Relationships between Common Biological Reference Points Used as Thresholds and Targets of Fisheries Management Strategies

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Mace, P.M. 1994. Relationships between common biological reference points used as thresholds and targets of fisheries management strategies. Can. J. Fish. Aquat. Sci. 51: 110–122.

Relationships between various biological reference points (BRPs) used to define thresholds and targets of fisheries management strategies were examined for a range of combinations of life history characteristics. Rank orderings of the selected BRPs were strongly influenced by the degree of density dependence in the underlying spawning–recruitment (S–R) relationship. The validity of $F_{0.1}$, F_{max}, $F_{20\%}$ (the fishing mortality at which spawning per recruit is 20% of the maximum), and other reference fishing mortality rates as approximations to F_{msy} or as thresholds of overfishing is highly dependent on life history characteristics, particulary the degree of density dependence in the S–R relationship. It is recommended that $F_{40\%}$ be adopted as a target fishing mortality rate when the S–R relationship is unknown and that threshold levels of biomass be related to the estimated or assumed degree of density dependence in the S–R relationship. Two new methods of calculating threshold biomass levels are suggested as alternatives to the familiar 20% B_0 rule.

Nous avons examiné les relations entre divers points de référence biologique (PRB) servant à définir les seuils et les cibles des stratégies de gestion des pêches pour une gamme diverse de combinaisons de caractéristiques biologiques. Les ordres de classement des PRB choisis étaient fortement influencés par le degré de dépendance par rapport à la densité dans le rapport des géniteurs aux recrues posé au départ. La validité de $F_{0.1}$, F_{max}, $F_{20\%}$ (la mortalité par pêche à laquelle le rapport géniteurs-recrues est de 20 % du maximum) et d'autres taux de mortalité par pêche, servant de référence comme approximations de F_{rms} ou comme seuils de la surpêche, dépend fortement des caractéristiques du cycle biologique, et particulièrement du degré de dépendance par rapport à la densité dans le rapport géniteurs-recrues. Il est recommandé d'adopter comme taux cible de mortalité par pêche $F_{40\%}$ lorsqu'on ne connaît par le rapport géniteurs-recrues, et de mettre en rapport les niveaux seuils de la biomasse avec les degrés estimés ou supposés de dépendance par rapport à la densité dans le rapport géniteurs-recrues. Nous proposons deux nouvelles méthodes pour calculer les niveaux seuils de la biomasse, méthodes qui peuvent remplacer la règle familière de 20 % B_0.

There are two general classes of risk or loss that need to be considered when formulating fisheries management strategies: the risk that yields will fall below the maximum attainable level and the risk that the stock will fall below some minimum size. To some extent, the first represents a risk to the fishery and the second a risk to the stock; however, if the stock "collapses", then it is likely that the fishery will also "collapse". Essentially, the former risk is the risk of not attaining a desirable target; the latter is the risk of falling below an undesirable threshold. The challenge for fisheries scientists and managers is to find a fishing strategy that achieves either both objectives or a compromise between the objectives. The usual approach has been to base fishing strategies on biological reference points (BRPs) such as target or threshold fishing mortality rates (F) and/or target or threshold biomass levels (B). These BRPs are often stated to be "conservative", "risky", or "near-optimal" but there are rarely sufficient data to make a sound judgement, and the same reference point may be categorized differently depending on the stock under consideration and the investigators' perceptions about the resilience of the stock.

The purpose of this paper is to evaluate the ability of selected BRPs to achieve long-term average yields approximating maximum sustainable yield (MSY) while at the same time avoiding overfishing thresholds associated with an unacceptable or undesirable stock condition. In part, this study is an extension of previous work by Deriso (1982, 1987), Beddington and Cooke (1983), Clark (1991), and others who have investigated the relationships between the true (deterministic) MSY and other BRPs. The main extensions here are the inclusion of a wider array of BRPs, a wider range of life history characteristics, and more explicit consideration of the ability of the reference points to achieve fishing targets while simultaneously avoiding overfishing thresholds. Thresholds and targets are expressed in terms of both F and B, and new methods for representing biomass thresholds are proposed.

The BRPs discussed include the constant fishing mortality rate that produces MSY (F_{msy}), the fishing mortality rate that equals the natural mortality rate ($F = M$), two reference fishing mortality rates from yield per recruit (YPR) analysis ($F_{0.1}$ and F_{max}), reference fishing mortality rates from spawning per recruit (SPR) analysis (e.g., $F_{20\%}$ and

110

Can. J. Fish. Aquat. Sci., Vol. 51, 1994

$F_{35\%}$), the threshold fishing mortality rate associated with extinction of the stock (referred to here as F_τ), the equilibrium biomass levels corresponding to the first four of these reference fishing mortalities (B_{msy}, $B_{F=M}$, $B_{0.1}$, and B_{max}), and various percentages of B_{msy}, virgin biomass (B_0), and virgin recruitment (R_0). Although the analysis is based on deterministic models, it can also be used to guide the formulation of control laws in stochastic systems, e.g., the choice of an appropriate threshold in control laws that limit the frequency at which biomass is permitted to fall below the threshold. The analysis may also provide guidance on the selection of reference points in situations where essential information on life history characteristics is lacking.

Methods

The question of which BRPs are best in which situations is complex. To make the problem tractable, the following major simplifications were adopted: economic objectives were not considered explicitly, fishing strategies were formulated as constant F strategies, and results are presented in terms of deterministic equilibria. The target or goal of a fishing strategy is specified to be some constant F that will achieve a long-term average yield approximating MSY while at the same time staying "far away" from the ultimate threshold of F_τ (which has a corresponding equilibrium B of zero). The obvious candidate for this target is F_{msy}; however, F_{msy} cannot be estimated unless the spawning–recruitment (S–R) relationship is known, and for certain S–R relationships, it could be dangerously close to the threshold. The problem is to choose a measurable F that provides the best compromise between approximating F_{msy} and avoiding stock collapse for a range of plausible S–R relationships and other life history characteristics.

The procedure developed to address this problem used standard age-structured population models with some parameters fixed and others varied between runs. Beginning-of-year numbers at age were calculated from

$$(1) \qquad N_{t+1} = N_t e^{-(F+M)}$$

where N = numbers, t = age, M = rate of natural mortality (0.1, 0.2, or 0.3), and F = rate of fishing mortality.

Annual growth was represented by the von Bertalanffy equation:

$$(2) \qquad W_t = W_\infty (1 - e^{-K(t-t_0)})^b$$

with

$$W_\infty = a'L_\infty^{b'}$$

where W = weight, L = length, W_∞ = asymptotic weight, L_∞ = asymptotic length (fixed at 50 cm), K = Brody growth coefficient (0.1, 0.2, or 0.3), t_0 = growth intercept (fixed at 0), and a' and b' = parameters (fixed at $a' = 0.01$, $b' = 3$).

Catch numbers at age, C_t, were calculated from the catch equation

$$(3) \qquad C_t = \frac{F}{F+M}(1-e^{-(F+M)})N_t.$$

Partial recruitment and maturity were both assumed to be knife-edged (0 below a given age and 100% above) with the age of recruitment, t_r, always equal to the age of matu-

rity, t_m (3, 5, or 7). Spawning biomass was represented by the average mature biomass present during the year, calculated by multiplying equations (1) and (2), summing over mature ages, and multiplying the result by $(1 - e^{-(F+M)})/(F+M)$. Similarily, the yield in weight was calculated by multiplying equation (3) by equation (2) and then summing over ages.

For the main series of runs, recruitment was modelled using a Beverton–Holt S–R relationship (Beverton and Holt 1957):

$$(4) \qquad R = \frac{S}{\alpha + \beta S}$$

where R = recruitment in numbers, S = spawning biomass, and α and β = parameters with $1/\alpha$ = slope at the origin and $1/\beta$ = asymptotic recruitment (fixed at 10^8 recruits). Since the recruitment and maturity schedules coincided, the average recruited biomass and spawning biomass were identical, as were the (recruited) biomass per recruit (BPR) and the spawning biomass per recruit (SPR). The latter two quantities were obtained from the equation

$$(5) \qquad \text{BPR} = \text{SPR} = \left(\frac{1 - e^{-(F+M)}}{F+M} \right) \sum_{t=t_r}^{\infty} (N_t \, e^{-(F+M)(t-t_r)} W_t)$$

with

$$N_t = 1 \text{ at } t=t_r \ (=t_m).$$

Virgin recruitment (R_0) and virgin biomass (B_0 or S_0) were defined by the intersection of the S–R curve with the line through the origin having slope equal to the inverse of the spawning biomass per recruit at $F = 0$ ($\text{SPR}_{F=0}$). Thus,

$$(6) \qquad B_0 = S_0 = \text{SPR}_{F=0} \cdot R_0.$$

The extinction parameter, τ, was defined as the ratio between the slope (or equivalently the survival ratio, R/S) corresponding to $\text{SPR}_{F=0}$ (i.e., $1/\text{SPR}_{F=0}$) and the slope at the origin (i.e., $1/\alpha$). Therefore, τ is equivalent to

