 1957).

| Genera/Species | $\Delta C$ range | Mesh size range (cm) | n | M/K | $C_{50}$ range |
|---|---|---|---|---|---|
| *Leiognathus* spp. | 0.033-0.146 | 4.0- 7.0 | 5 | 1.95 | 0.51-0.66 |
| *Lutjanus* spp. | 0.005-0.081 | 4.0-10.0 | 6 | 2.55 | 0.34-0.67 |
| *Nemipterus* spp. | 0.016-0.312 | 4.0- 8.3 | 20 | 2.30 | 0.31-0.74 |
| *Saurida* spp. | 0.022-0.196 | 4.0-10.0 | 13 | 1.75 | 0.36-0.65 |
| *Penaeus* spp. | 0.094-0.281 | 3.2- 4.3 | 7 | 1.60 | 0.63-0.95 |
| *Pleuronectes platessa* | 0.013-0.026 | 7.2-14.1 | 4 | 0.95 | 0.23-0.44 |
| *Melanogrammus aeglefinus* | 0.053 | 8.3 | 1 | 1.00 | 0.48 |

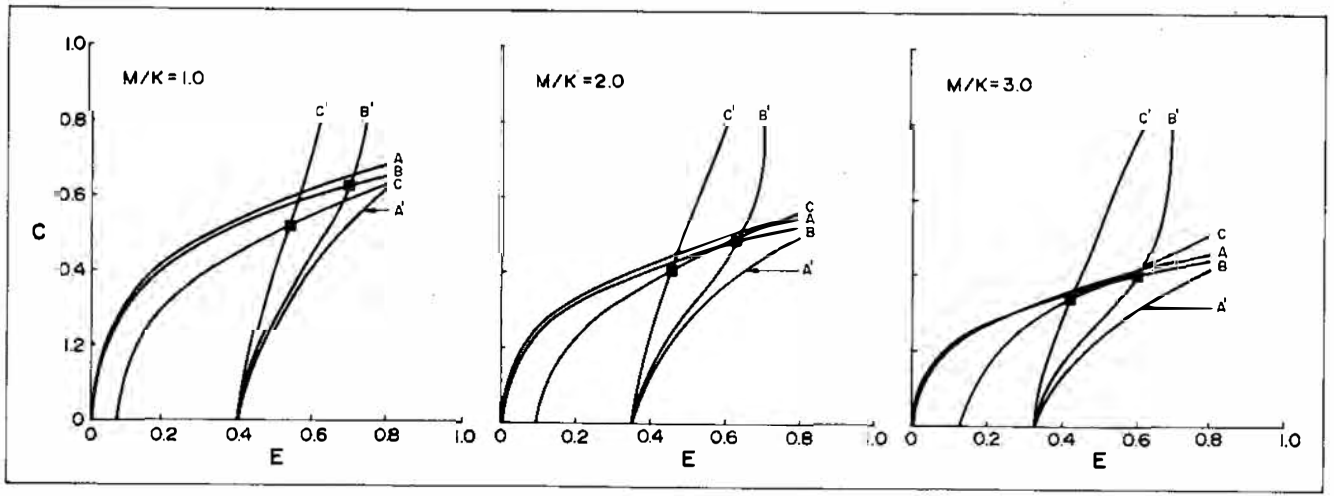


Fig. 4. Change in position of eumetric fishing lines in the E, C plane with increasing selection range (ΔC). The lines marked A, B and C indicate the location of optimum C's at fixed E, while the lines marked A', B' and C' indicate the location of optimum E's at fixed C values. The ΔC values are 0 for A and A', 0.02 for B and B' and 0.10 for C and C'. See text.

## Discussion

The results presented in the preceding section illustrate that the incorporation of complete selection ogives in yield-per-recruit assessments of short-lived, low $L_\infty$, tropical species is important. This is because these animals have characteristically large values of $\Delta C$, $C_{50}$ and M/K ratios. Viewed in relative terms, for instance, a 1-cm difference between $L_{75}$ and $L_{50}$ in a fish with 10 cm $L_\infty$ (short-lived, tropical fish) corresponds to a $\Delta C$ of 0.10. In a fish with $L_\infty$ = 100 cm (temperate, long-lived species) the corresponding $\Delta C$ would only be 0.01. Hence, given the same selection range, the bias in assuming knife-edge selection would be much greater for fishes with lower $L_\infty$ values.

It should be noted that the selection range usually increases with increasing $L_c$ or C, based on empirical observations. Hence, when performing assessments the $\Delta Y'/R$ (%) values are bound to be higher than indicated for a constant $\Delta C$ with increasing $C_{50}$ in Fig. 2.

