

# Spawning Stock Biomass per Recruit in Fisheries Management: Foundation and Current Use

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Goodyear, C. P. 1993. Spawning stock biomass per recruit in fisheries management: foundation and current use. p. 67-81. In S. J. Smith, J. J. Hunt and D. Rivard [ed.] Risk evaluation and biological reference points for fisheries management. Can. Spec. Publ. Fish. Aquat. Sci. 120.

Spawning stock biomass per recruit (SSBR) estimates the expected lifetime reproductive potential of an average recruit ( $P$ ), which is an important correlate of population growth potential. The ratio of the fished to unfished magnitude of  $P$  is the spawning potential ratio (SPR) and is a measure of the impact of fishing on the potential productivity of a stock. Current use of SPR merges concepts developed to quantify the compensation required for population persistence given anthropogenic increases in mortality with observations of stock productivity and SSBR for fisheries in the western North Atlantic. It has a firm theoretical basis and is evaluated against yield per recruit and contrasted with other traditional biological reference points. SPR is widely used in U.S. fisheries managed under the Magnuson Fishery Conservation and Management Act, usually in the context of a percentage of the unfished SSBR. Its implementation is intended to be risk-averse through selection of minimum acceptable levels above which stocks maintain acceptable productivity. The behavior of the underlying principles suggests SPR values below about 0.2 should be avoided unless there is evidence for exceptionally strong density-dependence in the stock. Critical levels have typically been set in the range of 0.2 to 0.3 primarily based upon the experience in the northwest Atlantic.

La biomasse du stock reproducteur par recrue (BSR/R) évalue le potentiel reproducteur prévu pour la durée de vie d'une recrue moyenne ( $P$ ) qui est un important corrélat du potentiel de croissance d'une population. Le rapport entre la grandeur de  $P$  pour un groupe exploité et un groupe non exploité est le rapport du potentiel reproducteur et une mesure de l'effet de la pêche sur la productivité potentielle d'un stock. L'utilisation actuelle du rapport du potentiel reproducteur combine des concepts élaborés pour mesurer la compensation nécessaire à la persistance d'une population étant donné les augmentations anthropogéniques de la mortalité aux observations de la productivité du stock et de la biomasse du stock reproducteur par recrue pour les pêches de l'Atlantique nord-ouest. Ce concept a une base théorique solide et il est évalué par rapport au rendement par recrue et est mis en contraste avec d'autres points de référence biologiques classiques. Le rapport du potentiel reproducteur est largement utilisé aux États-Unis pour les pêches qui sont gérées en vertu de la Magnuson Fishery Conservation and Management Act, en général dans le contexte d'un pourcentage de la biomasse du stock reproducteur par recrue qui n'est pas exploitée. Son application est destinée à limiter les risques en choisissant des taux minimum acceptables au-dessus desquels les stocks conservent une productivité acceptable. Le comportement des principes sous-jacents porte à croire qu'il faut éviter que le rapport du potentiel reproducteur soit inférieur à 0,2 environ à moins que l'on démontre que le stock est exceptionnellement très dépendant de la densité. Des taux critiques ont en général été établis dans la plage de 0,2 à 0,3 fondés surtout sur l'expérience dans l'Atlantique nord-ouest.

**T**he fundamental question in formulating advice to managers on harvest levels that can produce desired catches over a long-term period concerns the level of the reproductive capacity of the stock sufficient to maintain levels of high productivity. As evidenced by the classic works of Ricker (1954) and Beverton and Holt (1957), such stock-recruitment considerations have long been a matter of concern for fishery scientists. However, in practice, stock-recruitment data for most stocks display a wide scatter of points that belie underlying functional dependencies. This scatter often defeats statistical demonstration of the relation of recruitment to stock size and has not generally been convincing to managers. For these reasons, spawning stock size has not generally been an explicit consideration in developing advice for total allowable catches.

The problem of evaluating the dependence of recruitment on stock size has not been the sole province of those trying

to grapple with safe harvest levels. Some industrial practices, notably the temporary withdrawal of condenser cooling water by poorly located steam-electric power plants, can result in the deaths of enormous numbers of larval and juvenile fishes and have initiated considerable scientific debate (e.g., Barnthouse et al. 1988). Measures to minimize these losses could in some instances impose direct economic costs on the order of billions of dollars.