$$(7) \qquad \frac{\text{SPR}_\tau}{\text{SPR}_{F=0}}$$

where SPR_τ = threshold level of SPR (corresponding to the slope at the origin) and $\text{SPR}_{F=0}$ = maximum possible SPR (corresponding to zero fishing). The product 100τ is also referred to as the "threshold %SPR" (e.g., Mace and Sissenwine 1993). F_τ is the corresponding fishing mortality rate. It follows that the parameter α in equation (4) is related to τ by

$$(8) \qquad \alpha = \text{SPR}_{F=0} \cdot \tau.$$

Solving equation (4) at (B_0, R_0) using substitutions based on equations (6) and (8) results in two alternative expressions for R_0:

$$(9) \qquad R_0 = \frac{\text{SPR}_{F=0} - \alpha}{\beta \cdot \text{SPR}_{F=0}}$$

$$\text{or } R_0 = \frac{1}{\beta}(1-\tau).$$

$F_{0.1}$ and F_{max} were derived from YPR analysis (equation (A1) in Appendix A) by the standard method. $F_{20\%}$ and $F_{35\%}$ were defined as the fishing mortality rates corresponding to 20 and 35%, respectively, of $\text{SPR}_{F=0}$ from SPR analysis. The equilibrium recruitment at these and any other reference levels of F is given by
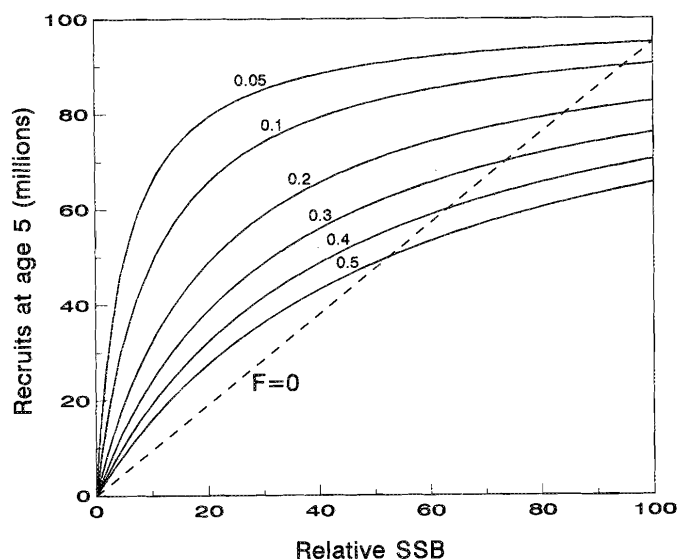
Can. J. Fish. Aquat. Sci., Vol. 51, 1994

111

FIG. 1. Effects of τ on the shape of the Beverton–Holt S–R relationship (numbers above the curves are the values of τ). The broken line is the line with slope $1/\mathrm{SPR}_{F=0}$; the intersection of this line with the S–R curves defines the location of (B_0, R_0), or equivalently (S_0, R_0), and therefore represents the upper limit of the range of the S–R curves.

$$(10) \quad R_{F_{\text{ref}}} = \frac{\mathrm{SPR}_{F_{\text{ref}}} - \alpha}{\beta \cdot \mathrm{SPR}_{F_{\text{ref}}}}$$

$$\text{or } R_{F_{\text{ref}}} = \frac{1}{\beta}\left(1 - \tau \cdot \frac{\mathrm{SPR}_{F=0}}{\mathrm{SPR}_{F_{\text{ref}}}}\right).$$

Corresponding levels of equilibrium yield and equilibrium biomass are given by the products

$$(11) \quad Y^*_{F_{\text{ref}}} = \mathrm{YPR}_{F_{\text{ref}}} \cdot R_{F_{\text{ref}}}$$

and

$$(12) \quad B^*_{F_{\text{ref}}} = \mathrm{BPR}_{F_{\text{ref}}} \cdot R_{F_{\text{ref}}}.$$

F_{msy} is obtained as the value of $F = F'$ that maximizes the expression

$$(13) \quad X = F' \cdot (\mathrm{BPR}_{F'} - \alpha).$$

The corresponding MSY is

$$(14) \quad \mathrm{MSY} = \frac{X}{\beta}.$$

Finally, the extinction threshold, F_τ, is obtained by finding the value of $F = F''$ that satisfies the equation

$$(15) \quad \mathrm{SPR}_{F''} = \alpha.$$

In another series of runs, the Ricker S–R model (Ricker 1954) was used in place of the Beverton–Holt model. The Ricker S–R relationship is given by

$$(16) \quad R = aSe^{-bS}$$

where a and b = parameters with a = slope at the origin and $b = (ae^{-1}/R_{\text{max}})$, where R_{max} is the maximum recruitment (fixed at 10^8 recruits). For a given level of τ defining the slope at the origin, the extinction threshold fishing mortality rate (F_τ) is the same for both S–R models, but F_{msy} will differ. For the Ricker model, F_{msy} is the fishing mortality rate, F', that maximizes

$$(17) \quad X = F' \cdot \log_e(a \cdot \mathrm{SPR}_{F'}).$$

Use of the Ricker model also required modification of equations (8), (9), and (10).

Based on previous studies, it was judged that the population parameters with the highest sensitivity were likely to be M, K, and τ. In the first series of runs, reference levels of F and B were calculated for all combinations of $M = 0.1$, 0.2, or 0.3; $K = 0.1$, 0.2, or 0.3; and $\tau = 0.05$–0.5 in increments of 0.05, with all other parameters held constant. In the second series, the effects of changing the ages of recruitment and maturity were examined for the case $M = K = 0.2$ and $\tau = 0.05$–0.5. For the third and final series, the Ricker S–R model was used in place of the Beverton–Holt model for the cases $M = K = 0.1$, 0.2, or 0.3 and $\tau = 0.05$–0.5. All equilibrium biomass levels were expressed in terms of $\%B_0$ (here equivalent to $\%S_0$).

The range of values selected for τ was based on the studies of Mace (1991) and Mace and Sissenwine (1993) where the median through the origin of observed S–R data was used as an estimate of the slope at the origin (i.e., the limit of the survival ratio as S approaches 0) and therefore the extinction thresholds denoted by SPR_τ and F_τ. The extremes of τ used here are close to the extremes estimated in these two studies. The upper limit of $\tau = 0.5$ implies extremely low compensation (survival at low stock sizes only about twice that at the virgin size), while $\tau = 0.05$ implies high compensation (survival at low biomass about 20 times the virgin rate). A default threshold of $\tau = 0.2$ (survival at least five times the virgin rate) is commonly assumed (e.g., in overfishing definitions in fisheries management plans in the United States).

Results

Main Runs with Beverton–Holt S–R Model

When spawning stock biomass (SSB) was expressed in relative terms (e.g., as $\%B_0$ or $\%S_0$), the shape of the Beverton–Holt relationship was independent of both M and K, i.e., M and K only affected the scale on the SSB axis, not the absolute amount of recruitment. In contrast, the shape of the relationship was strongly influenced by τ (Fig. 1). For $\tau = 0.5$, the relationship is almost linear through the origin over its entire range, while for $\tau = 0.05$, recruitment is almost constant down to a level of about 20% B_0.

F_{msy} and F_τ both decrease with increasing τ and increase with K and M (Fig. 2). Both reference fishing mortalities have the highest sensitivity to τ, next to M, and last to K. For low values of τ (about 0.05–0.1), the extinction threshold fishing mortality rate, F_τ, was usually high, sometimes exceeding $F = 3$. F_{msy} was usually well below F_τ, ranging from 16.4% F_τ to about 43% F_τ over all parameter combinations. $F_{0.1}$, F_{max}, $F_{20\%}$, and $F_{35\%}$ are not influenced by τ, but all increase with both M and K. For each M–K combination, $F_{0.1}$, $F_{35\%}$, and $F = M$ were of similar magnitude, with $F_{35\%}$ usually slightly higher than $F_{0.1}$, and $F_{0.1}$ slightly lower than $F = M$ for $K = 0.1$, almost identical for $K = 0.2$, and slightly higher for $K = 0.3$. F_{max} was only defined for four of the nine M–K combinations and was usually near the $F_{20\%}$ level.

