# *Approximations to sustainable yield for exploited and unexploited stocks*

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ABSTRACT

*Preliminary assessments of the potential yield from unexploited and underexploited stocks are frequently needed, especially for marine resources in tropical and subtropical areas where the fisheries statistics required for a complete assessment are often unavailable. To date most of such estimates have relied on the approximation $MSY \simeq 0.5\ MB\infty$ to provide a first estimate of potential yield, knowing virgin stock size $B\infty$ and natural mortality rate $M$, and assuming the logistic model applies.*

*A comparative study of existing applications of the logistic model in the fisheries literature shows that for many arcto-boreal resources, this approximation usually provides an underestimate of potential yield; but under other circumstances, particularly for short-lived species, this approximation may seriously overestimate MSY.*

*More explicit formulations for potential yield at the MSY point are presented here based on the logistic model, but more important, a new criterion for management is proposed, namely the Yield at Maximum Biological Production ($Y_{MBP}$). It is suggested that in order to avoid serious ecological perturbations, the fishery should be operated at the point where total production from the stock (predators+fishery) is maximized. This occurs at a level of effort below that providing MSY: the difference in effort between the two points increasing as the natural mortality rate (and hence the distance from the apex of the food pyramid) increases. Some ecological implications of the parameters obtained from fitting the logistic model are pointed out, and their relevance to fisheries management briefly discussed.*

*The case is presented for a more careful comparison between production models on different marine resources, in terms of the mortality rates experienced, both in the absence of fishing ($M$), and at the MSY point ($Z_{MSY}$). This could lead to a valuable set of data from which potential yield estimates for related stocks could be drawn with more certainty.*

KEY WORDS : Fishery management — Population dynamics — Stock assessment — Production (biological) — Tropical zones.

RÉSUMÉ

ÉVALUATIONS DE LA PRODUCTION ÉQUILIBRÉE DES STOCKS EXPLOITÉS ET NON EXPLOITÉS

*On a souvent besoin d'évaluations préliminaires de la production potentielle des stocks non exploités et sous-exploités, particulièrement dans le cas de ressources marines des régions tropicales et sub-tropicales où l'on ne dispose pas des statistiques de pêche qui en permettent une évaluation exhaustive. Jusqu'ici de telles évaluations ont pour la plupart utilisé la formule approchée: $MSY = 0,5\ MB\infty$ (MSY, maximum sustainable yield; en français PME, production maximale équilibrée) qui donne une première estimation de la production potentielle en fonction, de la taille du stock vierge $B\infty$, et du taux de mortalité naturelle $M$, dans l'hypothèse où le modèle logistique est applicable.*

*Comme le montre la comparaison de diverses applications du modèle logistique recueillies dans la littérature, cette approximation sous-estime généralement la production potentielle de nombreuses ressources arcto-boréales; par contre dans d'autres situations, notamment lorsqu'il s'agit d'espèces à courte durée de vie, cette approximation peut sérieusement surestimer MSY.*

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*Cette étude présente des formulations plus explicites de la production maximale équilibrée MSY, fondées sur le modèle logistique, mais surtout propose un nouveau critère de gestion : l'exploitation au maximum de la production biologique ($Y_{MBP}$). Il est suggéré que pour éviter de sérieuses perturbations d'ordre écologique, la pêche doive être menée au point où la production totale du stock (prédation+pêche) est maximale. Ce qui se produit pour un effort de pêche de niveau inférieur à celui aboutissant à MSY : la différence en termes d'effort entre ces deux valeurs augmentant avec le taux de mortalité naturelle (et donc l'éloignement du sommet de la pyramide trophique). Sont soulignées quelques-unes des implications écologiques des paramètres obtenus par ajustement du modèle logistique, et leur pertinence pour la gestion des pêches est brièvement discutée.*

*Il est suggéré qu'à partir d'une étude comparative encore plus approfondie des modèles de production appliqués à différentes ressources marines, en termes de taux de mortalité observés d'une part hors de toute exploitation (M), et d'autre part au niveau du MSY ($Z_{MSY}$), pourrait être rassemblé un précieux ensemble de données qui servirait de base plus sûre aux estimations des productions potentielles des stocks homologues.*

MOTS-CLÉS : Gestion pêches — Dynamique populations — Estimation stocks — Production (biologique) — Zone tropicale.

## 1. INTRODUCTION

The familiar equation widely used in the estimation of potential yields of under or unexploited fish stocks is that used first by GULLAND (1971), namely that the Maximum Sustainable Yield, MSY $\simeq$ 0.5 $MB_\infty$, where M is the instantaneous natural mortality rate for the stock, and $B_\infty$ the virgin biomass. The basic philosophy behind this approximation was that MSY must be a function of both the unexploited biomass ($B_\infty$) and the turnover rate (which in turn is related to M), in the unfished population. Following the logistic model, it can be shown that in order to obtain the MSY, the biomass of the exploited stock should be half that for the virgin stock, i.e. 0.5 $B_\infty$. It is then supposed that at MSY, $F_{MSY}$ is roughly equal to M. Developments of this approximation are also currently used for stocks that are already being exploited to give a rough idea of their potential MSY: thus, MSY $\simeq$ .5 $Z\bar{B}$, where Z = M+F, and since Y = $F\bar{B}$, this has been rewritten as MSY $\simeq$ .5 (Y+$M\bar{B}$) (CADIMA, *in* TROADEC, 1977). Since $Z\bar{B}$ is one definition of the total production P from the stock, this development of Gulland's equation assumes that MSY $\simeq$ 0.5 P: this in turn implies that F/Z $\simeq$ 0.5 and F $\simeq$ M at the MSY point. The equation is therefore strictly equivalent to the original one, and under the same logic is "exact" under logistic assumptions only if the value of $\bar{B}$ refers to a stock exploited at the MSY level. Its use as an approximation therefore becomes progressively more suspect with departure from MSY conditions.

GULLAND (1971) suggested that the above equation could be adjusted for use with different species bearing in mind the known value of analytic parameters for the stock, and hence being able to calculate the yield per recruit for the stock in question. Thus, MSY $\simeq$ $XMB_\infty$ and $X = \frac{F_{MAX}}{M} \cdot \frac{B_{MAX}}{B_\infty}$, where $F_{MAX}$ and $B_{MAX}$ are the fishing mortality and biomass under conditions corresponding to the maximum yield per recruit and can be obtained from the yield per recruit tables of BEVERTON and HOLT (1964), and varies from roughly 20 % to 90 % in Gulland's table, but is likely to have a more restricted range in practice. This approach certainly provides more flexible estimates of potential yield taking into account the relative production from a fixed number of recruits with different M/K and $l_c/L_\infty$ characteristics, but as noted by FRANCIS (1974), this more refined approximation is still only valid if constant or density independent recruitment occurs, which is not necessarily the case. In fact, experience tends to suggest that the chances of having long-term average recruitment success may be reduced, or recruitment become more variable, as MSY conditions are approached.