With the implementation of the U.S. National Environmental Policy Act of 1969 (U.S. Congress 1970), scientists were required to assess the impacts of such losses on the affected populations and the fisheries and ecosystems they supported. It became immediately clear that the key questions involved the nature and force of the density-dependent processes that may be available to offset the increases in mortality; i.e., the relation between stock size and subsequent recruitment. The inadequacy of existing knowledge prompted



research by both government and industry to develop methods to quantify the population level consequences of such losses. This research led to an initial conference in Gatlinburg, Tennessee (Van Winkle 1977) where several authors dealt directly with the issue (Campbell et al. 1977; Christensen et al. 1977; Goodyear 1977; Lawler et al. 1977; McFadden 1977). Subsequent studies included reviews of compensatory phenomena (Saila et al. 1987; Jude et al. 1987) and of mathematical models that may be applied to the problem (Chen 1987). The research continues to receive significant support from the COMPMECH program of the Electric Power Research Institute, Palo Alto, California.

One of the studies at the initial conference presented a method to quantify the degree to which anthropogenic mortality required compensatory changes in natural mortality or fecundity for population persistence (Goodyear 1977). The method utilized the observation that population stability requires that mortality be exactly offset by reproduction (on average). This fact was exploited to develop an estimator for compensation (the Compensation Ratio, CR) based on changes in the reproductive potential of the average recruit ( $P$ ). This knowledge permitted exploration of several important stock-recruitment considerations without the need to know the form of the curve or its parameters (Goodyear 1977, 1980). Although proposed as a potentially useful fisheries management tool in the original paper, implementation required empirical estimates for critical levels against which to judge the significance of any particular level of CR. Such estimates were not then available.

Meanwhile, expansion of the fisheries off the U.S. coast of the Northwest Atlantic in the late 1960's and early 1970's precipitated declines in landings of several important species (Brown 1990). This spurred increased emphasis on evaluation and advice on the condition of the spawning stocks (e.g., Shepherd 1982; Anon. 1983, 1987, 1988abc, 1989abc; Sissenwine and Shepherd 1987; Brown 1990). Several of these studies noted the relation between productivity and SSBR (Shepherd 1982; Overholtz et al. 1986; Mathews 1991), and others observed declines in productivity when SSBR fell below a general range of 20–40% of the unfished level (Gabriel 1985; Gabriel et al. 1984, 1989; Anon. 1987).

Appropriately estimated, SSBR is equivalent to Goodyear's (1977) definition of potential fecundity per recruit ( $P$ ); consequently, the observations of declining productivity with declining SSBR provide estimates of the critical levels. These developments and an urgent need to establish quantifiable conservation objectives to rebuild depleted Gulf of Mexico red drum (*Sciaenops ocellatus*) and red snapper (*Lutjanus campechanus*) stocks led to additional evaluations of the underlying theory, much of which was incorporated into stock assessments or other management advice (e.g., Goodyear 1987, 1990; Goodyear and Phares 1990). This paper summarizes the results of this work.

## The Spawning Potential Ratio

### Basis

Goodyear's (1977) compensation ratio (CR) is an index of the degree of compensation required of a fished population to persist. It is a measure of the overall change in the survival and fecundity parameters that must occur for a population undergoing exploitation to stabilize at a new equilibrium. The development of the CR details the assumptions involved in such analyses and is condensed here for convenience. The CR is defined as:

$$CR = \frac{P_{\text{unfished}}}{P_{\text{fished}}}$$

$P_{\text{unfished}}$  = potential recruit fecundity in the absence of fishing mortality;  
 $P_{\text{fished}}$  = potential recruit fecundity in the exploited stock.

Potential recruit fecundity ( $P$ ) is defined as the number of eggs that could be produced by an average recruit in the absence of density dependence. It carries the designation "potential" to highlight the notion that it includes both the actual average lifetime production of eggs per recruit at equilibrium population densities plus those eggs that would have been produced by an average recruit in the absence of any density-dependent suppression of maturities or fecundities at age or of survival in post-recruit ages. It is determined as:

$$P = \sum_{i=1}^n E_i \sum_{j=0}^{i-1} S_{ij}$$

where:

$n$  = number of ages in the unfished population;  
 $E_i$  = mean fecundity of females of age  $i$  in the absence of density-dependent inhibitions of growth;  
 $S_{ij}$  =  $\exp(-(F_{ij} + M_{ij}))$ , density-independent annual survival probabilities of females of age  $i$  while they were age  $j$ ;  
 $F_{ij}$  = the fishing mortality rate of females of age  $i$  when they were age  $j$ ; and  
 $M_{ij}$  = the natural mortality rate of females of age  $i$  when they were age  $j$ .