Points of intersection with F_τ indicate parameter combinations where reference levels of F cease to be sustainable (in the deterministic sense). For F_{max} to be sustainable,
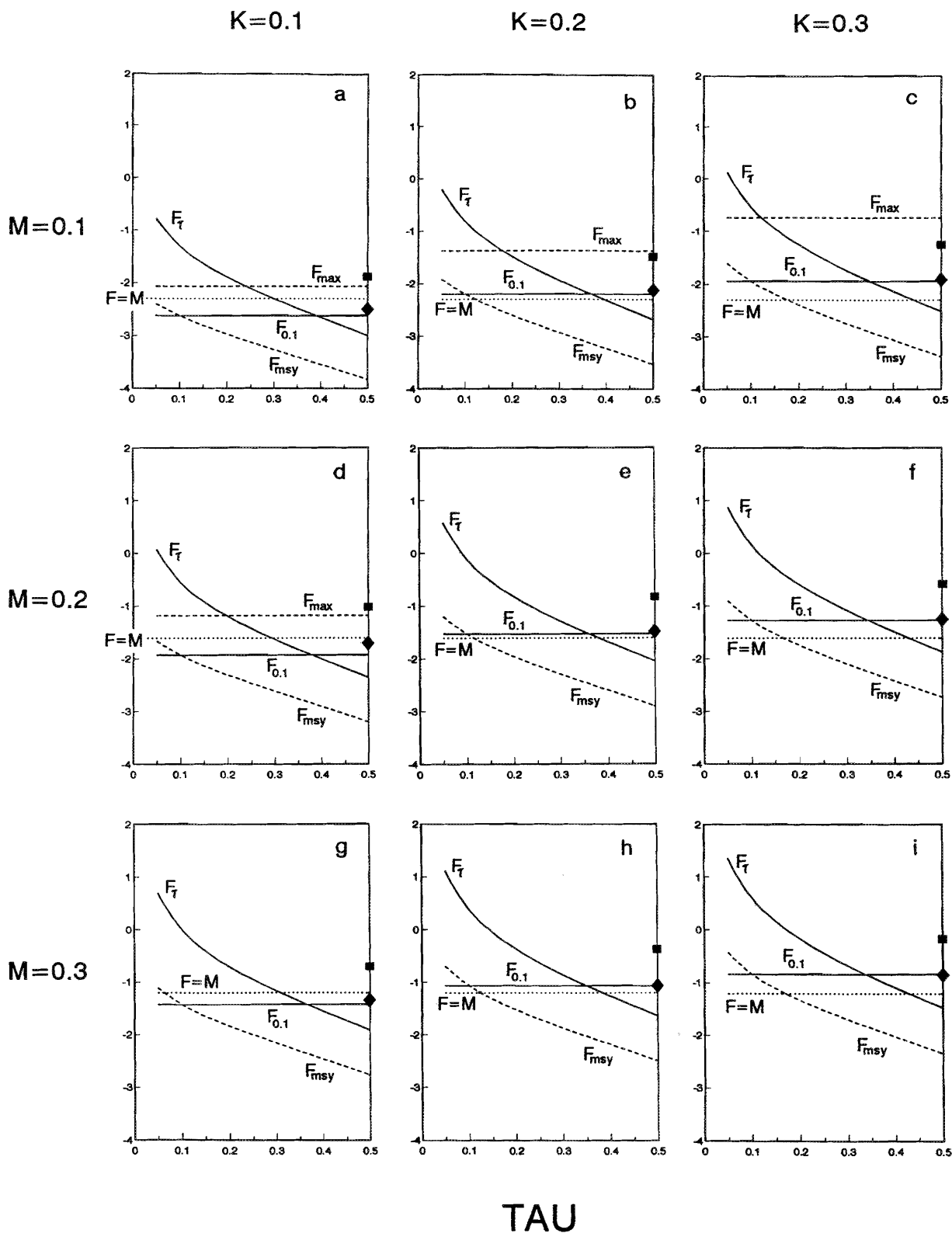
112

FIG. 2. Effects of various combinations of M, K, and τ on estimates of reference levels of fishing mortality (F) for the Beverton–Holt model: F_τ (solid curve), F_{msy} (broken curve), $F=M$ (dotted line), $F_{0.1}$ (solid straight line), F_{max} (broken straight line), and $F_{20\%}$ and $F_{35\%}$ (represented respectively by squares and diamonds on the right-hand side of the graphs). Fishing mortality was plotted on a log scale to make the figures readable.
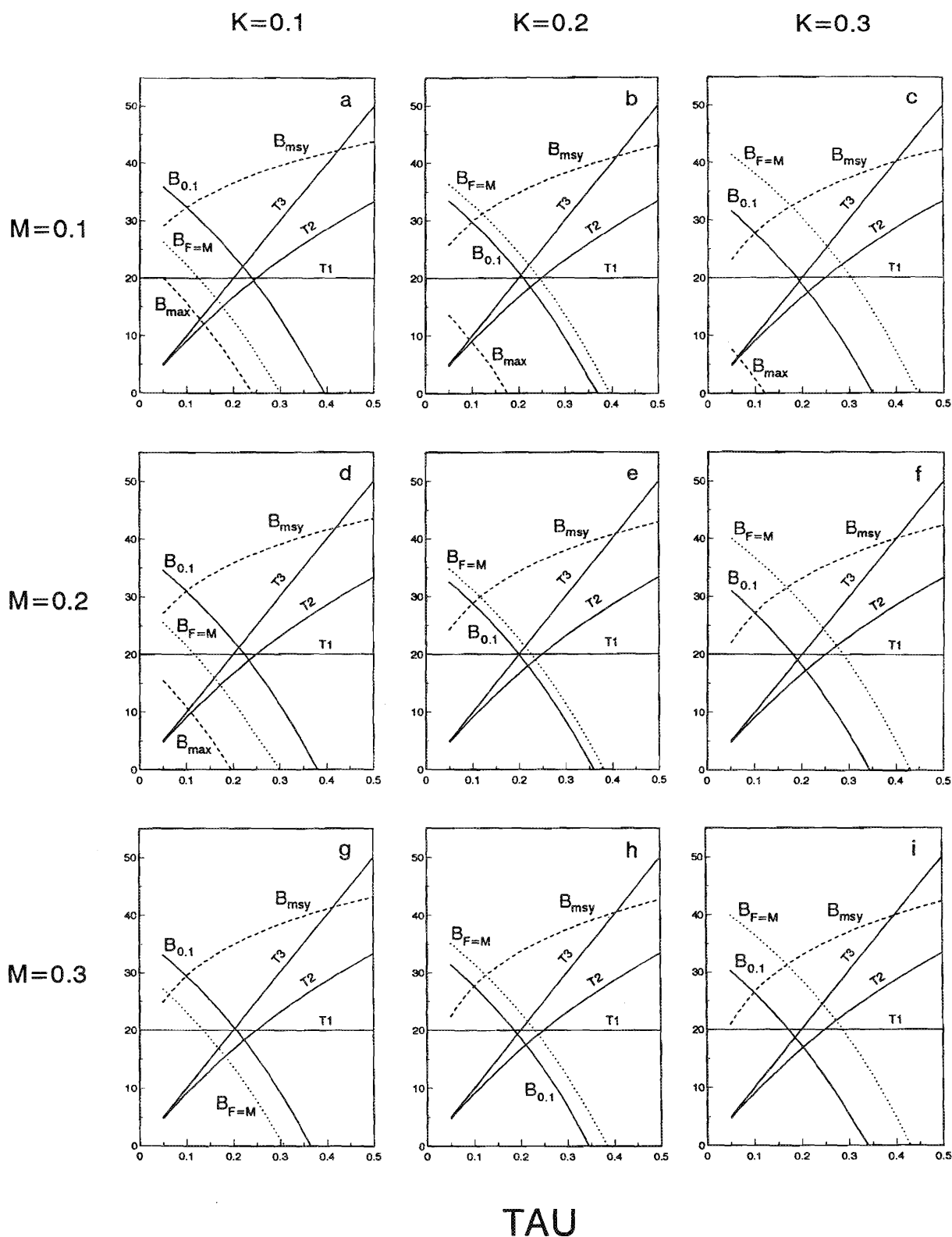
Can. J. Fish. Aquat. Sci., Vol. 51, 1994

113

FIG. 3. Effects of various combinations of M, K, and τ on estimates of equilibrium levels of biomass (B) expressed as $\%B_0$ (or $\%S_0$) for the Beverton–Holt S–R model. Estimates of B_{msy} (heavy broken line), $B_{F=M}$ (dotted line), $B_{0.1}$ (light solid line), and B_{max} (light broken line) are the equilibrium biomass levels attained with the corresponding reference fishing mortality rates in Fig. 2. T1 represents the common threshold level of 20% B_0; T2 is the $\%B_0$ attained at 50% R_{max}; T3 is the line given by $\%B_0 = 100\tau$.

114

Can. J. Fish. Aquat. Sci., Vol. 51, 1994

τ must be less than 0.15–0.25 depending on the parameter combination considered (Fig. 2). $F_{0.1}$ is sustainable for all parameter combinations with τ less than about 0.4. $F = M$ is sustainable for values of τ up to about 0.3, 0.38, and 0.43 for $K = 0.1$, 0.2, and 0.3, respectively.

F_{max} exceeded F_{msy} for all parameter combinations, as is always the case for the Beverton–Holt S–R relationship. $F_{0.1}$ was identical to F_{msy} at $\tau = 0.1$, less than F_{msy} for $\tau < 0.1$, and greater than F_{msy} for $\tau > 0.1$. This result held over all parameter combinations and is true in general whenever recruitment and maturity schedules coincide and the S–R relationship is given by the Beverton–Holt model (see Appendix A). $F = M$ was greater than F_{msy} for τ exceeding about 0.05–0.16, depending on K.

