Calculating Mortality Rates and Optimum Yields from Length Samples

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An equation is derived for yield per recruit of a fishery (or other exploited animal population) as a function of fishing intensity and age of first capture. The equation has the advantage that it does not require explicit estimates of natural mortality or individual growth rate parameters. Linear length growth is assumed until maximum size is reached, and mortality parameters are expressed relative to growth rate. Mortality parameters are estimated from average length samples of separate populations experiencing different fishing efforts in the same fishery. The equation may be used to compare existing fishing efforts and age of first capture with optimal values. Samples of the catfish *Bagrus docmac* from Lake Victoria (East Africa) are used to illustrate the method.

Key words: yield equation, Beverton–Holt, fish lengths, Lake Victoria, *Bagrus docmac*, fishing effort, recruitment age

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L'auteur dérive une équation décrivant le recrutement par recrue dans une pêcherie (ou dans toute autre population animale exploitée) comme fonction de l'intensité de pêche et de l'âge de la première capture. L'équation a l'avantage de ne pas requérir d'estimés formels de la mortalité naturelle ni de paramètres de croissance individuelle. On suppose que la croissance en longueur est linéaire jusqu'à ce que la taille maximale soit atteinte et on exprime les paramètres de mortalité par rapport au rythme de croissance. Les paramètres de mortalité sont estimés à partir de la longueur moyenne d'échantillons de populations distinctes soumises à des efforts de pêche différents au sein d'une même pêcherie. L'équation peut servir à comparer des efforts de pêche et l'âge de première capture avec des valeurs optimales. Pour illustrer la méthode, l'auteur se sert d'échantillons du silure *Bagrus docmac* capturés dans le lac Victoria (Afrique orientale).

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THE equation of Beverton and Holt (1957) has become standard in recent years for calculating average weight yield per recruit as a function of fishing effort and the age of first capture (critical age). However, a limitation of this equation has been that it requires precise values for growth and mortality parameters, values that are difficult to measure. Ssentongo and Larkin (1973) made an important step toward easier measurement of these parameters by estimating the ratio of mortality rate to growth rate (Z/K) on the basis of average length in a population sample.

If K and fishing mortality (F) can be measured by some other means, the knowledge of Z/K can be used to calculate natural mortality (M), and the resulting values of M, K, and F used in the Beverton–Holt equation. A similar procedure could be followed if Z and F were measured by other means. The approach of Ssentongo and Larkin has the advantage that it is not necessary to measure Z and K directly, but it has the limitation that it is necessary to measure at least one of them by some other means.

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The method described below is designed to calculate weight yield per recruit on the basis of only average length without measuring Z, K, F, or M directly. This is achieved on the basis of the average lengths associated with at least two different levels of fishing effort. It has the advantage that the effects of fishing effort and critical age upon yield can be calculated to a first approximation on the basis of a few weeks of sampling.

Yield Equation

Assume a recruitment of R individuals per unit time. They experience a constant natural mortality (M) throughout the period they are vulnerable to the fishery, as well as a constant fishing mortality (F) starting at critical age t_c. Mortality is the same for all fish older than t_c, regardless of age.

The number of the original R individuals reaching age t_c is

$$(1) \qquad R_c = Re^{-Mt_c}.$$

The number of individuals at any age t after t_c is

$$(2) \qquad N(t) = R_c e^{-Z(t-t_c)},$$

where $Z = M + F$ is the total mortality. Substituting (1) in (2),

$$N(t) = Re^{Ft_c - Zt}. \tag{3}$$

The number of fish dying at each age t is

$$Z(t) = \frac{-dN}{dt} = RZe^{Ft_c - Zt}, \tag{4}$$

of which a fraction M/Z is due to natural mortality and a fraction F/Z to fishing mortality. The number of fish captured, as a function of age, is therefore

$$F(t) = FRe^{Ft_c - Zt}. \tag{5}$$

The total yield from a cohort during its lifetime is the integral of all fish captured times their weight

$$Y = \int_{t_c}^{\infty} [F(t) \cdot W(t)]dt. \tag{6}$$

As an approximation to the von Bertalanffy curve often used for fish, length growth is assumed linear until a maximum length of L_∞. All fish in the population are assumed to reach the same maximum length, and weight is assumed proportional to the cube of length.