Two related problems seem to emerge from use of these approximations: the first relates to the question of whether MSY is always a desirable point to aim for in a developing fishery ; the second is to find out whether the above approximation is equally valid for all values of M.

## 2. ALTERNATIVE BENCHMARKS TO MSY

Various approaches in the literature towards defining a level of effort that is below that calculated to give the MSY all confirm the common concern and misgivings about the MSY benchmark. Some different approaches that provide other benchmarks are briefly referred to in the following:

The idea that the economically optimal effort level is to the left of MSY was first proposed by GORDON (1954) on economic grounds.

An arbitrary benchmark ($F_{0.1}$) was proposed to take account of the fact that in yield models in general, the marginal yield drops significantly as the MSY or $Y_{max}$ point is approached (GULLAND and BOEREMA, 1973).

Environmentally-caused instability in recruitment in conjunction with errors in estimation of parameters of the yield models means that in practice MSY cannot be attained, and the long-term Maximum Average Yield (MAY) will always be less than MSY (SISSENWINE, 1978).

Some idea of the probable average location of the new $f_{opt}$ is given by DOUBLEDAY (1976) who concluded that in situations where recruitment fluctuates, attempts to harvest the MSY each year from a stock leads to disaster. He found for the stochastic version of the SCHAEFER (1954) model that 2/3 $f_{MSY}$ is a safer target, giving a yield little smaller than the theoretical (and in practice unsustainable!) MSY benchmark.

Realising that all other benchmarks are referred with respect to MSY, we should add that $F_{MSY}$ at best represents the level of fishing mortality not to be exceeded on a long-term basis because of its drawbacks in biological and economic terms.

## 3. THE YIELD AT MAXIMUM BIOLOGICAL PRODUCTION ($Y_{MBP}$)

The recent approach to production modelling suggested by CSIRKE and CADDY (1983) involving a direct fit of yield against Z in the absence of effort data suggests a fundamental criterion for optimality to consider in setting harvesting levels for a fish stock. It is widely accepted now that there are alternative and preferable benchmarks lying to the left of $F_{MSY}$ in management of fish stocks, for example, arbitrary but widely accepted criteria such as the $F_{0.1}$ or 2/3 $f_{MSY}$ points, both of which are believed to be reasonably close to Maximum Economic Yield (MEY). In light of the growing preoccupation with multispecies management, and in particular, the impact of fishing on equilibrium in predator-prey systems, it seems worthwhile to attempt to define a level of harvesting that offers the best chance of co-existence of a fishery with the on-going trophic interactions of the harvested stock. One criterion would be to try and define the level of fishing that yields the maximum productivity of the stock to both man and other predators on the resource being harvested. Accepting that a great deal of information will be needed before this point can be defined exactly, nonetheless a simple extension of the logistic model appears to offer the possibility of defining such a point and its corresponding characteristics, given the natural mortality rate for the stock, and historical information on its response to varying intensities of fishing.

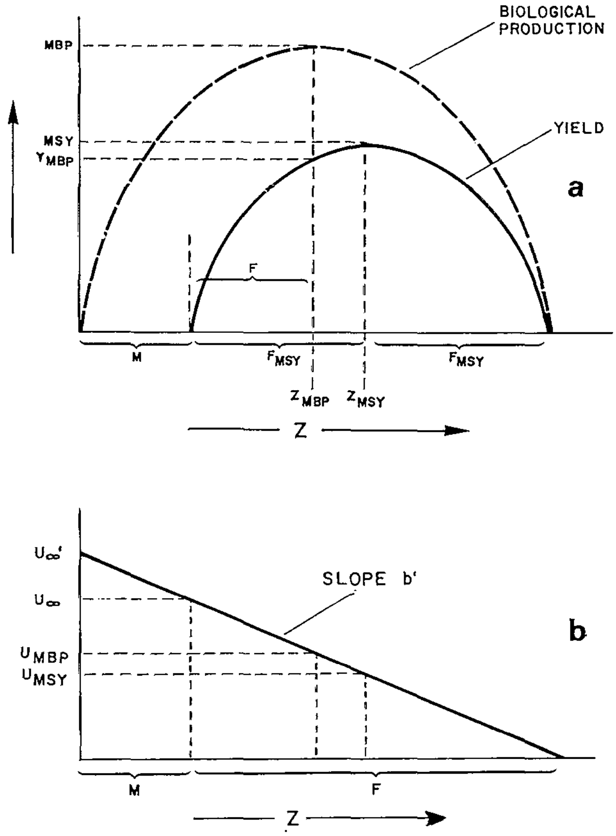


FIG. 1. a: total production and yield from a fish stock under the logistic population model, as a function of total mortality rate (Z), illustrating that the point of Maximum Biological Production (MBP) corresponds to a lower yield ($Y_{MBP}$) than the MSY level. b: the corresponding relationship between catch rate (U) and total mortality rate is shown.
a: *production globale et production exploitée d'un stock de poissons dans le modèle logistique, en fonction du taux de mortalité totale (Z), illustration de ce qu'au point de production biologique maximale (MBP) correspond une production exploitée ($Y_{MBP}$) inférieure au MSY.*
b: *la relation correspondante entre capture par unité d'effort (U) et taux de mortalité totale.*

A plot of yield versus Z (fig. 1) implies—in terms of the overall mortality rate suffered by a population—that fishing mortality is added in sequence to an already existing natural mortality rate suffered before the fishery begins (Figure 1a), so that the intercept of the curve with the Z-axis gives an estimate of M, which is to the right of the origin. Details of this new approach are given in CSIRKE and CADDY (1983), who also suggest a second alternative of fitting the logistic model, based on regressing the catch rate on Z.

As noted by PAULY (1979), the usual concept underlying production models—namely that surplus production is effectively zero for the virgin stock—ignores the fact that for most stocks, predation is harvesting a significant proportion of prey biomass even in the absence of fishing, so that overall production is certainly far from negligible under these conditions. Hence, although the virgin biomass $B_\infty$ (and the virgin catch rate $U_\infty$) remain as defined in the usual models, we can postulate for convenience of description of our new approach a value $U'_\infty$ which is an extrapolation to a purely hypothetical "catch rate" or abundance index when $Z = 0$ (fig. 1b). Evidently, $U'_\infty = U_\infty + b'M$, where $b'$ is the slope of the plot of catch rate U against Z (or F).