The convention of employing  $F_{ij}$  in the computation of  $P$  allows the estimate of  $P$  to reflect the historical pattern of fishing mortality on the year classes comprising the population. For equilibrium analyses all  $F_{ij}$  would equal  $F_j$  for all  $j$ , and the equations simplify to referencing only the age dimension. The compensatory density dependence that brings about population stability can be manifested as changes in early life stage (pre-recruit) survival, or as changes in survival or fecundity in the later life stages. It is probably impossible to forecast the

partitioning of each possible compensatory response between increased survival and fecundity by life stage for a virgin stock that is to be the target of a new fishery. However, in a heavily exploited stock the reduced density of older fish often relaxes any density-dependent suppression of growth, survival, and fecundity that may have existed in these older age classes in the virgin population. As a consequence, the parameter values needed to solve for  $P$  can often be derived from studies of an existing stock if exploitation has been sufficient to fully utilize any potential density-dependent growth and survival that might occur within the adults. Specifically, no further reduction in abundance would cause the recruits to be subject to less natural mortality, grow faster, be more fecund, or mature earlier. It is assumed that half the eggs will be female. For most applications this assumption has little importance since the initial fraction of females will cancel when ratios are taken. However, this assumption does pose a problem for those species that transform from one sex to the other during their lifetime.

Recall that for population persistence each egg in the parental generation must on average produce a single egg in the filial generation. Thus, if a population can persist in both the fished and unfished state, the ratio of the average potential lifetime fecundities of pre-reproductive recruits of the same age is a direct measure of the compensation that occurred between the two states to allow persistence in the fished state; hence the term compensation ratio. The response of the CR to fishing mortality is illustrated in Fig. 1. Its actual shape will vary by species. A CR value of 100 means that in order for the population to persist at the corresponding level of fishing mortality the mean survival probability of an average recruit must increase a hundredfold over that existing in the unfished condition.

The calculation of spawning stock biomass per recruit for a fished stock is analogous to the computation of  $P$ , except that the units may be in terms of the biomass of the entire adult stock, the biomass of mature females in the stock or the biomass of the eggs they produce. SSBR calculations are typically made to characterize the reproductive potential of a stock. When it is estimated in terms of the biomass of the eggs, it differs from  $P$  only by the mean weight of the eggs. Note that this term would cancel when the compensation ratio is taken. Given this observation, it is clear that for practical purposes SSBR and  $P$  are effectively identical. These two terms are henceforth treated synonymously with the understanding that the estimates of SSBR that do not conform to the precise definition of  $P$  are intended as surrogates for the estimate of potential recruit fecundity. The spawning potential ratio (SPR) is then estimated as the reciprocal of CR; i.e.,

$$SPR = \frac{P_{\text{fished}}}{P_{\text{unfished}}} = \frac{SSBR_{\text{fished}}}{SSBR_{\text{unfished}}}$$

SPR has a maximum value of unity and declines toward zero as fishing mortality increases. As the SPR declines with

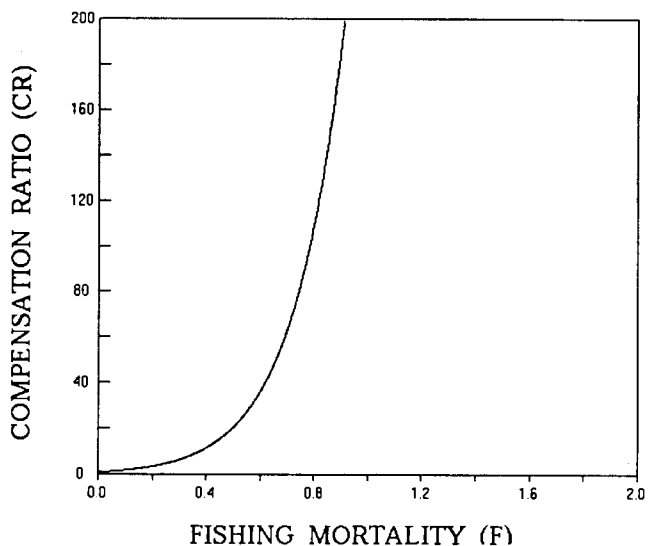


Fig. 1. Effect of fishing on the level of compensation required for population persistence in striped bass (*Morone saxatilis*) as a function of fishing mortality (modified from Goodyear 1977).

increased fishing mortality, the required compensatory decline in density-dependent mortality or increased fecundity per spawner increases.