$$\begin{aligned} L(t) &= L_\infty t \quad \text{when} \quad 0 \le t \le 1, \\ L(t) &= L_\infty \quad \text{when} \quad t > 1. \end{aligned} \tag{7}$$

$$\begin{aligned} W(t) &= W_\infty t^3 \quad \text{when} \quad 0 \le t \le 1, \\ W(t) &= W_\infty \quad \text{when} \quad t > 1. \end{aligned} \tag{8}$$

Note that a unit of time is that required to grow from a hypothetical size 0 to maximum length (L_∞). The mortality rates F, M, and Z are now instantaneous rates with respect to this special time scale. The size at age 0 is hypothetical because it represents a linear extrapolation to $t = 0$, which does not necessarily correspond to the actual birth of the fish. It does not matter whether length growth conforms to equation (7) below age t_c, as long as it is approximately linear above t_c.

Although the abrupt cessation of growth postulated by equations (7) and (8) may be a departure from reality, the consequent error should be reasonably small, particularly at high natural mortalities where few fish reach maturity. Furthermore, the precise growth pattern of most species is not known sufficiently well in practice to justify a more elaborate assumption.

Substituting (5) and (8) in (6),

$$Y = \int_{t_c}^{1} [FRe^{Ft_c - Zt} t^3 W_\infty]dt + \int_{1}^{\infty} [FRe^{Ft_c - Zt} W_\infty]dt. \tag{9}$$

The two terms are necessary because of the discontinuity in growth. The first term corresponds to the yield of fish still growing and the second term to the yield of full-grown fish.

Evaluating the integrals in (9) and expressing Z as $M + F$,

$$Y = RW_\infty Fe^{Ft_c}\left[e^{-(M+F)t_c}\left(\frac{t_c^3}{M+F} + \frac{3t_c^2}{(M+F)^2} + \frac{6t_c}{(M+F)^3} + \frac{6}{(M+F)^4}\right) - e^{-(M+F)}\left(\frac{3}{(M+F)^2} + \frac{6}{(M+F)^3} + \frac{6}{(M+F)^4}\right)\right]. \tag{10}$$

This is the yield equation. R, W_∞, and M are constants in the equation; t_c and F are decision variables.

Characteristics of Yield Equation

Figure 1 shows yield as a function of the decision variables: critical age (t_c) and fishing mortality rate (F). Yield is expressed as a function of the highest possible yield, RW_∞, which is the yield to be attained if the fish are able to grow to full size without any mortality and then experience only fishing mortality. The critical age shown in Fig. 1 does not extend past 1 because the optimal critical age is always 1 or less. Furthermore, since all fish of age 1 and older are the same size, there is no way in practice to make the critical age >1 on the basis of mesh sizes.

Figure 1A shows yield per recruit when $M = 0$. Although natural mortality would never be 0 in reality, Fig. 1A is of interest as a theoretical limit to the yield equation. Yield reaches the maximum possible value of unity if fishing begins at full growth ($t_c \ge 1$). Fishing mortality is of no consequence in this situation. Yield is also nearly the maximum, even though $t_c < 1$, whenever the fishing mortality rate is close to 0. Yields decline continuously as the critical age decreases or the fishing mortality rate increases.

A yield of unity can never be attained when M is >0. In fact, natural death rates place severe restrictions on the best yield that can be realized even by adjusting critical age and fishing mortality (Fig. 1A and B). For any given value of M, the maximum yield is $t_c^3 e^{-Mt_c}$, which occurs at $t_c = 3/M$ (subject to the constraint $t_c < 1$) and $F = \infty$. Therefore, as natural mortality increases, the maximum yield decreases and (when $M > 3$) is found at smaller critical ages.

If the critical age is fixed, the best fishing mortality increases as natural mortality increases. (However, the yield equation gives only yield per recruit and does not take into account the effect of fishing upon recruitment. Heavy fishing in conjunction with a high natural mortality, though optimal for yield per recruit, may reduce recruitment.)