By introducing the new parameter $U'_\infty$, we can draw a second production curve with the same value for parameter $b'$ as the first, but going through the origin. This intercepts the Z-axis at the same point as the first curve when production falls to zero, namely, at a value of $Z = M+2\,F_{MSY}$ (fig. 1a, 1b). Inspection of this second curve readily reveals that its maximum occurs to the left of the point of MSY. We can consider this as the point of Maximum Biological Production (MBP), including natural deaths plus harvested yield for the population as a whole. In one sense, this is the most 'healthy' point on the yield curve, since here the exploited population is at its most productive. The equivalent fishery related yield (the Yield at Maximum Biological Production: $Y_{MBP}$) is related to MBP by:

$$Y_{MBP} = E.MBP, \text{ where } E = F_{MBP}/Z_{MBP}$$

From this, it follows with the logistic model, that the point MSY occurs when the total production of the population is already declining. Looking at Figure 2, we can see that the rate of decline in total production at MSY becomes progressively more pronounced as M increases: $F_{MBP}$ occuring progressively earlier in the evolution of fishing effort with increasing M. The question to be asked is whether the effort corresponding to MBP is not a safer point on the yield curve than MSY to aim for, at least in an initial assessment. Certainly it seems worthwhile defining it more precisely.

Consider the conventional formulation for SCHAEFER's (1954) model in terms of effort: $U_t = U_\infty - bf_t$, and express it in terms of the fishing mortality F and the catchability coefficient q. We then have:

$$U_t = U_\infty - b'F_t.$$
$$\text{or } U_t = U_\infty - b'(Z_t\text{-}M).$$
$$\text{where } b' = \frac{b}{q}.$$

Evidently the parabola of biological production in Figure 1a, since it is congruent with the parabola of yield, corresponds under the Schaefer model to an overall abundance $U_t$ given by:

$$U_t = U'_\infty - b'Z_t = (U_\infty + b'M) - b'Z_t.$$

Noting that biological production (i.e. biomass dying naturally and caught per time interval) from a population in a steady state can be defined as $P_t = B_tZ_t$, and if catch rate $U_t$ is proportional to Biomass $B_t$, we can formulate an index of production $U_tZ_t$ given by:

$$U_tZ_t = (U_\infty + b'M)Z_t - b'Z_t^2. \quad (2)$$

which describes a parabola with a maximum production level that corresponds to $Z_{MBP}$. This, in practical terms, is easier to fit than the upper curve in Figure 1a, which requires data on the biomass or catchability coefficient for a stock, and corresponds to:

$$B_tZ_t = \frac{(U_\infty + b'M)}{q} Z_t - \frac{b'}{q} Z_t^2. \quad (3)$$

The percentage change in production for a given change in Z is evidently the same for curves generated by equations (2) and (3), so that equation (2) may be readily used in most fisheries estimates involving biological production if the logistic model is assumed.

It can also be noted (S. GARCIA, pers. comm.) that the line between any point on the biological production curve and the origin in Fig. 1a has a slope equal to the biomass (slope = P/Z). Therefore the slope of the tangent to the curve going through the origin is equal to $B'_\infty$, the theoretical biomass when $M = 0$, and the slope of the tangent to the yield curve going through $Z = M$ is equal to the virgin stock biomass ($B_\infty$). The biomass at Maximum Biological Production ($B_{MBP} = B'_\infty/2$), and the biomass at MSY level ($B_{MSY} = B_\infty/2$) can be defined in the same way.

## 4. OTHER FORMULATIONS OF THE LOGISTIC

It is interesting to relate the parameters of the revised Schaefer model $U_\infty$ and $b'$, to those of the "relative logistic" model of Graham, in particular the parameter r in:

$$Y_E = r\,\frac{\bar{B}(B_\infty - \bar{B})}{B_\infty}.$$

CSIRKE and CADDY (1983) note that this is easily transformed into:

$$Y_E = B_\infty\,F - \frac{B_\infty\,F^2}{r}.$$

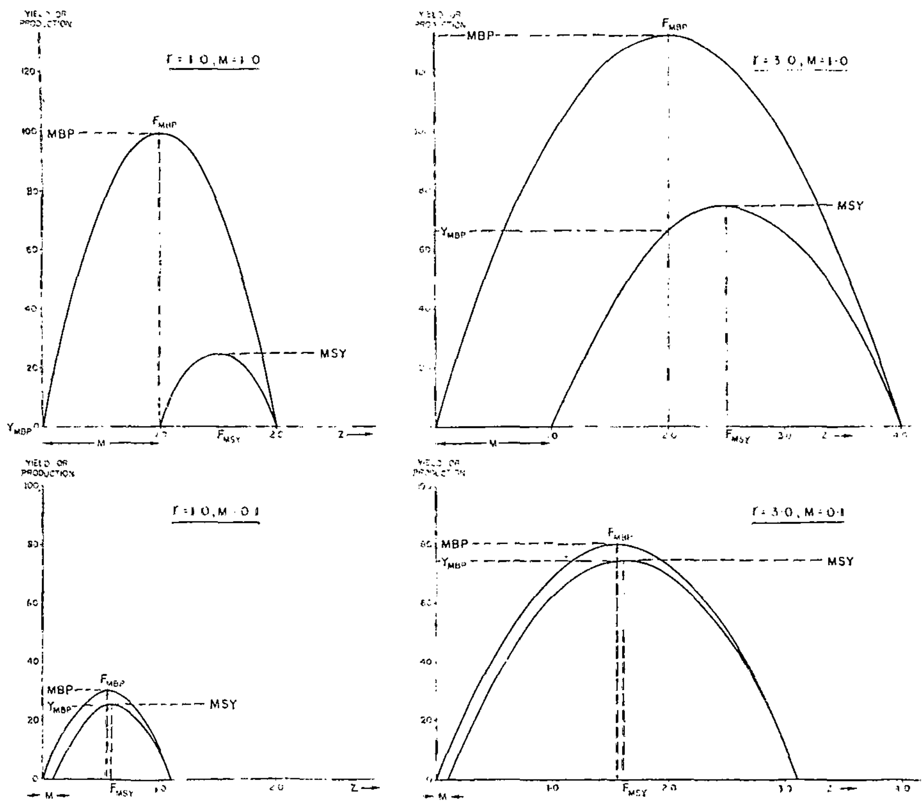


FIG. 2. — Diagrammatic representation of logistic curves for biological production and yields as a function of 4 sets of extreme values for the population parameters M and r.