The spawning potential ratio is an alternative measure of the reproductive fitness of a stock that is conceptually based on the degree of departure from the virgin condition. It is a measure of the extent to which fishing has reduced the potential reproductive output of an average recruit from that which would have existed in the absence of fishing. This measure does not require knowledge of the size of the virgin stock. It is based on the premise that the size of a stock is the emergent property of the force exerted by the growth potential of its excess reproductive capacity against the limitations imposed by the environment, including fishing. This approach attacks the stock-recruit question from a different perspective than the traditional statistical analysis of stock-recruit data pairs. The often observed statistical independence of stock and recruitment and the required functional dependence of recruitment on stock are not conflicting concepts, but rather are each valid attributes of the recruitment problem. The observations of stock and recruitment focus on the realized production of recruitment and are confounded by environmental variation and measurement error.

SPR on the other hand focuses on the influence of fishing mortality on the slope of the spawner-recruit curve at its origin; i.e., in the absence of compensatory density dependence. In this situation the initial slope of the stock-recruit relation is proportional to the average lifetime fecundity of the recruits (Goodyear 1980). For example consider the hypothetical population of Fig. 2 which is near the origin of a stock recruitment curve. In this example, fishing mortality is scaled so that it reduces the expected lifetime fecundity of the offspring to 1/3 of that in the unfished stock. In the fished state the cluster of parental stock sizes and environmental influences that produced the recruits depicted by the solid circles would produce the cluster of recruits represented by the "x" symbols. A line

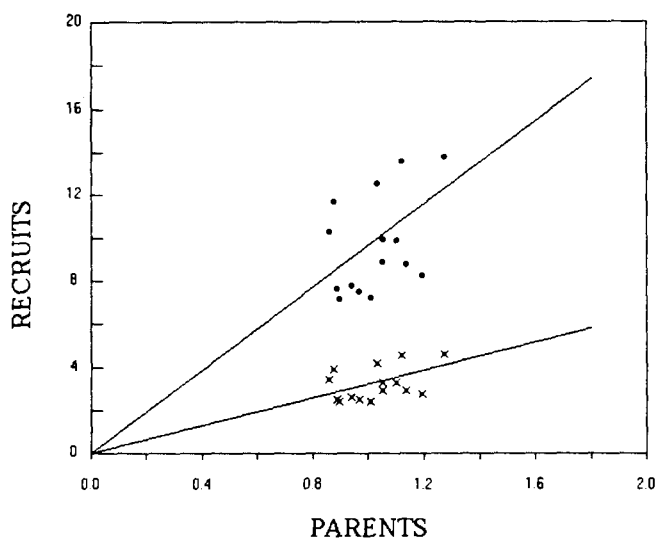


Fig. 2. Hypothetical stock-recruit data in the absence of density dependence with (x) and without fishing (·) plotted with corresponding regressions through the origin.

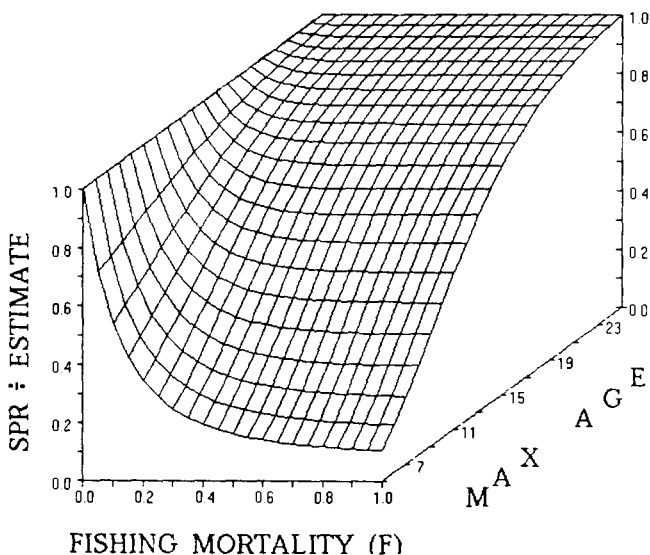


Fig. 3. Bias in SPR estimates from employing maximum ages too young to represent the unfished age distribution.

drawn through the mean of the unfished cluster has a slope of 10, and a line drawn through the mean of the fished cluster has been reduced by fishing to a slope of 3.3. Note that in this example recruitment is in excess of that needed for replacement for both situations, thus neither situation would necessarily lead to extinction. However, the growth rate for the unfished stock is greater than for the fished stock since it produces three times more mature offspring per spawner than does the fished stock. Further, the force of this differential in growth potential on the environmental resources might cause the two situations to reach even much different average equilibrium stock sizes with different temporal dynamics. The impact of fishing on the potential growth rate of a population is therefore different from its effect on the average population size, but it is also inexorably tied to it by ecological processes.