B_{msy}, the equilibrium biomass corresponding to F_{msy}, increases monotonically with τ when expressed as a percentage of B_0 (Fig. 3), although it is dome shaped when expressed in absolute terms because B_0 itself decreases with τ. B_{msy} was never less than the commonly used threshold of 20% B_0 (e.g., Beddington and Cooke 1983), but it approached this level (T1 in Fig. 3) for certain parameter combinations (e.g., $M = K = 0.3$ and $\tau = 0.05$ where B_{msy} was 20.9% B_0). It is interesting to note that the magnitude of $B_{0.1}/B_0$ was influenced relatively little by M or K, always intersecting 20% B_0 near $\tau = 0.20$ (range 0.18–0.24). In contrast, the point where $B_{F=M}$ fell below 20% B_0 ranged between about $\tau = 0.12$–0.30, depending on the M–K combination. B_{max} was almost always less than 20% B_0.

Effects of Age of Recruitment

A (simultaneous) change in the age of recruitment (t_r) and the age of maturity (t_m) alters the percentage of growth achieved at the age of recruitment (Table 1). Increasing t_r $(=t_m)$ resulted in increases in $F_{0.1}$ relative to $F = M$, increases in the range of τ values over which $F = M$ was sustainable, increases in the level of τ at which $F_{msy} = M$, decreases in the equilibrium level of B_{msy} as a fraction of B_0, and decreases in the range of τ values over which $B_{F=M}$ fell below 20% B_0 (Fig. 4). However, over the 4-yr range of ages tested, none of the differences were pronounced.

Extension to Ricker

F_{msy} is the only reference F level that differs between the Beverton–Holt and Ricker models. For the parameter combinations considered in Fig. 2, F_{msy} estimates based on the Ricker S–R function were invariably higher than those derived from the Beverton–Holt S–R function, being at least twice as high for $\tau = 0.05$ and converging to a difference of at least 10% at $\tau = 0.5$. The reason for the difference is that for the same maximum R and slope at the origin (relative to the $F = 0$ replacement line), the excess of recruitment over the replacement level required in the absence of fishing is usually greater for the Ricker function, except at the extremes of spawning biomass (Fig. 1 and 5). The difference is particularly pronounced at low values of τ. In fact, for parameter combinations where F_{max} was defined, Ricker S–R estimates of F_{msy} usually exceeded F_{max} at $\tau = 0.05$, although they were always less than F_{max} for $\tau = 0.1$ or more (Fig. 6). Similarly, the level of τ at which F_{msy} intersected $F_{0.1}$ was higher for the Ricker model (occurring within a remarkably small range of τ of about 0.17–0.19 over the full set of parameter combinations), compared with the Beverton–Holt model (consistently, $\tau = 0.1$).

TABLE 1. Percentage of growth in length ($\%L_t/L_\infty$) and weight ($\%W_t/W_\infty$) achieved at the age of recruitment for the combinations of the Brody growth coefficient (K in equation (2)) and age of recruitment (t_r in equation (5)) considered in Fig. 2–4 and 6.

	$\%L_t/L_\infty$	$\%W_t/W_\infty$
$K = 0.1$		
$t_r = 5$	39.4	6.1
$K = 0.2$		
$t_r = 3$	45.1	9.2
$t_r = 5$	63.2	25.3
$t_r = 7$	75.3	42.8
$K = 0.3$		
$t_r = 5$	77.7	46.9

In comparison with the Beverton–Holt results (Fig. 3), the ratio B_{msy}/B_0 from the Ricker model was less sensitive to τ, but all other biomass ratios were considerably more sensitive to τ, ranging from as much as 70% B_0 at $\tau = 0.05$ to zero at $\tau = 0.25$–0.45 (Fig. 6).

Threshold Levels of Biomass

One problem with using a fixed $\%B_0$ (e.g., 20% B_0) as a threshold is that as compensation decreases (τ increases) and/or the age of recruitment is reduced, F_τ and F_{msy} both decline dramatically and any fixed F has a decreasing chance of being sustainable (Fig. 2, 4, and 6). It seems more logical to use a biomass threshold that increases as resilience decreases. One approach that takes account of the degree of compensation (i.e., the slope of the S–R relationship near the origin) is to express the threshold as a fixed percentage of the maximum recruitment (R_{max}). The S–R relationship can then be used to translate this into the corresponding $\%B_0$ (see Apprendix B). Threshold values of $\%B_0$ based on an arbitrary theshold recruitment level of 50% R_{max} (labelled T2) have been superimposed on Fig. 3, 4, and 6. Thresholds based on the Ricker S–R model (Fig. 6) differed only slightly from those based on the Beverton–Holt model (Fig. 3 and 4). For both models, T2 decreases in the same direction as τ but is independent of M and K. The relationship to B_{msy} is similar for all M–K parameter combinations: it approximates 50% B_{msy} for τ in the range of about 0.2–0.25 for the Beverton–Holt model and τ in the range of about 0.3–0.4 for the Ricker model and is less than 50% B_{msy} for smaller values of τ and greater than 50% B_{msy} for larger values. $B_{F=M}$ is generally below the suggested threshold for τ greater than about 0.3 and above the threshold for $\tau < 0.2$.

A simpler alternative solution to the problem of specifying a threshold level of $\%B_0$ that is less dependent on the exact form of the underlying S–R relationship is to set it at the same value as τ expressed as a percentage (i.e., $\%B_0 = 100\tau$; T3 in Fig. 3, 4, and 6). This is equivalent to equating threshold levels of $\%B_0$ with threshold levels of $\%SPR$ (equation(7)), although it is not strictly valid to use the two interchangeably (Appendix B). Equating the two results in a threshold biomass that is similar to that associated with 50% R_{max} (T2) at low τ, but much higher at high τ (Appendix B; Fig. 3, 4, and 6). However, T3 may be a reasonable threshold in cases where the form of the S–R
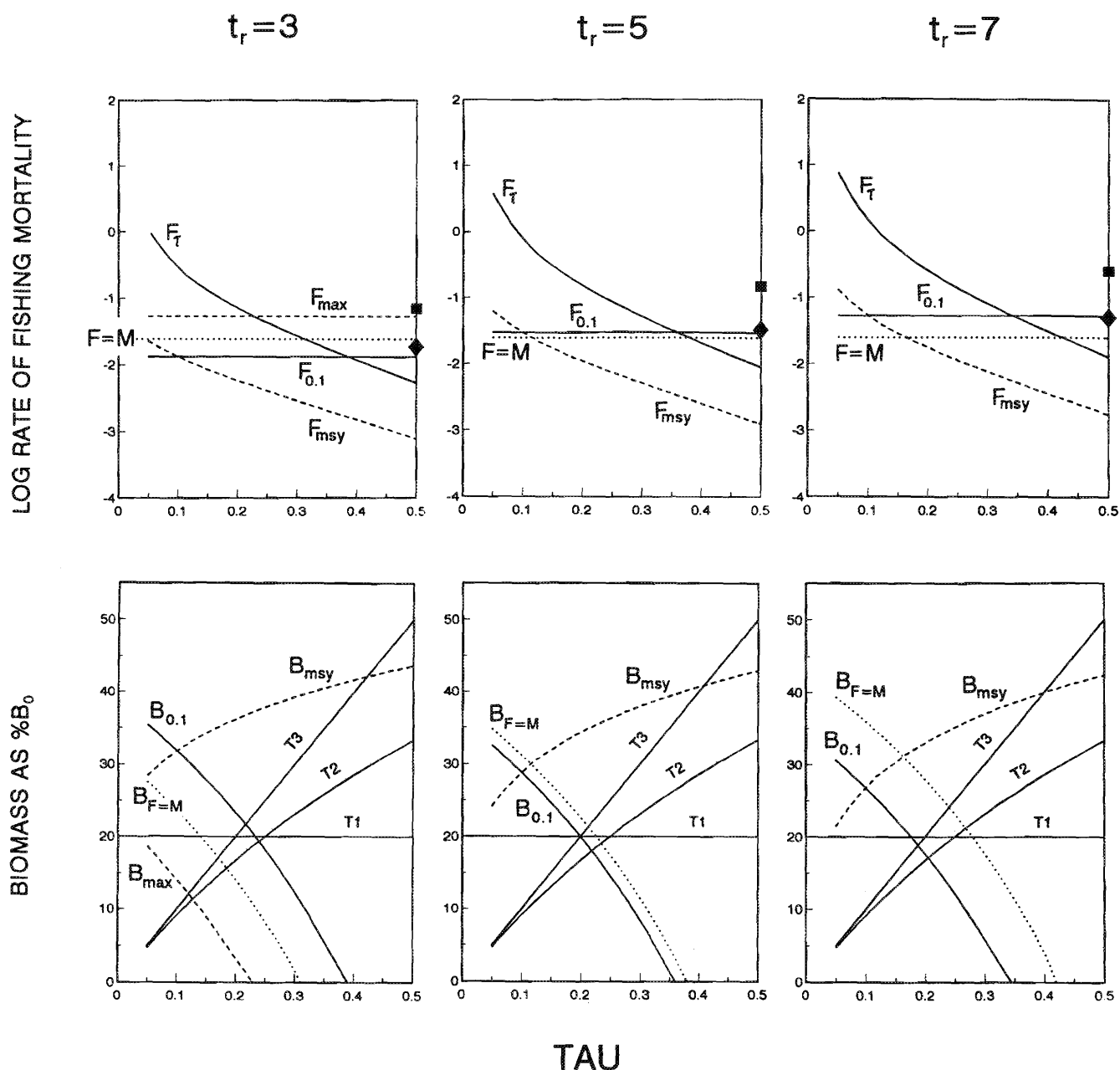
FIG. 4. Effects of the age of recruitment ($t_r = 3$, 5, or 7) on estimates of reference levels of fishing mortality (F) and equilibrium levels of biomass (B) expressed as %B_0 for the Beverton–Holt model. See legends to Fig. 2 and 3 for details.

relationship is unknown. Like T2, it has the property of increasing with τ and represents a situation where recruitment is likely to have fallen appreciably relative to virgin or maximum levels. T2 is equivalent to 20% B_0 at $\tau = 0.25$ for the Beverton– Holt relationship and τ about 0.3 for the Ricker relationship; T3 is equivalent to 20% B_0 at $\tau = 0.2$.