*Représentation schématique des courbes logistiques de production globale et de production exploitée, pour 4 paires de valeurs extrêmes des paramètres M et r.*

Dividing by f we get:

$$U_E = \frac{Y_E}{f} = \frac{B_\infty F}{f} - \frac{B_\infty F^2}{rf}.$$

$$U_E = qB_\infty - q\frac{B_\infty}{r}F.$$

$$\text{i.e. } U_E = U_\infty - \frac{U_\infty}{r}F.$$

which, by comparison with our revised Schaefer model: $U_t = U_\infty - b'F$, gives:

$$\frac{U_\infty}{r} = b' \text{ or } r = \frac{U_\infty}{b'}.$$

i.e. our ratio $\frac{U_\infty}{b'}$ is identical to the value r in the "relative logistic", which, since $b' = 0.5\,\frac{U_\infty}{F_{MSY}}$, and $r = 2\,F_{MSY}$ (CSIRKE and CADDY, 1983), implies that r measures the dimensions of the base of the yield parabola, and hence is inversely related to the degree of convexity of the yield parabola for a given value of $U_\infty$.

We can now reformulate equation (3) for production in terms of these new parameters as:

$$P_t = B_t Z_t = B_\infty\left(1 + \frac{M}{r}\right)Z_t - \left(\frac{B_\infty}{r}\right)Z^2_t \quad (4)$$

This may be compared with the production model for fishery yield:

$$Y_t = B_t F_t = B_\infty F_t - \left(\frac{B_\infty}{r}\right)F^2_t.$$

Both of these curves are plotted in Fig. 2 for 4 arbitrary values of M and r, with $B_\infty = 100$ units, and the corresponsing bechmarks for the system are calculated in Table II.

It is worth noting that b' is the decline in catch rate resulting from applying a unit fishing mortality rate $F = 1.0$ to the stock, and can be obtained in practice by a functional regression of annual catch rate on annual Z for a series of years. The total production for the system is theoretically obtainable as the product of the weighted estimate of total mortality (Z) for all exploited age groups, and an independent estimator of total biomass. Since the latter is unlikely to be easily obtainable, we have suggested earlier obtaining an index of total production, $U_tZ_t$ which will behave in the same way as the total production for the stock, if catch rate is a good index of biomass.

Some other useful expressions that emerge from the characteristics of these two production curves are:

### Estimation of key mortality rates

(a) *Expressions for $F_{MBP}$ (Fishing mortality rate at Maximum Biological Production)*

$$Z_{MBP} = 0.5\,(2\,F_{MSY} + M) = 0.5\,M + F_{MSY}.$$
$$Z_{MBP} = 0.5\,(r + M).$$
$$\text{i.e. } F_{MBP} = 0.5\,(r - M).$$
$$F_{MBP} = 0.5\left[\frac{U\infty}{b'} - M\right]. \quad (5)$$

Equation (5) is suggested to operate under the constraint that $M \leqslant r$, since otherwise negative values for $F_{MBP}$ will be obtained, implying that the level of mortality corresponding to Maximum Biological Production (MBP) was exceeded even before the fishery began. This is of course theoretically feasible. In the long-term however, it seems reasonable to suppose that a common evolutionary strategy (the "benign predator" strategy) would be to maintain prey population close to its maximum long term productivity. Although there seems little evidence to support or deny this theory, $M \geqslant r$ tends to imply an assymetric yield curve, and/or the possibility of rapid population declines at moderate F, that would invalidate simple logistic theory.

Also, since:

$$U_\infty = q\,B_\infty.$$
$$Z_{MBP} = \frac{0.5\ q\,B_\infty}{b'} + 0.5\,M. \quad (6)$$
$$\text{and } F_{MBP} = \frac{0.5\ q\,B_\infty}{b'} - 0.5\,M. \quad (7)$$

(b) *Expressions for fishing mortality rate at MSY*

We have noted that the catch rate U and fishing mortality rates F in any given year are related by:

$$U_t = U_\infty - b'F_t = U_\infty - b'(Z_t - M).$$

and at MSY by:

$$U_{MSY} = 0.5\,U_\infty = U_\infty - b'\,F_{MSY}.$$
$$\text{i.e., } U_\infty = 2\,b'\,F_{MSY} = b'\,r.$$
$$U_t = 2\,b'\,F_{MSY} - b'\,(Z_t - M).$$
$$= b'\,(2\,F_{MSY} - Z_t + M).$$
$$\text{and } F_{MSY} = \frac{U_t}{2\,b'} + 0.5\,(Z_t - M). \quad (8)$$

### Estimating the Maximum Sustainable Yield (MSY)

(c) *A formulation for MSY from an exploited stock*

$$MSY = \bar{B}_{MSY}\,F_{MSY} = 0.5\,B_\infty\,F_{MSY}.$$
$$\text{where } F_{MSY} = \frac{MSY}{0.5\ B_\infty}.$$

substituting in (8) for $F_{MSY}$:

$$MSY = \frac{B_\infty}{4}\left[\frac{U_t}{b'} + Z_t - M\right]. \quad (9)$$

(d) *Expression for potential MSY from a virgin stock*

Logistic theory implies that MSY is being harvested when $\bar{B} = 0.5\ B_\infty$,

and since $r = 2\,F_{MSY}$

$$MSY = F_{MSY}\,.\,0.5\,B_\infty = r\,B_\infty/4. \quad (10)$$

This expression is analogous to the first Gulland approximation for yield at MSY.

### Characteristics of the point of Maximum Biological Production (MBP)

Following a somewhat limited definition of production from a single-species system, namely the amount of biomass produced by the population in the harvestable phase (i.e. ignoring production of gametes and pre-recruits), and accepting the simplifications of constant natural mortality rate for the exploited phase, and logistic population growth, we can arrive at the expressions defined in the following sections:

#### Yield at maximum biological production (MBP)

(a) *Catch rate at $Y_{MBP}$ in terms of the present rate*

Noting that:

$$U_{MBP} = U_\infty - b'\,F_{MBP}.$$

and substituting for $F_{MBP}$, using equation (5):

$$U_{MBP} = U_\infty - b'\left[\frac{0.5\ U_\infty}{b'} - 0.5\ M\right].$$
$$\text{i.e., } U_{MBP} = 0.5\,[U_\infty + M\,b']. \quad (11)$$

(b) *Definition of $Y_{MBP}$*

$$Y_{MBP} = B_{MBP}\,F_{MBP} = \frac{U_{MBP}}{q}\,.\,F_{MBP}$$

TABLE I

Summary of some basic equations derived from the logistic model in comparison with both the MSY benchmark, and the point of Maximum Biological Production (MBP).