The general pattern of the effects of critical age and fishing mortality on yield (Fig. 1B and C) is the same for all natural mortalities >0. Yield is nearly independent of the critical age at low fishing mortalities but depends upon the critical age at higher fishing mortalities. At critical ages greater than the optimal t_c, yield increases continuously (but with diminishing returns) as fishing mortality increases. However, at critical ages less than the optimal t_c, yield is greatest at an intermediate fishing mortality, and the best fishing mortality rate decreases as t_c decreases.

For example, when $M = 1$ (Fig. 1B), the optimal yield

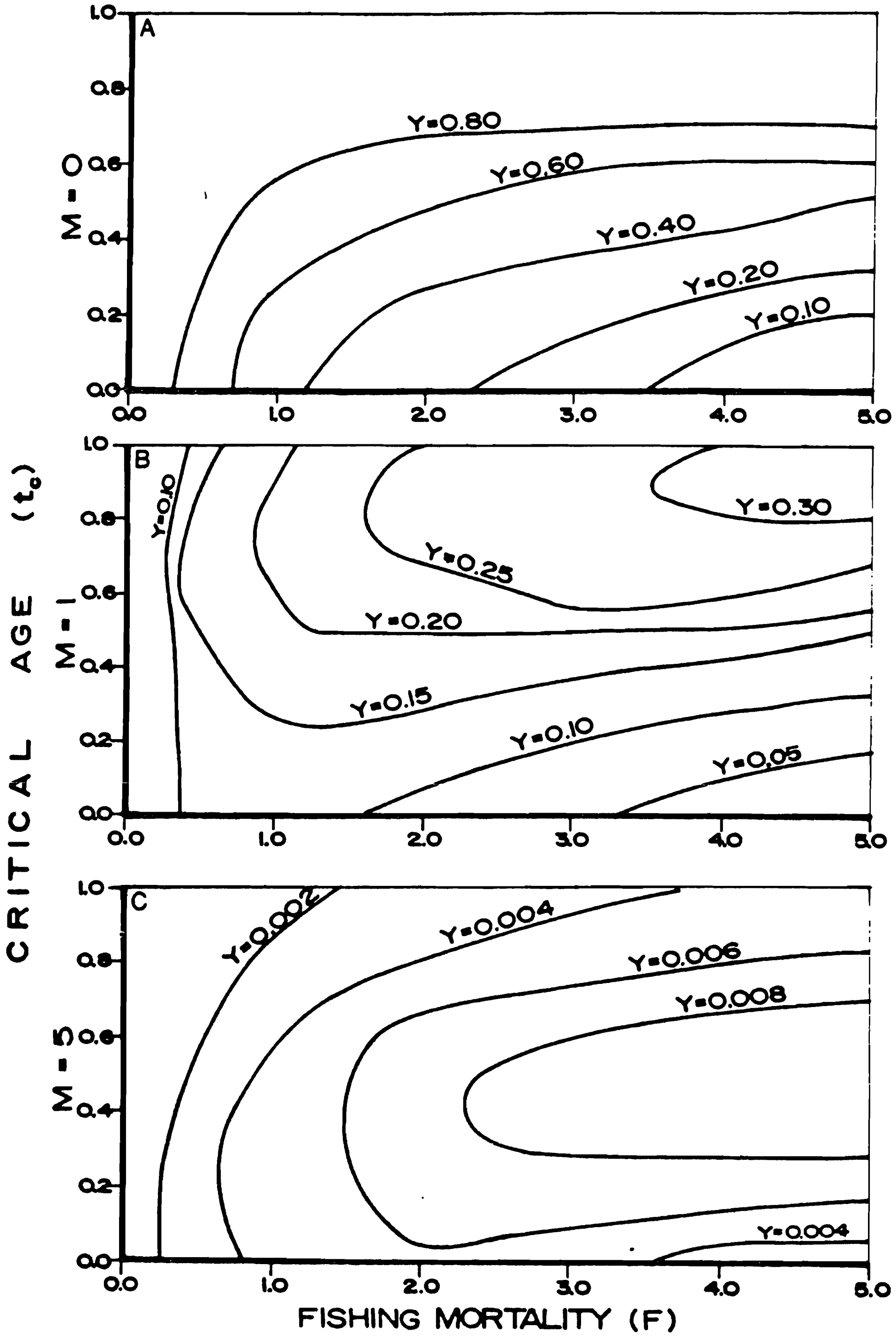

FIG. 1. Isopleths of yield per recruit (Y/RW_∞) as a function of critical age (t_c) and fishing mortality rate (F).