Discussion

Which Values of τ Seem Credible?

Conclusions about whether particular BRPs are "conservative" or "risky" are highly dependent on the magnitude of τ (and, to a lesser extent, on other life history characteristics). To date, there have been few studies that can be

used as a basis for selecting or rejecting particular values or ranges of τ. Even when S–R data are available, estimation of τ is hindered by (i) measurement errors, (ii) recruitment variability, (iii) lack of adequate contrast in S, and (iv) uncertainty about the form of the S–R relationship as a result of (i), (ii), and (iii). Shepherd (1982) proposed using the 90th percentile survival ratio of the S–R data points to estimate the slope of the S–R function at the origin; however, Sissenwine and Shepherd (1987) pointed out that S–R data points in the upper 10th percentile may just reflect anomalously favorable environmental conditions, not the ability to the population to sustain fishing under average environmental conditions. The latter authors proposed using the average or median observed survival ratio (R/S) as a safer estimate of the maximum survival ratio. In fact, the average or median

116

Can. J. Fish. Aquat. Sci., Vol. 51, 1994

survival ratio is likely to be a biased estimator of the maximum survival ratio unless the S–R observations are restricted to low stock sizes where the S–R relationship can be approximated by a straight line through the origin. Otherwise, it will be conservatively biased for S–R observations that exhibit concavity (compensation) and liberally biased for S–R observations that are convex (depensation).

Mace (1991) and Mace and Sissenwine (1993) calculated median survival ratios for 83 sets of S–R observations taken from exploited fish stocks. Of these, 56% exhibited no significant departure from linearity through the origin, 44% exhibited significant concavity, and none exhibited significant convexity. However, the average value of τ (the inverse of the median survival ratio divided by $SPR_{F=0}$, i.e., their threshold %SPR expressed as a proportion) was almost identical for cases with and without concavity, so the two groups were not treated separately. The overall average value of τ was 0.19, and the 80th percentile of the results was approximately 0.3. Estimates for highly resilient species such as Atlantic cod (*Gadus morhua*) were frequently in the range τ = 0.05–0.15. Mace and Sissenwine (1993) recommended the observed average (rounded to 0.2) as a default overfishing theshold for stocks believed to have at least average resilience, but with insufficient S–R observations to estimate τ explicitly, and the 80th percentile result (τ = 0.3) for little-known stocks.

Clark (1991) rejected τ = 0.5 as too high for any fish stock (the parameter *A*, adopted by Clark from Kimura's (1988) reparameterization of the Beverton–Holt S–R relationship, is related to τ by the expression $\tau = 1 - A$) because the stock would be driven to extinction by a fishing mortality rate less than *M*. For the model and parameter combinations considered here, the highest τ at which *F* = *M* was sustainable ranged from about 0.3 to 0.43 (Fig. 2, 4, and 6). The validity of using the criterion of sustainability of *F* = *M* to set an upper bound on τ is debatable, but most fish stocks that have sustained fisheries for long periods have also sustained fishing mortality rates at least equal to *M*.

Choice of a lower bound is even more difficult. Clark (1991) used τ = 0.06 as the lower bound, rejecting the alternative of τ = 0.03 as too low for the majority of stocks because there would be "hardly any ill effect" of fishing at *F* = 1.0. However, 10-yr average fishing mortality rates exceeded *F* = 1.0 in 11% of the cases examined by Mace (1991) and Mace and Sissenwine (1993). The lower limit of τ = 0.05 used here implies a threshold fishing mortality rate exceeding *F* = 1 for all but two of the 11 unique $M–K–t_r$ combinations considered (Fig. 2 and 4); the minimum was F_τ = 0.46 for the combination *M* = *K*=0.1, t_r = 5. Empirical estimates of τ were less than 0.05 in 9% of cases listed in Mace (1991). Thus, τ = 0.05 may not represent a lower bound for some stocks. However, it may be a reasonable lower bound to use in sensitivity analyses for cases lacking observations near the origin, since the assumption that the S–R relationship continues to be concave near the origin may not be valid. In multispecies systems where one species has been observed to replace another when the latter has been reduced to low levels, it is possible that the S–R relationship became depensatory (convex) near the origin.

In conclusion, I believe that there is no basis for rejecting values of τ within (or maybe even slightly beyond) the range 0.05 to about 0.35, a priori. Because the midpoint of this
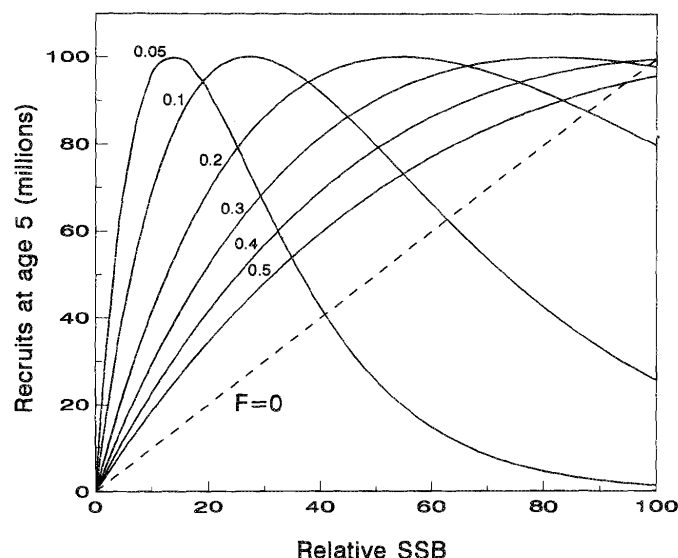

FIG. 5. Effects of τ on the shape of the Ricker S–R relationship (numbers above the curves are the values of τ). See legend to Fig. 1 for an explanation of the broken line.

range (τ = 0.2) is similar to the average estimate of τ obtained by Mace (1991) and Mace and Sissenwine (1993), it will be used as the main reference for the remainder of the discussion.

Which BRPs Are "Best"?

The range of F_{msy} taken over all model–parameter combinations with τ in the range 0.05–0.35 was 0.029–1.46 and was always less than 47% F_τ (Fig. 2, 4, and 6). Thus, F_{msy}, the strategy that achieves the highest long-term average yield, can probably be considered "safe" for the range of parameter combinations considered here in that it falls well below F_τ. The corresponding equilibrium biomass level, B_{msy}, never crossed the commonly used threshold level of biomass of 20% B_0 (T1 in Figs. 3, 4, and 6); however, it was very close in some cases (the closest approach being 20.9%), suggesting that it should not automatically be assumed that F_{msy} is "safe" if there is reason to believe that stock productivity will be negatively impacted at levels below 20% (or more) B_0. Adoption of threshold levels higher than 20% B_0 (e.g., Quinn et al. 1990) may lead to a convergence between target and threshold levels of biomass if an F_{msy} fishing strategy is used. This appears to be less of a potential problem when recruitment dynamics are governed by the Ricker model rather than the Beverton–Holt model, because B_{msy}/B_0 was much higher and less variable for the Ricker model (Fig. 3 and 6).