*Formulaire comparatif de quelques expressions fondamentales dérivées du modèle logistique, au niveau du MSY, et au niveau de la production biologique maximale (MBP).*

| Variable Defined | At point of Maximum Biological Production ($Y_{MBP}$) | At Maximum Sustainable Yield (MSY) | Conventional Approximations to MSY |
|---|---|---|---|
| 1. **Optimum catch rate** | $U_{MBP} = 0.5\,(U_\infty + Mb')$ | $U_{MSY} = U_\infty - b'\,F_{MSY}$ | $U_\infty/2$ |
| 2. **Fishing mortality rate** expressed as a function of: | | | |
| Unexploited stock | $F_{MBP} = 0.5\,(r - M)$ | $F_{MSY} = \frac{0.5\,U_\infty}{b'} = \frac{r}{2}$ | |
| Exploited stock | | $F_{MSY} = \frac{U_t}{2b'} + 0.5\,(Z_t - M)$ | |
| 3. **Total mortality rate** | $Z_{MBP} = 0.5\,(r + M)$ | $Z_{MSY} = 0.5\,r + M$ | |
| 4. **Biomass** | $B_{MBP} = \frac{B_\infty}{2}(1 + \frac{M}{r})$ | $B_\infty/2$ | |
| 5. **Yield**, expressed as a *function of:* | | | |
| Unexploited stock | $Y_{MBP} = \frac{r\,B_\infty}{4}\left[1 - (\frac{M}{r})^2\right]$ | $MSY = \frac{r\,B_\infty}{4}$ | $MSY = 0.5\,M\,B_\infty$ |
| Exploited stock | $Y_{MBP} = MSY\left[1 - (\frac{M}{r})^2\right]$ | $MSY = 0.25\,B_\infty\left[\frac{U_t}{b'} + Z_t - M\right]$ | $MSY = 0.5\,(Y + M\,B)$ |
| 6. **Production** | $MBP = \frac{B_\infty}{4r}\,(r + M)^2$ | $P_{MSY} = \frac{MSY}{E_{MSY}}$ | |

TABLE II

Calculated parameter values for production and yield for the 4 hypothetical curves in Fig. 2.

*Valeurs calculées de différents paramètres de production pour les 4 courbes théoriques de la fig. 2.*

| Parameter values for $B_\infty = 100$ | | M = 0.1, r = 1.0 | M = 0.1, r = 3.0 | M = 1.0, r = 1.0 | M = 1.0, r = 3.0 |
|---|---|---|---|---|---|
| $Z_{MBP} = 0.5\,(r + M)$ | $Z_{MBP}$ : | = 0.55 | = 1.55 | = 1.0 | = 2.0 |
| $F_{MBP} = 0.5\,(r - M)$ | $F_{MBP}$ : | = 0.45 | = 1.45 | = 0 | = 1.0 |
| $MSY = \frac{rB_\infty}{4}$ | MSY : | = 25 | = 75 | = 25 | = 75 |
| $F_{MSY} = r/2$ | $F_{MSY}$ : | = 0.5 | = 1.5 | = 0.5 | = 1.5 |
| $Y_{MBP} = \frac{rB_\infty}{4}\left[1 - (\frac{M}{r})^2\right]$ | $Y_{MBP}$ : | = 24.75 | = 74.91 | = 0 | = 66.7 |
| $\bar{B}_{MBP} = \frac{B_\infty}{2}\,(1 + \frac{M}{r})$ | $B_{MBP}$ : | = 55.0 | = 51.70 | = 100 | = 66.7 |
| $MBP = \frac{B_\infty}{4r}\,(r + M)^2$ | MBP : | = 30.25 | = 80.1 | = 100 | = 133.4 |

Substituting for $F_{MBP}$ from equation (7):

$$Y_{MBP} = \frac{U_{MBF}}{q}\left[\frac{0.5\ q\ B_\infty}{b'} - 0.5\ M\right].$$

then substituting for $U_{MBP}$ from equation (11):

$$Y_{MBP} = \frac{0.5\ U_\infty + 0.5\ M\ b'}{q}.\left[\frac{0.5\ q\ B_\infty}{b'} - 0.5\ M\right].$$

$$= \frac{0.25\ U_\infty\ B_\infty}{b'} - \frac{0.25\ M\ U_\infty}{q} + 0.25\ M\ B_\infty$$

$$- \frac{0.25\ M^2\ b'}{q}.$$

but $q = \frac{U_\infty}{B_\infty}$ and $b' = \frac{U_\infty}{r}$.

therefore : $$Y_{MBP} = \frac{r\ B_\infty}{4}\left[1 - \left(\frac{M}{r}\right)^2\right]. \quad (12)$$

### The point $Y_{MBP}$ in Terms of MSY

Starting with equation (12), and noting that:

$$B_\infty = \frac{4\ MSY}{r}.$$

$$Y_{MBP} = MSY\left[1 - \left(\frac{M}{r}\right)^2\right] = \frac{B_\infty}{4}\left[\frac{r^2 - M^2}{r}\right]. \quad (13)$$

### The Maximum Biological Production (MBP)

From equation (13), noting that the biomass at MBP is given by:

$$B_{MBP} = \frac{Y_{MBP}}{F_{MBP}}.$$

we have $$B_{MBP} = \frac{B_\infty}{4}\left(\frac{r^2 - M^2}{r}\right)\left(\frac{1}{0.5\ (r - M)}\right).$$

$$B_{MBP} = \frac{B_\infty}{2}\left(1 + \frac{M}{r}\right).$$

Since the total production at this population biomass is given by:

$$MBP = Z_{MBP} \cdot \bar{B}_{MBP},$$

we have $$MBP = \frac{B_\infty}{4\ r}(r + M)^2.$$

A summary of some key relationships are given in Table I. Table II and Fig. 2 give simple examples of their application. It is presupposed in applying these new relationships that some more detailed information on population parameters of closely related stocks exist, that can form the basis for an estimate of sustainable yield. This will certainly be more likely as detailed studies accumulate in the literature, and in this case, the methods proposed here will be useful in the transitional phase until a more detailed assessment is possible along conventional lines.