of 0.37 occurs at $t_c = 1$ and $F = \infty$. If t_c is forced to be 0, the best F shifts down to $F = 0.83$. By comparison, when $M = 5$ (Fig. 1C), the optimal yield is only 0.011 and occurs at $t_c = 0.6$ and $F = \infty$. The best F is 1.83 when t_c is forced to be 0.

Estimation of Total Mortality

Natural mortality is the yield equation's key parameter. To estimate natural mortality it is necessary first to estimate total mortality. The total mortality rate of a

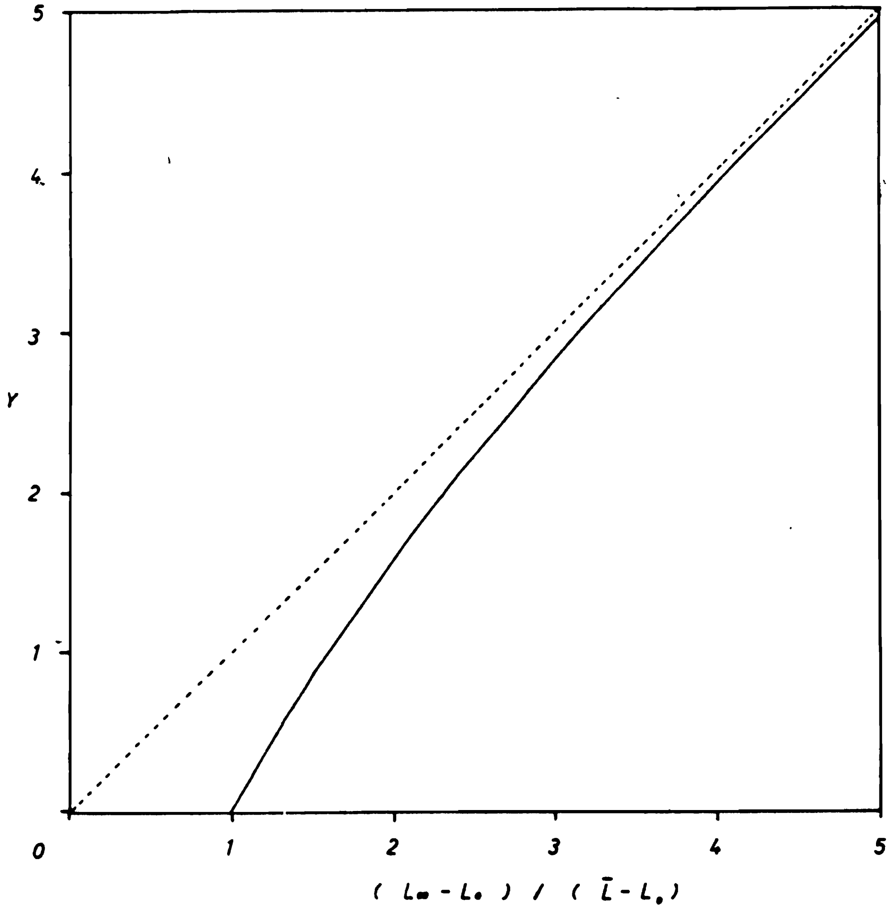

FIG. 2. Solution to equation (14) for estimating total mortality ($\hat{Z}$) using $(L_\infty - L_0)/(\bar{L} - L_0)$ and equation (14a).

population can be estimated from its average length.