The basic concept involved in the application of SPR stems from the observation that significant changes in vital rates must occur on a fished stock, if it is to persist. The average parental egg in a population must produce an egg in the filial generation for population persistence. Fishing reduces the probability that individuals will survive to each age subsequent to entry into the fishery. If growth and natural mortality remain constant at the levels of the unfished stock, the number of eggs produced by the filial generation would always be fewer than their parents. As a consequence, to prevent population collapse the egg to pre-recruit survival probability and/or fecundity at age must rise in response to the lowered expected lifespan of the recruits. In the interest of brevity, the following discussion will assume that compensatory changes are manifested only as changes in early life stage survival probabilities. This simplifies the discussion but does not diminish the applicability of the basic concept.

This compensatory rise in the egg-to-pre-recruit survival probability is itself an emergent property of the dynamics of whatever actually happens during the growth and development from egg to recruit. However, it must occur for a population to sustain itself. Recruitment may or may not decline with increasing fishing, but this component of population survival must increase. The concept is really quite simple. If an average pre-reproductive recruit produced one-tenth as many eggs in the fished versus unfished population, then the survival probability of the eggs must increase tenfold to permit the population to persist in the fished state.

Stability is a relative concept here. It does not imply that recruitment in the population is the same from year to year, either in the fished or unfished state. The concept is that if the fishery can persist indefinitely at a given level of fishing mortality, then there is a corresponding long-term average egg-to-recruit survival that meets the replacement requirement. If no compensatory change in the mean survival rate were to occur for the preceding example, recruitment would fall 90% each generation from what it would otherwise have been. After two generations recruitment would be only 1% of its unfished state with the same environmental history.

The examples in the subsequent discussion that require data on the life history characteristics of a species use data from the red snapper fishery of the U.S. waters of the Gulf of Mexico (Goodyear and Phares 1990). Computations adopt a convention of 30 age classes in the stock because the sum of the contribution of all older ages to egg production is less than 2.5% for the unfished population. Natural mortality ( $M$ ) is 0.20 for all ages, and a length-fecundity relation is used to estimate the age-specific reproductive potentials of the average recruit at age from mean length at age. Forecasts of future trends, though arbitrary for the purposes of this document, assume initial conditions based upon VPA analysis of fishing mortality and numbers at age for this stock.

The last age class included in the analysis ( $n$ ) should be old enough so that the sum of the reproductive contribution of all older age classes represents a vanishingly small part of the reproductive potential of the unfished age structure. Selection of a younger maximum age, perhaps based upon the

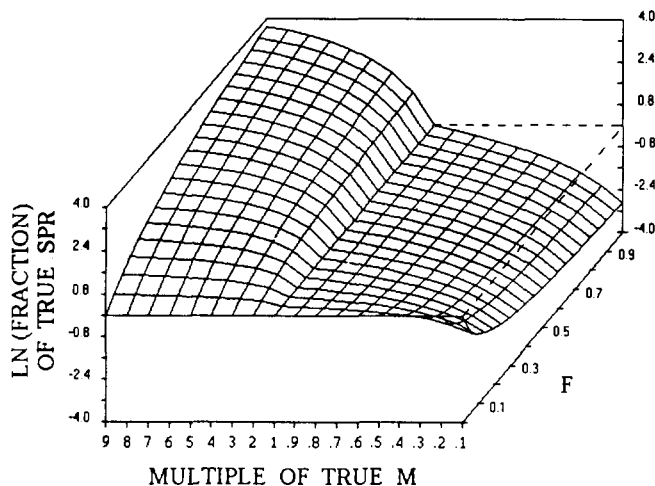


Fig. 4. Bias in SPR estimates from employing erroneous estimates of natural mortality ( $M$ ).

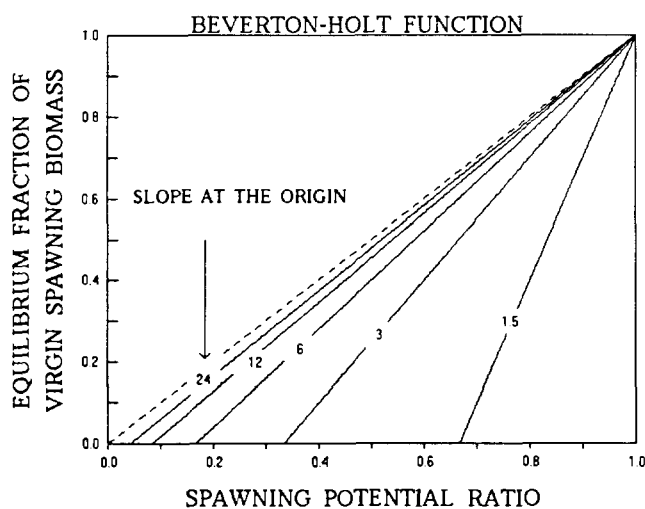


Fig. 5. Equilibrium fraction of virgin spawning biomass as a function of SPR for several slopes at the origin for the Beverton-Holt spawner-recruit model.