## 5. r AND k SELECTION THEORY

The papers of MacArthur and Wilson (1967) and Pianka (1970, 1972) give a good description of the way in which the life strategies of most organisms, to a greater or lesser extent, tend towards one of two extremes: one increasing individual survival at the expense of reproduction, the other maximizing reproductive potential at the expense of individual survival.

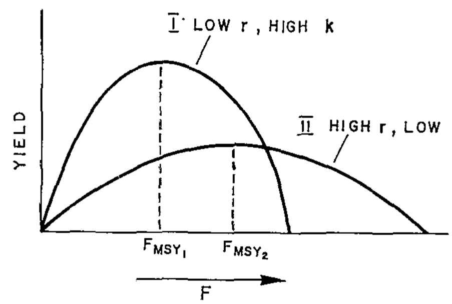


Fig. 3. — The logistic model and r-k theory, illustrated by 2 species with different r/k ratios. Species I dominate the environment at low levels of exploitation, but is replaced progressively by II as fishing intensity increases.

*Le modèle logistique et la théorie r-k, illustré par 2 espèces dotées de rapports r/k différents. L'espèce I est dominante aux faibles niveaux d'exploitation, mais est remplacée par II quand augmente l'intensité de pêche.*

Pianka (1970) in particular notes that fish tend to "span the range of the r-k continuum", and Gunderson (1980) shows empirically that this paradigm is valid for a limited selection of northern boreal species, for which he found that natural mortality rate and longevity respectively are the parameters most directly related to gonad index, as would be predicted by r- and k- theory. Mathematically, r and k are the parameters of the Verhulst-Pearl logistic equation $\frac{dN}{dt} = rN - \frac{rN^2}{k}$ defining of course our logistic model, and broadly speaking, populations approaching the two ends of the "r-k continuum" may be expected to resemble those shown in Figure 3.

Noting that if we substitute $N_\infty = k$ = carrying capacity of the environment, and $a = r/N_\infty$, we arrive at a formulation analogus to the conventional Schaefer model: i.e.,

$$\frac{dN}{dt} = rN\frac{(N_\infty - N)}{N_\infty} = \frac{rN}{N_\infty}(N_\infty - N) = aN(N_\infty - N).$$

Although the parameters of this model were originally expressed in terms of numbers and will not have the same values as for the conventional fisheries biomass model, it seems likely that the ratio of k to r, in the Verhulst-Pearl logistic represents the quotient:

$$\frac{k}{r} \propto \frac{\text{Carrying capacity of the environment (or maximum density the environment can support)}}{\text{Rate of increase in r (or convexity of the parabola).}}$$

and should show similar trends to the ratio $\frac{U_\infty}{r}$ derived from the biomass model, and will measure the distance of a species along the r-k continuum. As such, we would expect a species with a high value for $\frac{U_\infty}{r}$ would also be a species with a high natural mortality rate, and vice versa. Comparative studies of production models to test this and other hypotheses (such as $F_{MSY} \simeq M$) would seem to merit serious attention, but in our limited attempts to extract estimates of $r (= 2\ F_{MSY})$ from data in the literature, it was difficult to be sure from the data presented whether the variations in $F_{MSY}$ observed were due to lack of proper calibration of effort data in the usual plots of catch rate versus effort, due to poor fit of the model to the data in question (few authors publish estimates of goodness-of-fit for production models), or whether there is a real underlying difference in the populations composed. A similar uncertainty relates to the values of natural mortality used for many species and how they have been obtained. Despite these problems, we have attempted in Figure 4 to make a preliminary comparison of r and M for different species and stocks principally to see whether the relationship $F_{MSY} \simeq M$ is a reasonable approximation or not. Estimates of $F_{MSY}$ were rarely possible directly from fitted values of r, but had to be obtained either from $F_{MSY} = q\ f_{MSY}$, if q is known, or if parallel cohort and production model analyses have been carried out, by obtaining the mean value of fishing mortality for all age groups, $F_t$, in those years when effort levels lay close to the calculated MSY level of the fitted production model.

Table III summarizes the basic data used. It was clear, even from our non-exhaustive review of the literature on production models, that there are few examples where both a reliable estimate of M and of $F_{MSY}$ can be obtained, and this is particularly the case for tropical stocks, for the reasons mentioned earlier. We have also deliberately confined our summary to those models where the Schaefer (as opposed to the logarithmic or other versions of the production model) have been used, and the following generalizations were suggested from the data set investigated:

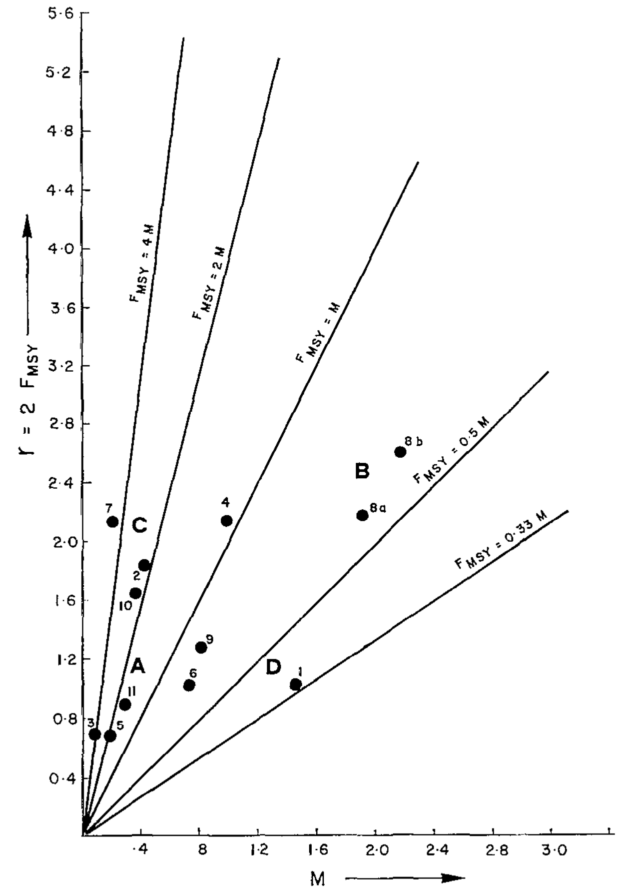


FIG. 4. – Summary of the characteristics of 11 production curves extracted from the literature expressed in terms of the natural mortality rate.