It is best to include only fish greater than length L_0 in the estimation procedure if smaller fish are suspected to be underrepresented in the sample due to escapement. Assuming continuous recruitment and $t_0 = L_0/L_\infty \geq t_c$ (i.e., all fish in the sample are large enough to be subject to the constant fishing mortality F), the probability density function of the population above length L_0 is

$$p(t) = Ze^{-Zt}. \tag{11}$$

The average length of the population above length L_0 is

$$\bar{L} = \int_{t_0}^{\infty} [p(t)L(t)]dt. \tag{12}$$

Substituting (7) and (11) in (12)

$$\bar{L} = \int_{t_0}^{1} [Ze^{-Zt}tL_\infty]dt + \int_{1}^{\infty} [Ze^{-Zt}L_\infty]dt. \tag{13}$$

Evaluating the integrals in (13) and solving for Z, the estimate of total mortality ($\hat{Z}$) is

$$\hat{Z} = \frac{L_\infty}{L - L_0}\left[1 - e^{-\left(\frac{L_\infty - L_0}{L_\infty}\right)\hat{Z}}\right]. \tag{14}$$

Although equation (14) does not have an explicit solution it is easily solved by iteration using $L_\infty/\bar{L} - L_0)$ as an initial guess. $\hat{Z}$ is within 1% of $L_\infty/(\bar{L} - L_0)$ when $\hat{Z}(L_\infty - L_0)/L_\infty > 5$.

The solution to equation (14) can also be obtained using Fig. 2. Starting with $(L_\infty - L_0)/(L - L_0)$, the value of Y is read from Fig. 2 and natural mortality then calculated as

$$\hat{Z} = Y\left(\frac{L_\infty}{L_\infty - L_0}\right). \tag{14a}$$

The time unit for the estimate of total mortality is the time required to grow from hypothetical size 0 to full length (L_∞). For example, if the instantaneous mortality rate is 2.0/yr and full size is reached at 3.0 yr, $Z = 6.0$.

Estimation of Natural Mortality

To estimate M it is necessary to sample two or more populations at different times and/or locations. The parameters of individual growth, as well as the natural mortalities of the populations, are assumed to be the same, but the fishing efforts (f) and consequent average lengths must be distinctly different. After estimating total mortality for each population using equation (14), the unknown natural mortality (M) and gear efficiency (k) can be estimated by fitting the regression equation

$$Z = M + kf. \tag{15}$$

The Z intercept gives an estimate of M (i.e. the hypothetical mortality when fishing intensity is 0), and the slope gives the conversion factor between fishing effort (f) and fishing mortality (F), $F = kf$. Confidence limits for M and k can be calculated by standard linear regression techniques.

It may be that natural mortality is influenced by fishing and therefore is not the same in all the populations. If so, the resulting curvilinear relationship between Z and f can be fitted by polynomial regression and M estimated by extrapolation to $f = 0$.

Summary of the Method

Restating equation (10), the yield equation, in terms of k and f,

$$Y = RW_\infty kfe^{kft_c}\left[e^{-(M+kf)t_c}\left(\frac{t_c^3}{M+kf}+\frac{3t_c^2}{(M+kf)^2}+\frac{6t_c^3}{(M+kf)^3}+\frac{6}{(M+kf)^4}\right) - e^{-(M+kf)}\left(\frac{3}{(M+kf)^2}+\frac{6}{(M+kf)^3}+\frac{6}{(M+kf)^4}\right)\right]. \tag{16}$$

The method is simple. First, samples of two or more populations having approximately the same growth and natural mortality parameters but experiencing different fishing efforts are taken to estimate the average length of each population. Equation (14) is used to estimate the total mortality (Z) of each population, and equation (15) is then used to estimate natural mortality (M) and the gear efficiency coefficient (k). M and k are the two essential parameters for calculating yield.

Note that although the parameters R and W_∞ must be known to calculate the absolute value of yield, they need not be known to calculate relative values of yield for different values of the decision variables, critical age (t_c) and fishing effort (f). Graphs can be prepared of relative yield against t_c and f (Fig. 1) and the optimal values of t_c and f compared with existing values in the fishery.

An Example

Equation (15) can be used to estimate M and k most effectively when at least one of the locations is heavily fished and one lightly fished. The calculations presented below are based on bottom-trawl samples of the catfish *Bagrus docmac* from two parts of Lake Victoria, East Africa: (1) the heavily fished Kavirondo Gulf and (2) the lightly fished Emin Pasha Gulf. Samples from different times of the year were pooled to average out seasonal fluctuations in average length. Although this simple example is based on only two sample points, serious applications of the method should use as many points as possible.