maximum age observed in a sample from a fished population, will introduce a positive bias into the estimate of SPR. The extent of this bias as a function of fishing mortality and the oldest age included in the estimate of SPR is illustrated for red snapper in Fig. 3. This sensitivity to the oldest age class included in the analysis is the result of the fact that both the cumulative effect of fishing mortality on cohort survival and the reproductive importance of each individual increases with age. As a consequence, omission of the older ages can cause significant bias in the estimation of SPR. The oldest age in a population is a function of the initial cohort size and survivorship. In the unfished population, survivorship is solely a function of natural mortality. As a consequence, error in the estimate of natural mortality can cause significant bias in the estimate of SPR, particularly at high levels of fishing mortality (Fig. 4).

## SPR and the Equilibrium Spawning Biomass

As already noted, SPR is a measure of the depression of the potential growth rate of a population caused by exogenous mortality. It is not directly tied to population size. However, if environmental perturbations lack temporal trends then a particular average stock size would be expected for any given constant level of SPR. The particular association between SPR and average stock size will be dependent upon the nature of the density-dependent suppression of population growth. Thus it would be both stock and area specific.

One manifestation of the anticipated relation could arise because the reduced growth potential of the fished population would cause slower recovery from negative environmental perturbations. Similarly the fished population would be slower to respond to temporary shifts toward improved environmental conditions. The overall result of these responses would be to reduce the average population size in the fished condition. Since the depression of the growth rate is measured by SPR, the mean stock size would decline with declining SPR. However, the primary factor controlling the magnitude of the response to a change in SPR is the actual change in the growth potential of the population. The magnitude of this change is the joint property of the magnitude of SPR and the slope of the spawner-recruit relation in the absence of density-dependent suppression of survival and fecundity. Thus, the expected mean population size for any given level of SPR for any particular stock-recruitment function is determined by the slope of the spawner-recruit curve at its origin and some scalar effect related to the size of the environment.

These principles can be illustrated for the traditional Ricker and Beverton-Holt stock-recruit models (Ricker 1975). The Ricker model used is of the form

$$R = \alpha P e^{\beta P}$$

and the Beverton-Holt model is of the form:

$$R = 1/(\alpha + \beta P)$$

To facilitate the examination of the relation among the variables, the scalar effect of the environment was removed by normalizing the equilibrium stock sizes to the virgin stock. Two analyses were performed for each model. The first was to plot the equilibrium fractions of the virgin spawning biomass as a function of SPR for several levels of the slope of the spawner-recruit curve at the origin (Fig. 5 and 6). The second was to plot the equilibrium fractions of the virgin spawning biomass as a function of the slope at the origin for several levels of SPR (Fig. 7 and 8).

For both models the equilibrium spawning biomass declines monotonically with declining SPR (Fig. 5 and 6) for all slopes of the spawner-recruit curve at the origin. However, the initial rate of decline observed for any given spawner-recruit slope is less for the Ricker model (Fig. 6) than for the Beverton-Holt model (Fig. 5) and the difference is more pronounced at higher slopes at the origin. This characteristic

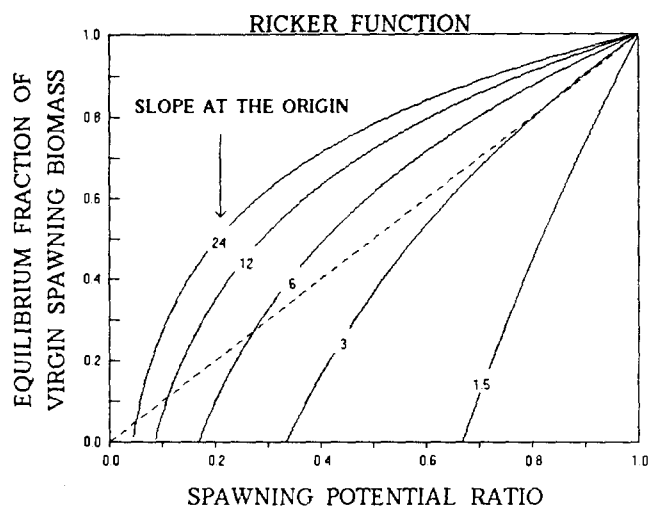


Fig. 6. Equilibrium fraction of virgin spawning biomass as a function of SPR for several slopes at the origin for the Ricker spawner-recruit model.