*Caractéristiques de 11 courbes de production en fonction du taux de mortalité naturelle, d'après la littérature (légendes des numéros, voir tabl. III).*

(1) There is no evidence as already noted by FRANCIS (1974), that $F_{MSY} \simeq M$ is a valid approximation for very many stocks, although for most species of groundfish considered from north temperate regions, and some north temperate pelagics, this is a reasonably conservative approach to estimating a 'safe' level of harvesting if M is known. We cannot however at this time extend this generalization to tropical or subtropical stocks, until more detailed studies are available.

(2) For some species (especially several important small pelagic stocks), it is evident that the above approximation does not always provide a safe guideline for management. However, we may note here that the high natural variability of some of these stocks, and the fact that they lie close to the base of the food chain, makes them more vulnerable

TABLE III

Parameters of a short selection of logistic production models extracted from the fisheries literature (equilibrium conditions assumed).
*Paramètres de quelques modèles logistiques de production sélectionnés dans la littérature sur les pêches (en supposant les situations à l'équilibre).*

| | Species & Stock | MSY | $f_{MSY}$ | q | $Z_{MSY}$ | M | $F_{MSY}$ | r | Author |
|---|---|---|---|---|---|---|---|---|---|
| 1 | Pandalid shrimp, California | $2.46 \times 10^6$ lbs | $6.05 \times 10^3$ hrs | $8.50 \times 10^{-5}$ | | 1.44 | 0.514 | 1.03 | Fox (1970) |
| 2 | Californian sardine | $6.11 \times 10^5$ short tons | 1,175 boat months | $9.86 \times 10^{-4}$ | | 0.5 | 0.924 | 1.847 | Fox (1970) |
| 3 | Redfish (ICNAF area 3M) | 15,000 t | 3,800 days | | 0.44 (1972) | 0.10 | 0.34 | 0.68 | Parsons et al. (1976) |
| 4 | Peruvian anchoveta | $11 \times 10^6$ t | $17 \times 10^6$ gross registered ton-trips | 0.06284 | | 1.0 | 1.07 | 2.14 | Murphy (1973) |
| 5 | P. halibut | 305 t | 25.5 x 10 t/hr | | 1.90 (1974-75) | 0.8 | | | Butterworth (1980) |
| 6 | Octopus (Northern CECAF) | 114,154 t | 1,100 unidades espanolas | | 1.27 (1972) | 0.5-1.0 (.75) | 0.52 | 1.04 | Pereiro & Bravo de Laguna (1980) |
| 7 | Yellowtail flounder (S. New England) | 15,400 t | ≈ 5,300 standard days fished | | 1.25 (1959-61) | 0.2 | 1.05 | 2.10 | Pentilla & Brown (1972) |
| 8 | Penaeid shrimp, (Ivory Coast) | | Close to MSY | a) Brown shrimp<br>b) White shrimp | 1.9 (1976) | 1.1<br>2.2 | 2.2<br>1.3 (1973) | <br>2.6 | Brunnenmeister (1981) |
| 9 | Moroccan sardine (Zone A) | 227,000 t | 2,910 units | | | 0.8 | 0.64 age 2-3 (1974-75) | 1.28 | CECAF (1978) |
| 10 | Atlantic menhaden | 620,000 t | 1,000 vessel-weeks | | | 0.37 | 0.8 | 1.6 | Stevenson (1981) |
| 11 | Sangala (*Lates niloticus*, Lake Tanganyika) | 52 t | 5.5 boats | | | 0.3 | .45 | .90 | Henderson et al. (1972) |

Year (in brackets) is period when MSY was approached most closely.

to environmentally-produced instabilities, thus reducing the value or possibility of precise definition of MSY or $F_{MSY}$ anyway.

## TYPICAL VALUES OF R AND THEIR RELATIONSHIP TO M

Estimates of $r (= 2\ F_{MSY})$ were obtained from a number of fits of the Schaefer model already in the literature, for which estimates of $F_{MSY} = r/2$ could be obtained either directly from age composition analysis or by $F_{MSY} = q\ f_{MSY}$. The number of estimates found was necessarily limited, but showed some interesting features. Given that the numbers of fits is very limited, four groups seem to emerge which roughly correspond to types A-D in Figure 4.

(a) *Low r and low M.* This fairly homogenous group, including slow-growing, long-lived species (redfish, nile perch, Pacific halibut) are generally speaking piscivorous and close to the top of the food web. Although they generally have a low resistance to heavy exploitation, $F_{MSY}$ occurs at a relatively high level, in excess of the natural mortality rate M for the population.

(b) *High r and high M* short-lived and fast-growing species that sustain heavy fishing effort (our lone example is a Penaeid shrimp). Although we cannot generalize from this one example, we may suspect that when data are available from some other tropical stocks, they may lie to the right hand side of Figure 4.

(c) *Medium-high r, low M.* Includes a variety of species with moderately long life spans, species including pelagics (California sardine, Icelandic herring, South African anchovy) and a flat fish. Despite the fact that $F_{MSY} > M$, some of these have at one time sustained an intensive fishery, including some which have subsequently shown stock collapses, suggesting that population instability of species predominantly close to the base of the food web may not be entirely due to overfishing.

(d) *Low r and high M.* Once again, a very small sample, consisting of short-lived species with unstable population sizes where, once again, relative effects of environment may be greater than that of fishing. This category may be particularly relevant to tropical and sub-tropical species.

Quite clearly, the use of Figure 4 as an indicator of the likely level of $F_{MSY}$ as a function of the natural mortality rate for a given organism or group of organisms, is strictly limited at present, but may be expected to increase in usefulness as further case studies are completed. We may note however, following May *et al.* (1979), that the single-species MSY concept is most useful for populations at the top of the trophic ladder. For populations other than these, *(op. cit.)* "preservation of the ecosystem would seem to require that stocks not be depleted to a level such that the populations productivity, or that of other populations dependent on it, be significantly reduced"; keeping in mind that "any stock subject to predation may well be below MSY in its natural state". Although the definition of MSY implied here differs from that used conventionally, which usually considers the yield surplus to the effect of natural mortality, it is also quite clear that yield to a fishery if unharvested, is consumed within the system. To this extent, also, the first quotation above explicitly suggests adoption of a management criterion based on overall productivity and not just fisheries yield; and this is what we have attempted to provide in this paper.