Yields are expressed as Y/RW_∞, i.e. as a proportion of the maximum yield that would be possible if there were no natural mortality.

	Kavirondo Gulf		Emin Pasha Gulf
Sample size	3440		74
Min length used in samples (L_0)		34.5 cm	
Length at maturity (L_∞)		85.0 cm	
Avg length in sample ($\bar{L}$)	41.9 cm		47.4 cm
Total mortality (Z) estimated from equation (14)	11.5		6.5
Fishing effort (f) as nets per mile of shoreline	445		112
Natural mortality (M) estimated from equation (15)		4.8	
Efficiency coefficient (k) estimated from equation (15)		.015	

Because *Bagrus* is fished by a great variety of nets that capture it between a size of 5 cm and maturity, t_c is for all practical purposes 0. Calculating the optimal fishing intensity, assuming $t_c = 0$,

	Kavirondo Gulf		Emin Pasha Gulf
Present calculated yield (Y/RW_∞) by equation (16)	.0023		.0055
Optimal fishing effort (f) by equation (16)		113	
Optimum yield (Y/RW_∞) by equation (16)		.0055	

With an estimated natural mortality of 4.8, the best yield possible for *Bagrus* with the present critical age ($t_c = 0$) is only 0.55% of what would be possible if there were no natural mortality. Whereas fishing effort in the Emin Pasha Gulf is very close to the optimum, fishing effort in the Kavirondo Gulf is 4 times the optimum, and yield is only 42% of what it could be.

Figure 1C (based on $M = 5$, which is reasonably close to the $M = 4.8$ for *Bagrus*) gives an idea of the possibilities if critical age could be adjusted. If the critical age can be postponed to 60% of maturity, the maximum is double what it is when the critical age is 0 (Fig. 1C). Furthermore, maximum yield at $t_c = 0.60$ occurs at a value of $F = \infty$, which means that the fishing mortality of $F = 6.7$ in the heavily fished Kavirondo Gulf would no longer represent overfishing.

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I wish to thank G. Ssentongo, who stimulated me to formulate the yield equation presented in this paper.

BEVERTON, R. J. H., AND S. J. HOLT. 1957. On the dynamics of exploited fish populations. Her Majesty's Stationery Office, London. 533 p.

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APPENDIX: Estimates of total mortality (Z) for major commercial fish in Lake Victoria using equation (14) and average lengths

Source: Marten, G.G. 1976. Mortality rates and optimum yields from average lengths. East African Freshwater Fisheries Research Organization Annual Report (1975):22-24.

	Location	N	L_0	L_∞	Ave (L)	Est (Z)
Tilapia esculenta	EPG	359	22.5	35	28.0	5.4
Tilapia variabilis	KG	94	19.5	34	23.3	8.7
Tilapia nilotica	U	442	39.5	60	47.3	6.9
Bagrus docmac	KG	3440	34.5	85	41.9	11.5
Bagrus docmac	EPG	74	34.5	85	47.4	6.5
Clarias mossambicus	KG	227	54.5	110	72.0	6.0
Protopterus sp.	KG	217	99.5	160	118.7	7.9
Haplochromis sp.	KG	4794	4.75	16	7.05	6.9
Haplochromis sp.	PV	3072	4.75	16	7.50	5.7
Schilbe mystus	KG	258	19.5	35	23.6	8.3
Synodontis afrofischeri	KG	254	9.25	20	11.13	9.6
Synodontis victoriae	U	245	13.45	26	15.50	12.7
Engraulicypris argenteus	KG	569	4.75	9	5.75	8.9
Engraulicypris argenteus	PV	925	4.75	9	6.05	6.6

KG = Kavirondo Gulf, Kenya (1975)
PV = Port Victoria, Kenya (1975)
U = Uyoma, Kenya (1975)
EPG = Emin Pasha Gulf, Tanzania (1970)

N = Sample size
L_0 = Minimum length (cm) used in the fish sample
L_∞ = Maximum length (cm) to which the fish can grow
Ave (L) = Average length (cm) of fish exceeding L_0 in the sample
Est (Z) = Estimated total mortality