The fact that F_{msy} and F_τ increase dramatically as τ decreases suggests that biomass targets and thresholds should also be dependent on the degree of compensation exhibited or assumed. Two possiblities for a threshold level of %B_0 (or %S_0) suggested here are to use the %B_0 corresponding to 50% R_{max} based on a particular S–R relationship (T2 in Fig. 3, 4, and 6) or to equate the threshold percentage with τ (T3 in Fig. 3, 4, and 6). These two thresholds are similar at low τ but diverge progressively as τ increases. There is little basis for recommending one over the other, but the first could probably be used when there are sufficient data to fit
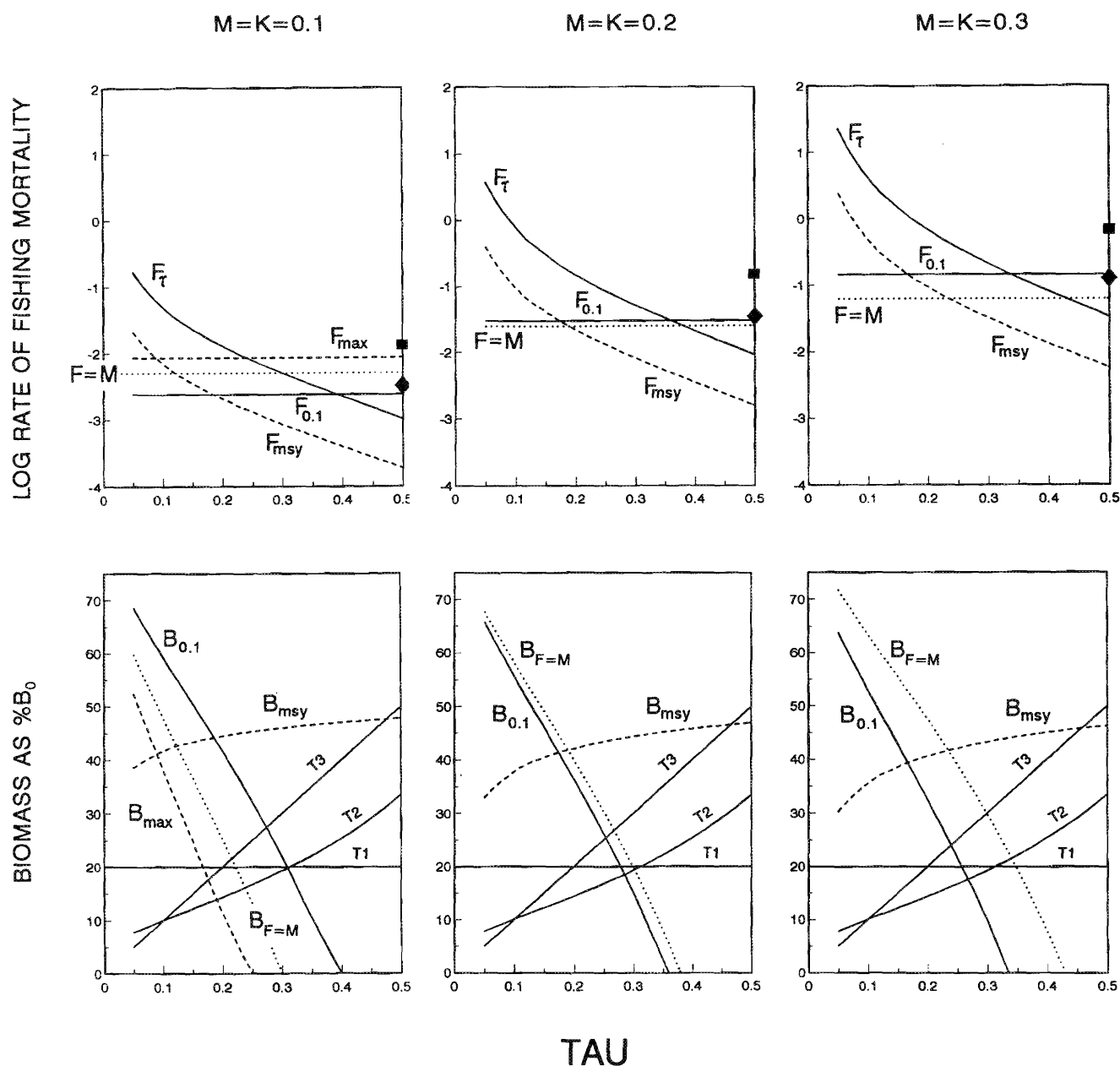
Can. J. Fish. Aquat. Sci., Vol. 51, 1994

117

$M=K=0.1$ $M=K=0.2$ $M=K=0.3$

TAU

FIG. 6. Effects of various combinations of M, K, and τ on estimates of reference levels of fishing mortality (F) and equilibrium levels of biomass (B) expressed as $\%B_0$ for the Ricker S–R model. See legends to Fig. 2 and 3 for details.

an S–R relationship and the second when it is necessary to make an assumption about the likely level of compensation exhibited by a stock. Both proposed thresholds represent situations where recruitment is likely to have fallen appreciably relative to virgin or maximum levels. T2 is the point corresponding to 50% of the maximum recruitment, and T3 represents a point where, for τ in the range 0.05–0.35, recruitment has fallen to between 51 and 61% R_0 for a Beverton–Holt relationship and about 35–69% R_{max} for a Ricker relationship (Appendix B).

If F_{msy} is not known (i.e., if there are insufficient S–R data to estimate it), what is the best alternative to use with respect to achieving a compromise between approximating F_{msy} and avoiding F_τ? It has often been stated that $F = M$ is a conservative reference fishing mortality. However, for

most parameter combinations, $F = M$ exceeded F_{msy}. $F = M$ was a conservative estimate of F_{msy} only when low values of τ were combined with high values of K. For $\tau = 0.2$ and $t_r = 5$, $F = M$ ranged from 35 to 66% F_τ. Therefore, it is probably reasonable to assume that $F = M$ is generally a conservative estimate of F_τ, but not necessarily a conservative estimate of F_{msy}. For some parameter combinations (low M and K, high τ), $F = M$ may be less conservative than is commonly assumed.

The advantages of using $F_{0.1}$ rather than $F = M$ are evident from Fig. 2, 4, and 6. $F_{0.1}$ incorporates the effects of the rate of growth and age of recruitment as well as natural mortality, so that it falls below M for slow-growing stocks or stocks with low age of recruitment and exceeds M for fast-growing stocks or stocks with high age of recruitment.

Similarly, reference points from SPR are likely to be superior to those from YPR because they incorporate maturity schedules in addition to the processes captured by YPR. Thus, BRPs derived from SPR take account of the effects of disparate recruitment and maturity schedules (age of 50% recruitment substantially above or below the age of 50% maturity) whereas those derived from YPR do not. Clark (1991) showed that $F_{35\%}$ and $F_{0.1}$ were generally quite close when recruitment and maturity schedules coincided but that the two diverged when there were appreciable differences between recruitment and maturity schedules. When the age of 50% maturity is less than the age of 50% recruitment, $F_{35\%}$ will generally exceed $F_{0.1}$; when the opposite is true, $F_{35\%}$ will be less than $F_{0.1}$. Therefore, strategies based on $F_{35\%}$ would result in stocks that mature before they recruit being fished much harder than stocks that recruit before they mature, whereas strategies based on $F_{0.1}$ would not distinguish between the two situations.

Given that (i) $F_{35\%}$ generally exceeded $F_{0.1}$ for the parameter combinations considered here (in which the ages of recruitment and maturity were always equal), (ii) $F_{0.1}$ averaged about $F_{38\%}$ for the empirical estimates obtained by Mace (1991) and Mace and Sissenwine (1993), and (iii) $F_{35\%}$ and $F_{0.1}$ both invariably exceeded F_{msy} at $\tau = 0.2$ for all the model–parameter combinations used here, I suggest a default fishing target of at least $F_{40\%}$ as a robust approximation to F_{msy} that will not exceed F_τ unless τ exceeds 0.4. This is similar to the default of $F_{35\%}$ suggested by Clark (1991) who showed that fishing at $F_{35\%}$ would achieve at least 75% of MSY for a wide range of deterministic S–R relationships. It is also identical to the recommendation he later made after extending his deterministic analysis by adding recruitment variability (Clark 1993). For the reasons given here and in Clark (1993), I suggest that $F_{40\%}$ represents a modest improvement over $F_{35\%}$.

F_{max} always exceeds F_{msy} for a Beverton–Holt S–R function, but F_{msy} may exceed F_{max} at low τ for the Ricker function (Fig. 6). The fact that F_{max} is generally larger than F_{msy} except when the S–R relationship is dome shaped and has strong density dependence is already well known (e.g., Deriso 1982). For the model–parameter combinations considered here, F_{max} was always above or only slightly below F_τ at $\tau = 0.2$ (Fig. 2, 4, and 6). This suggests that while F_{max} may often be too high as a target, it may sometimes be a useful threshold. Given that (i) BRPs based on SPR should generally be considered superior to those based on YPR, (ii) F_{max} is often not defined (whenever the instantaneous rate of growth exceeds the instantaneous rate of natural mortality), and (iii) F_{max} averaged about 21% SPR in the studies by Mace (1991) and Mace and Sissenwine (1993), it may be useful to consider a fishing mortality rate of about $F_{20\%}$ as a threshold for stocks that are reasonably certain to have at least "average" resilience. However, $F_{20\%}$ corresponds to the extinction threshold for $\tau = 0.2$; thus, it will not be sustainable over the upper half of the range $\tau = 0.05$–0.35. In the absence of adequate information on stock dynamics, a more prudent approach is to use a default overfishing threshold of $F_{30\%}$, as suggested by Mace and Sissenwine (1993). A threshold of $F_{30\%}$ has also been recommended by Thompson (1993) based on an examination of the dynamics of stocks where the S–R relationship is represented by a depensatory form of the Beverton–Holt function.