## 6. DISCUSSION

Production of biomass occurs independently of harvesting in any population, a fact that is treated at length in the literature on population energetics, but receives no specific mention in the theory of production modelling. In production models a population is treated as a "black box" which produces output (in the form of catch) as a direct function of human inputs (fishing effort). In fact of course deaths due to fishing are not different (except possibly with regard to their probability of occurrence with age) from those caused by natural causes (principally predation). This fact was recognized explicitly by Schaefer (1970), and Murphy (1973) in his study of the Peruvian anchovy fishery, when he calculated the equivalent "fishing effort" by birds, and added it to that exerted by man to arrive at an overall effort index which he used in fitting the total of fish landings and fish consumption by birds against this effort index. Extending this concept a little further to include all natural and human related deaths in an overall "effort index", it is more logical as in Csirke and Caddy (1983) to express the cumulative risk of death from all causes in terms of the total instantaneous mortality rate the population is subject to in a given year.

Various points of view have been expressed about the level of production of a population in the absence of fishing, of which the two most common points of view are:

(1) The one that suggests that at virgin biomass $B_\infty$ production must be negligible since the population is presumed to be dominated by large, old fish. This is clearly not the case, when there is a population of predators that is being supported by the productivity of the above species.

(2) The opposite intuitive approach as expressed for example by Pauly (1979), essentially implies that the biosphere (and presumably also the individual populations that make it up) have evolved to maximize long-term average productivity even in the absence of fishing (i.e., $Z_{MBP}$ occurs when $Z = M$ i.e. $F_{MBP} = 0$!). Some serious problems with this approach emerge under the logistic model: thus, taking the definition of productivity P in an unfished system $P = BM$, if the curve for overall production is symmetrical, by the time $F = M$ in a developing fishery (or $Z = 2M$), the population will have been reduced to a negligible size.

Evidently some intermediate interpretation will hold in most cases. The first postulate says nothing explicit about the relationship between F and M, except that it has become axiomatic to assume that $F = M$ at MSY. It seems clear from earlier sections that if this holds for a given population with specified r and M, it will not hold if one or other of these parameters changes in value (Francis, 1974). A solution for the relationship between M, r and $F_{MSY}$ is presented in this paper, or more usefully we believe, for M, and $F_{MBP}$ (the fishing mortality rate giving the Yield at the point of Maximum Biological Production). What is suggested by this simple extrapolation of the logistic model, and which has apparently gone unnoticed before, is that the point of Maximum Biological Production occurs progressively earlier than the point of Maximum Sustainable Yield as M increases. The relevance of this point to tropical fisheries where natural mortality rates are higher on average than for temperate species is obvious: serious biological perturbation and/or loss of yield are likely to occur well before MSY is reached for many such stocks. Although it is dangerous to argue ecological theory from oversimplified models such as the logistic, this approach suggests that fish species subject to a high predation rate (or M) are closer to their point of maximum production before fishing begins than is the case for longer-lived species, and may already be declining in overall productivity even at relatively low rates of fishing. This argument is however rather oversimplistic if we do not consider the value of r for the populations in question: evidently for a given M, species with a high r are more likely to be able to sustain high levels of fishing than those with a low r (Figure 4), and will reach the point of $F_{MSY}$ $(= \frac{r}{2})$ at a higher fishing intensity.

This has obvious implications for multispecies fisheries that will not be developed further here, except to note graphically (Figure 3), that species I with a low r and the same value of M, should react differentially to the same level of fishing mortality in terms of their ability to sustain their biomass in a fishery than species II with a high r. Species I should show a more marked and immediate decline in biomass and catch rate than II for a relatively moderate level of effort. Presumably now, if species II is a predator on species I, the ratio of their productivities at points $F_{MBP}$, and at each $F_{MSY}$ level will all be different. How will this affect firstly the trophic requirements of species II, and secondly the predation rate on species I? No answer is suggested here, since the dynamics of the predator-prey system depends on time-related processes, not static ones such as we are portraying here —sufficient to say that the ratio of equilibrium biomasses will certainly change with F with a resultant effect on the composition of the ecosystem.

The following points emerge from this discussion that are of immediate relevance to the technique of estimating potential yields from underdeveloped fisheries resources, (and this particularly applies to such fisheries in tropical areas), namely:

(1) the fishing effort recommended should be below that estimated to provide MSY. This is particularly the case for species well below the apex of the food pyramid, for which the so-called Maximum Sustainable Yield (MSY) may not in fact be sustainable;

(2) the shortfall between the recommended fishing effort and that effort level providing MSY, should increase as a function of the natural mortality rate of the species (or in other words, as the biological demands on the population by ecosystem predators increases), if serious changes in the ecosystem itself are to be avoided (1).

The parameter r ($= 2\ F_{MSY}$) governing the steepness of the yield parabola of the logistic, is also an important factor in determining the MSY level; and this is not taken into account in the conventional approximation ($MSY \simeq 0.5 MB_{\infty}$). This may lead to quite erroneous estimates in some cases, although from Fig. 4, it seems to be conservative (even very conservative!) for the large fisheries resources of arcto-boreal regions;

(3) the use of MSY itself as a benchmark for setting fishing effort levels is therefore only recommended for apical predators, and then only if economic considerations are not paramount, and the risks of accidental stock depletion are accepted;

(4) a number of arbitrary criteria have been suggested, that from experience result in a level of fishing effort that more closely corresponds to an economic optimum (e.g. $F_{0\cdot 1}$, $f_{2/3MSY}$), and are of course below $f_{MSY}$. We suggest here an easily calculated criterion, $F_{MBP}$; the fishing mortality rate at which the total biological production (yield plus predation) of the system is maximized under logistic model assumptions. This can be easily calculated from a knowledge of M and the shape parameter $r = 2F_{MSY}$;

(5) to date, to our knowledge, there have been no attempts to compare the results of independent studies using production models for different species; perhaps because in order to do so, some corresponding estimates of the analytical mortality parameters are needed in parallel with the annual figures for catch and effort, to permit standardization of

(1) *A priori*, there are no reasons why the ecosystem perturbations should necessarily be harmful, but in fact because intensive fishing may reduce the complexity of the system itself, and affect trophic relationships, from general ecological theory we may expect a decrease in system stability that may also have repercussions on the main species sought.

separate estimates of MSY and $f_{MSY}$ on a common basis, (i.e. in terms of the corresponding fishing mortality $F_{MSY}$ experienced by the population, as a function of the natural mortality rate M experienced by the stock). The preliminary foundations for such a comparative approach are provided in Table III, Fig. 4, and should be extended as new data becomes available, particularly for tropical areas. As a general recommendation, we suggest that in cases where production models are applied, if at all possible, some parallel information be collected that will enable an index of the current mortality rate to be calculated, in order that such a standardization may subsequently be possible. This comment is particularly relevant to tropical fisheries assessments, where the general lack of analytical parameters for "typical" populations must be regarded as one of the key impediments to estimates of sustainable yield however preliminary.

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