Most fisheries in the Southeast Asian region (and for that matter, other tropical and temperate regions) are multispecies in nature. Hence, what is generally of interest is the yield from the mix of species rather than that for a single component of the species mix. Several attempts at combining single-species assessments are available in the literature (e.g., Sainsbury 1984; Silvestre 1986; Sinoda et al. 1979; Federizon et al. 1986) for estimating the best mesh size (proportional to $L_c$ or C) and exploitation levels for multispecies stocks. These works rely on the use of the yield-per-recruit model with the usual assumption of knife-edge selection. The bias generated by such assumption in aggregate/combined single species assessments, hence, are expected to be far more serious (i.e., compounded).

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## References


Andersen, K.P. and E. Ursin. 1977. A multispecies extension to the Beverton and Holt theory of fishing, with accounts of phosphorus circulation and primary production. Medd. Dan. Fisk. Havunders 7: 319-435.

Baranov, F.I. 1918. On the question of the biological basis of fisheries. Nauchn. Issled. Ikhtiologichaskii Inst. Izv. 1:81-128 (In Russian).

Beverton, R.J.H. and S.J. Holt. 1957. On the dynamics of exploited fish populations. Fish. Invest. Ser. II, Vol. 19, 533 p.

Beverton , R.J.H. and S.J. Holt. 1966. Manual of methods for fish stock assessment. Part 2. Tables of yield functions. FAO Fish. Tech. Pap. 38 (Rev. 1): 67 p.

Federizon, R., G. Silvestre and V. Sambilay, Jr. 1986. MULTIMESH - A Basic program for the evaluation of optimum mesh size in multispecies fisheries, p. 139-164. *In* D. Pauly, J. Saeger and G. Silvestre (eds.) Resources, management and socioeconomics of Philippine marine fisheries, Univ. Philipp., Dept. Mar. Fish. Tech. Rep. 10: 224 p.

Garcia S. and L. Le Reste. 1981. Life cycles, dynamics, exploitation and management of coastal penaeid shrimp stocks. FAO Fish. Tech. Pap. 203: 215 p.

Gulland, J. A. 1969. Manual of methods for fish stock assessment. Part I. Fish population analysis. FAO Man. Fish. Science 4: 154 p.

Gulland, J.A. 1983. Fish stock assessment: A manual of basic methods. FAO/Wiley Series on Food and Agriculture. 223 p.

Jones, R. 1957. A much simplified version of the fish yield equation. Doc. P.21, presented at the Lisbon meeting of ICNAF, ICES and FAO. 8 p.

Paulik, G.J. and L.E. Gales. 1964. Allometric growth and the Beverton and Holt yield equation. Trans. Am. Fish. Soc. 93: 369-381.

Pauly, D. 1984. Fish population dynamics in tropical waters: a manual for use with programmable calculators. ICLARM Studies and Reviews 8: 325 p. ICLARM, Manila.

Pauly, D. 1980. On the interrelationships between natural mortality, growth parameters, and mean environmental temperature in 175 fish stocks. J. Cons. CIEM 39(2): 175-192.

Pauly, D. and M. Soriano. 1986. Some practical extensions to Beverton and Holt's relative yield-per-recruit model, p. 491-495. *In* J.L. Maclean, L. Dizon and L. Hosillos (eds.) The First Asian Fisheries Forum. Asian Fisheries Society, Manila.

Pope, J., A. Margetts, J. Hamley and E. Akyüz. 1975. Manual of methods for fish stock assessment, Part III. Selectivity of fishing gear. FAO Fish. Tech. Pap. 41 (Rev. 1), 65 p.

Ricker, W.E. 1975. Computation and interpretation of biological statistics of fish populations. Bull. Fish. Res. Bd. Canada (191): 382 p.

Russell, E.S. 1931. Some theoretical considerations on the overfishing problem. J. Cons. CIEM 6(1):3-20.

Sainsbury, K. 1984. Optimum mesh size of tropical multispecies trawl fisheries. J. Cons. CIEM 41: 129-139.

Silvestre, G. 1986. Preliminary analysis of the optimum mesh size for the demersal trawl fisheries of the Samar Sea, Philippines. Univ. Philipp., Dept. Mar. Fish. Tech. Rep. 7: 43-65.

Silvestre, G. and M. Soriano. 1988. Effect of incorporating sigmoid selection on optimum mesh size estimation for the Samar Sea multispecies trawl fishery. p 482-492 *In* S. Venema, J. Möller-Christensen and D. Pauly (eds.) Contributions to Tropical Fishery Biology: Papers by the participants of FAO/DANIDA Training courses. FAO Fish. Rep. 389, Rome.

Sinoda, M., S. M. Tan, Y. Watanabe and Y. Meemeskul. 1979. A method for estimating the best cod end mesh size in the South China Sea area. Bull. Choshi Mar. Lab. 11: 65-80.

Sparre, P. 1985. Introduction to tropical fish stock assessment. FAO/DANIDA Project: Training in Tropical Fish Stock Assessment - GCP/INT/392/DEN.

Tanaka, S. 1958. A mathematical consideration of the effect of mortality and growth on a fish population. Bull. Tokai Reg. Fish. Res. Lab. 20: 1-11

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