Dependence of Results on Input Assumptions

This study shows that the validity of various reference levels of F as approximations to F_{msy}, or as thresholds of overfishing, is highly dependent on life history characteristics. The sensitivity of F_τ and F_{msy} to the life history parameters considered here increased through the sequence K, M, τ. Ironically, the difficulty of estimating these three parameters increases in the same sequence. Choice of τ and the validity of F_τ as an estimate of the extinction threshold is particularly problematic. In reality, F_τ is almost always derived by extrapolating beyond the observations. The assumption that the survival ratio is maximized as S approaches zero ignores the observation that stocks reduced to low levels frequently "collapse", in the sense that they remain at low biomass for long periods of time. Stocks may collapse long before F reaches F_τ. Nevertheless, F_τ may be useful as a boundary condition, indicating the ultimate consequences of assuming or estimating particular levels of compensation.

This study also shows that the results are sensitive to the form of the S–R relationship. For S–R functions with maximum slope occurring at the origin, F_τ will always be given by an expression similar to equation (15); i.e., F_τ is the value of F that satisfies the expression SPR = the inverse of the slope at the origin. Thus, for a given set of life history parameters, F_τ values for Beverton–Holt and Ricker S–R functions are identical. For S–R functions that have maximum slope at $S > 0$ (e.g., those that are convex near the origin), F_τ will be associated with a nonzero equilibrium biomass. Even when F_τ values are similar, F_{msy} values may diverge considerably; F_{msy} estimates based on the Ricker model (Fig. 6) were as much as 2.3 times those based on the Beverton–Holt model (Fig. 2). For the same maximum R and slope at the origin relative to the no-fishing replacement line, the Ricker model represents a much more productive fish stock in terms of the excess of recruitment over the replacement level required in the absence of fishing (Figs. 1 and 5). Not only was F_{msy} consistently higher, so too were the corresponding levels of MSY, B_{msy} (except at $\tau = 0.05$ and 0.1), and B_{msy} as a percentage of B_0.

Extensions to Stochastic Systems

Deterministic models provide a simplified approach that represents a useful first step towards identifying potential pitfalls of proposed control laws for stochastic systems. In addition, depending on the skewness of the distributions used in the stochastic system, the deterministic results may often be close to the average or median of the stochastic results.

Part of the impetus for this study was the increasingly common usage of a threshold biomass level of 20% B_0. For the Beverton–Holt model, low τ and high K and age of recruitment result in B_{msy} approaching the 20% B_0 threshold (T1 in Fig. 3 and 4). Thus, a control law that restricted $P(B < 20\% \ B_0)$ to some upper limit would have a greater tendency to reject F_{msy} the more productive and robust the system. Worse yet, this control law would give increasingly conservative estimates of the optimum F as the age of recruitment was increased within a stock. It makes more sense to treat stocks differentially based on the relative degrees of resilience and/or productivity they exhibit. Either of the two recommendations suggested in this paper (the two thresh-

olds, T2 and T3, superimposed on Fig. 3, 4, and 6) could be used as the basis of control laws for stochastic systems. For example, the optimum F might be specified as that F that provides the closest approximation to F_{msy} subject to the constraint that $P(B < 100 \cdot \tau \cdot B_0) < 5\%$ (or less, since thresholds based on the slope at the origin or 50% R_{max} are unlikely to be conservative and should probably be treated as nearly as possible as absolute boundaries not to be crossed). The frequency at which B is likely to fall below such thresholds can be assessed qualitatively from diagrams like Fig. 3, 4, and 6. It may even be possible to use deterministic results to rank parameter combinations in terms of the relative probabilities of violating the thresholds, without resorting to stochastic simulations.

Conclusions and Recommendations

The merits of one BRP over another depend on a number of factors including life history characteristics (e.g., M, K, τ), whether or not or how well these are known, and the perceived importance of the risk of driving a stock below some minimum threshold level relative to the risk of sacrificing yield. In the common situation where there is adequate information to place bounds on all relevant life history parameters except those characterizing the S–R relationship, I recommend using a default target fishing mortality rate of $F_{40\%}$ and a default overfishing threshold SSB given by $\%S_0 = 100\tau$ as a basis for formulating risk-averse fishing strategies when the two types of risk are given similar weighting. $F_{40\%}$ is similar to $F_{0.1}$ when recruitment and maturity schedules coincide, approximates F_{msy} for τ in the range of about 0.05–0.2, and does not exceed F_τ unless $\tau > 0.4$. The proposed threshold SSB corresponds to a drop in recruitment to around half the virgin or maximum level for a wide range of parameterizations of both the Beverton–Holt and Ricker S–R functions (actual range about one third to two thirds; Appendix B).

The biggest problem is the choice of τ. By definition, τ determines the threshold fishing mortality. Therefore, speculation about the likely range of τ will have a direct influence on conclusions about the best choice for the threshold F. The current theoretical study does not provide a basis for altering the previous recommendation by Mace and Sissenwine (1993), who suggested using $\tau = 0.2$ as a default overfishing threshold for stocks believed to have at least average resilience and $\tau = 0.3$ as a threshold for little-known stocks. These values of τ would correspond to threshold biomass levels of 20% S_0 and 30% S_0, respectively (or the same %B_0 values, if B_0 is equivalent to S_0). However, there is a need to be cautious in the application of the less-conservative default threshold. The corresponding threshold fishing mortality $(F_{20\%})$ will exceed the extinction threshold (F_τ) if $\tau > 0.2$. In fact, if τ is believed to be near 0.2, it is probably unwise to use a threshold F as high as $F_{20\%}$, since thresholds sometimes have a tendency to become targets. Currently, $F_{20\%}$ is being adopted as a default overfishing threshold (and sometimes even a fishing target) in an increasing number of fisheries management plans in the United States. Of course, for stocks known or believed to have extremely high resilience, $F_{20\%}$ may be a conservative threshold.

If the S–R relationship is known, there is no need to use defaults, since F_{msy} and other BRPs can be estimated directly.

If the relationship can be fitted by an asymptotic or domed S–R function and there are adequate observations at low stock size, I suggest using the slope at the origin as a threshold F and the SSB corresponding to 50% R_{max} as a threshold biomass. Note, however, that these thresholds hardly represent conservative reference points, and so should generally be treated as absolute thresholds in the sense that the probability of crossing them should be vanishingly small.

If there are insufficient observations to characterize the S–R function over its entire range, the observed survival ratios can be used to estimate the replacement F (F_{rep}) in the manner outlined by Sissenwine and Shepherd (1987) and Gabriel et al. (1989) and implemented by Mace (1991) and Mace and Sissenwine (1993). The average (or median) observed survial ratio can then be used as the basis for a threshold F if it is believed that the stock is dangerously low, or well below historic observations, or as a target F if the observations have been collected from a fishery operating at near-optimal levels.

Acknowledgements

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120

Can. J. Fish. Aquat. Sci., Vol. 51, 1994

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Appendix A. Relationship between YPR and MSY for Beverton–Holt and Ricker *S–R* Functions

The following equations apply to the special case where recruitment and maturity schedules coincide so that the age of recruitment (t_r) equals the age of maturity (t_m) and the average recruited biomass per recruit (BPR) equals the average spawning biomass per recruit (SPR).

For the case of knife-edge recruitment, the yield per recruit (YPR) equation is given by

$$(A1) \qquad YPR = F\left(\frac{1-e^{-(F+M)}}{F+M}\right)\sum_{t=t_r}^{\infty}(N_t\ e^{-(F+M)(t-t_r)}\ W_t)$$

where

$$N_t = 1 \text{ at } t=t_r.$$

Substituting from equation (5) leads to simple relationships between YPR and SPR:

$$(A2) \qquad YPR = F\cdot SPR$$

and between SPR and the slope at the origin of the YPR relationship:

$$(A3) \qquad \left.\frac{d(YPR)}{dF}\right|_{F=0} = \left(\frac{1-e^{-M}}{M}\right)\sum_{t=t_r}^{\infty}(N_t\ e^{-M(t-t_r)}\ W_t).$$
$$= SPR_{F=0}.$$

Thus, $F_{0.1}$ is the fishing mortality rate that satisfies the relationship

$$(A4) \qquad \frac{d(YPR)}{dF} = 0.1\cdot SPR_{F=0}.$$

For the Beverton–Holt *S–R* model, F_{msy} is the fishing mortality rate, F', that maximizes the expression (equation (13))

$$X = F'\cdot(SPR_{F'} - \alpha).$$

Substituting from equations (A2) and (8) results in

$$(A5) \qquad X = YPR_{F'} - F\cdot\tau\cdot SPR_{F=0}.$$

Differentiating (A5) with respect to F and setting $dX/dF=0$ gives

$$(A6) \qquad \frac{d(YPR)}{dF} = \tau\cdot SPR_{F=0}.$$

Thus, from equations (A4) and (A6), $F_{msy} = F_{0.1}$ for the special case $\tau = 0.1$, $F_{msy} > F_{0.1}$ for $\tau < 0.1$, and $F_{msy} < F_{0.1}$ for $\tau > 0.1$.