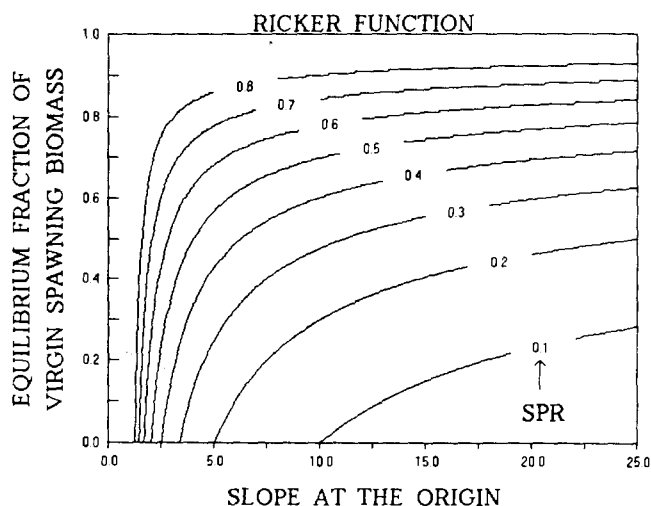


Fig. 8. Equilibrium fraction of virgin spawning biomass at several levels of SPR as a function of the slope of the Ricker spawner-recruit model at the origin.

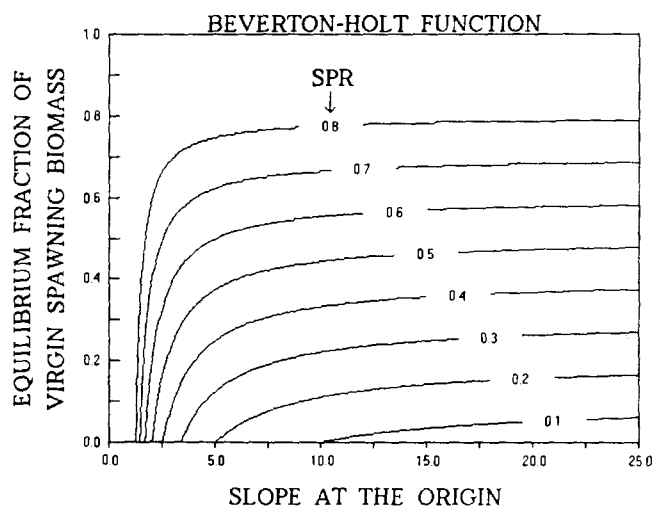


Fig. 7. Equilibrium fraction of virgin spawning biomass at several levels of SPR as a function of the slope of the Beverton-Holt spawner-recruit model at the origin.

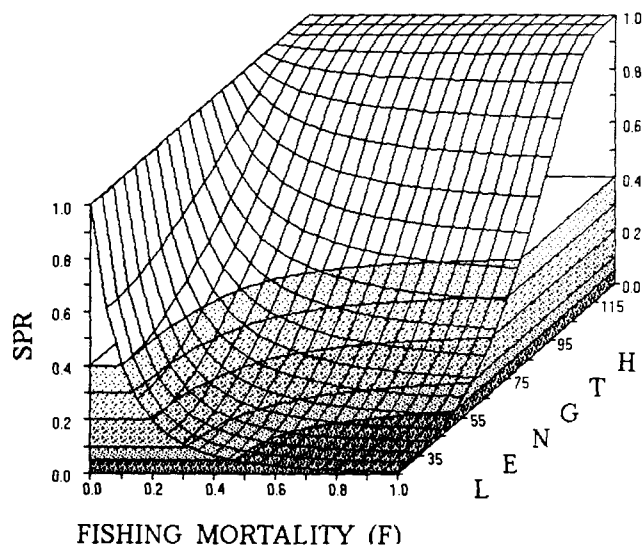


Fig. 9. SPR estimates for Gulf of Mexico red snapper as a function of fishing mortality and minimum size assuming no mortality for sublegal fish that are caught and released.

is the result of the dome-shaped form of the Ricker model. Inspection of Fig. 5–8 provides ample evidence that the equilibrium size of a stock cannot be reliably predicted from SPR where the stock-recruit relationship is not well known. The fractional reduction from the virgin condition may be more or less than the SPR depending on the form of the stock-recruitment relation and its slope at the origin. Note, however, that the Y-axis intercepts are the same for the two models in each of the figures. This is because the limiting value of SPR for population persistence for any stock-recruit relation is the reciprocal of the slope of the spawner-recruit curve at its origin.