These results can be generalized to the case where recruitment and maturity are not knife-edge; equations (A3), (A4), and (A6) will hold as long as the recruitment and maturity ogives are the same.

For the Ricker relationship, F_{msy} is the fishing mortality rate, F', that maximizes (equation (17))

$$X = F'\cdot\log_e(\alpha\cdot SPR_{F'}).$$

Using the same procedure as above gives a somewhat more complex relationship between MSY and YPR. F_{msy} is the fishing mortality rate that maximizes

$$\frac{d(YPR)}{dF} = \frac{YPR}{F}\left[1 - \log_e\left(\frac{YPR}{F\cdot\tau\cdot SPR_{F=0}}\right)\right].$$

Thus, $F_{0.1} = F_{msy}$ when

$$0.1\cdot SPR_{F=0} = \frac{YPR}{F}\left[1 - \log_e\left(\frac{YPR}{F\cdot r\cdot SPR_{F=0}}\right)\right].$$

Deriso (1987) provided a more detailed exploration of the relationship between $F_{0.1}$ and F_{msy} for the Ricker model.

Appendix B. Relationship between $\%B_0$ and Threshold $\%SPR$ for Beverton–Holt and Ricker *S–R* Relationships

Threshold levels of %SPR (SPR expressed as a percentage of $SPR_{F=0}$) are commonly equated with threshold levels of $\%B_0$ (e.g., a threshold of 20% SPR is used interchangeably with 20% B_0). However, if the threshold %SPR is the %SPR associated with the slope at the origin of the spawning–recruitment (*S–R*) relationship (equation (7)), it is obvious that the two do not equate because the corresponding equilibrium biomass is zero. The translation between the two depends on the shape of the underlying *S–R* relationship. An alternative threshold based on relative recruitment is defined here and used as a reference point for comparing levels of $\%B_0$ and threshold %SPR.

The suggested alternative threshold is the biomass level corresponding to 50% of the maximum recruitment estimated from a fitted *S–R* relationship (50% R_{max}). It makes sense to base threshold definitions on relative recruitment because one of the main reasons for choosing a non-zero biomass threshold is the belief that low biomass leads to an increased probability of "recruitment failure" or an average level of recruitment that is so low that stock rebuilding is impeded. The 50% level is arbitrary, but there is likely to be general agreement that stocks should not be permitted to fall below a biomass level that would produce an average recruitment of 50% of the expected maximum.

The following equations define γ, ζ, and τ, which are the threshold levels (proportions) of B_0 (here equivalent to S_0), R_{max}, and $SPR_{F=0}$, respectively:

$$S = \gamma B_0;\ 0 < \gamma < 1$$
$$(B1) \qquad R = \zeta R_{max};\ 0 < \zeta < 1$$
$$\left.\frac{dR}{dS}\right|_{S=0} = \frac{1}{\tau\cdot SPR_{F=0}} = \frac{1}{\tau\cdot(B_0/R_0)};\ 0 < \tau < 1$$

where S = spawning biomass, B_0 = virgin recruited biomass = virgin spawning biomass $(=S_0)$, R = recruitment in numbers, R_{max} = maximum expected recruitment, and τ = the ratio between the slope corresponding to $SPR_{F=0}$ (i.e., $1/SPR_{F=0}$ or R_0/B_0) and the slope at the origin $(dR/dS_{|S=0})$; thus, τ = the threshold %SPR expressed as a proportion.

These equations are used in conjunction with the Beverton–Holt and Ricker *S–R* functions (i) to calculate the $\%B_0$ corresponding to 50% R_{max} for various levels of threshold %SPR (i.e., to find γ when $\zeta = 0.5$ with τ known) and (ii) to calculate the $\%R_{max}$ resulting from the common assumption that $\%B_0$ is equivalent to the threshold %SPR (i.e., to find ζ when $\gamma = \tau$).

TABLE B1. Relationships between $\%B_0$, threshold $\%$SPR, and $\%R_{\max}$ (γ, τ, and ζ, respectively, expressed as percentages).

	Critical point = 50% $R_{\max}$ ($\zeta = 0.5$)			%B_0 = threshold %SPR ($\gamma = \tau$)	
Threshold %SPR (100τ)	%B_0 (100γ)		Threshold %SPR (100τ)	%$R_{\max}$ (100ζ)	
	Beverton–Holt	Ricker		Beverton–Holt	Ricker
5	4.8	7.8	5	51.3	35.1
10	9.1	10.1	10	52.6	49.7
20	16.7	14.4	20	55.6	63.4
30	23.1	19.3	30	58.8	68.4
40	28.6	25.3	40	62.5	69.1
50	33.3	33.5	50	66.7	66.6

1. Beverton–Holt S–R Relationship with $R_{\max} = 1/\beta$.

The Beverton–Holt S–R relationship is given by

(B2) $\quad R = \dfrac{S}{\alpha + \beta S}$

where α and β are parameters that define the maximum of the function and the slope at the origin by

(B3) $\quad \lim_{S \to \infty} R = 1/\beta = R_{\max}$

(B4) $\quad \dfrac{dR}{dS}\Big|_{S=0} = \dfrac{1}{\alpha}.$

Equations (B1) and (B4) result in

(B5) $\quad \alpha = \tau \dfrac{B_0}{R_0}.$

Combining equations (B1)–(B3) and (B5) gives

(B6) $\quad \begin{aligned} &\gamma = \tau \text{ when } \zeta = 0.5 \\ &\zeta = 0.5 \text{ when } \gamma = \tau. \end{aligned}$

2. Beverton–Holt S–R Relationship with $R_{\max}$ Given by the Intersection of the S–R Curve with the Line $R = (1/\text{SPR}_{F=0}) \cdot S$ (i.e., $R_{\max} = R_0$ is a Point on the Curve)

An expression for β is obtained by sustituting the point (B_0, R_0) and equation (B5) into equation (B2):

(B7) $\quad \beta = \dfrac{1 - \tau}{\tau^2 R_0}.$

It follows from equations (B1), (B2), (B5), and (B7) that

(B8) $\quad \begin{aligned} &\gamma = \dfrac{\tau}{1 + \tau} \text{ when } \zeta = 0.5 \\ &\zeta = \dfrac{1}{2 - \tau} \text{ when } \gamma = \tau. \end{aligned}$

At $\zeta = 0.5$, γ and τ are reasonably close as long as τ is less than about 0.2 (Table B1). When $\gamma = \tau$ and τ is in the range 0–0.35, ζ will be in the range 0.5–0.61. When (B_0, R_0) is a point on the curve defined by equation (B5), equation (B6) is a limiting case for equation (B8), occurring when $\gamma = \tau$ approaches 0.

3. Ricker S–R Relationship with $R_{\max}$ Given by the Maximum of the Function and R_0 Given by the Intersection of the S–R Curve with $R = (1/\text{SPR}_{F=0}) \cdot S$ (i.e., (B_0, R_0) is a Point on the Curve and $R_0 \le R_{\max}$)

The Ricker S–R relationship is given by

(B9) $\quad R = aSe^{-bS}$

where a and b are parameters that define the maximum of the function and the slope at the origin by

(B10) $\quad \dfrac{dR}{dS} = 0 \Rightarrow S = \dfrac{1}{b}; \; R_{\max} = \dfrac{a}{b} e^{-1}$

(B11) $\quad \dfrac{dR}{dS}\Big|_{S=0} = a.$

Equations (B1) and (B11) imply that

(B12) $\quad a = \dfrac{R_0}{\tau B_0}.$

Combining equations (B1), (B9), (B10), and (B12) gives

(B13) $\quad \zeta = \dfrac{\gamma}{\tau} \dfrac{R_0}{R_{\max}} e^{-(\gamma/\tau) \cdot (R_0/R_{\max}) \cdot e^{-1}}.$

Thus, γ must be found by iteration. For the case $\zeta = 0.5$, the divergence between γ and τ is somewhat greater for the Ricker function than for the Beverton–Holt function (Table B1). For $\gamma = \tau$ in equation (B13), $\zeta = (R_0/R_{\max}) \cdot e^{-(R_0/R_{\max}) \cdot e^{-1}}$. The range covered by ζ in this case exceeds the range calculated for the Beverton–Holt relationship (Table B1). For R_0 in the range 0.5–$1.0\, R_{\max}$ in equation (B13), ζ will be in the range 0.42–0.69.

In conclusion, for these common S–R functions, the level of $\%B_0$ ($\%S_0$) that equals the threshold $\%$SPR defined by the ratio between the slope at $\text{SPR}_{F=0}$ and the slope at the origin will correspond to an expected recruitment level that is appreciably below the maximum. For reasonable ranges of the threshold $\%$SPR (0.05–0.35), the expected recruitment corresponding to $\%B_0$ = threshold $\%$SPR will range from 51 to 61% R_0 for the Beverton–Holt function and from 35 to 69% $R_{\max}$ for the Ricker function.