### Equilibrium Analyses

SSBR and SPR decline with increasing fishing mortality and can be evaluated using methods analogous to traditional equilibrium analyses of yield per recruit. The spawning potential ratio is plotted as a function of length at recruitment and fishing mortality in Fig. 9 assuming no incidental fishing mortality exists for fish below the minimum size.

SPR decreases monotonically with increasing fishing mortality for all size limits that permit harvest. Similarly SPR decreases with decreasing minimum size for all levels of fishing mortality above zero. If significant mortality occurs for fish caught and released below the minimum size, then some fishing mortality is exerted below the minimum size and the

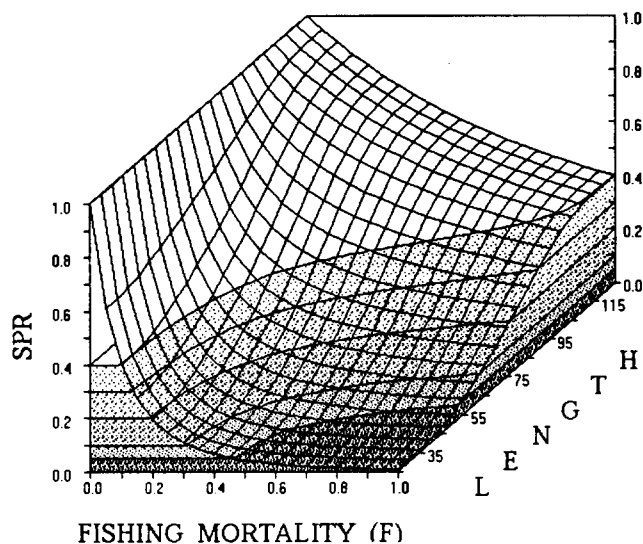


Fig. 10. SPR estimates for Gulf of Mexico red snapper as a function of fishing mortality and minimum size assuming a mortality of 10% for sublegal fish released after capture.

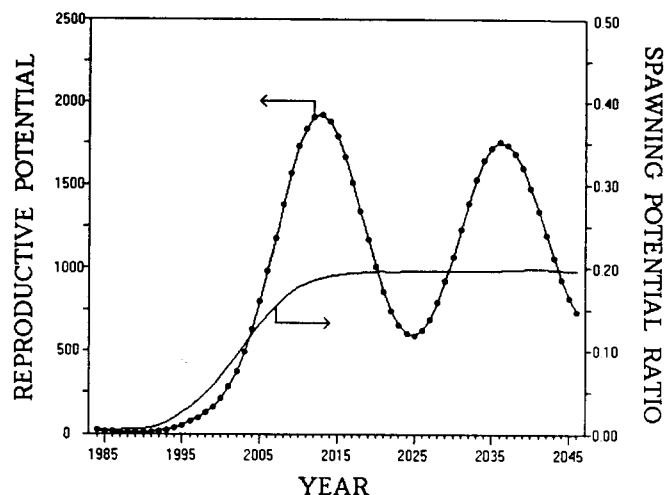


Fig. 12. Spawning stock biomass and SPR subsequent to management intervention for a depressed stock regulated by a strongly dome-shaped stock-recruit relationship.

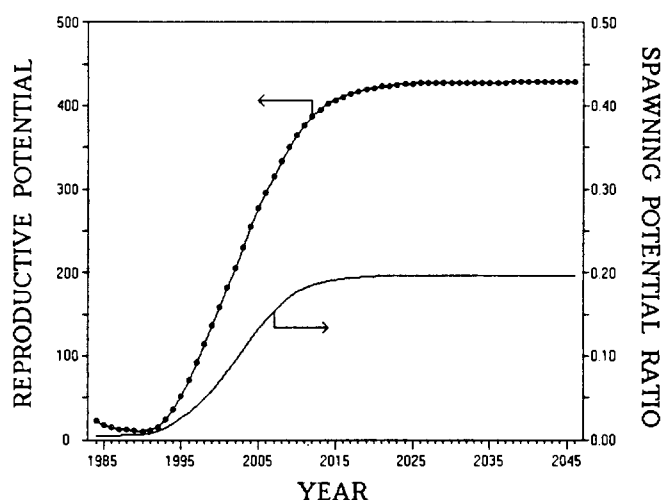


Fig. 11. Spawning stock biomass and SPR subsequent to management intervention for a depressed stock regulated by an asymptotic stock-recruit relationship.

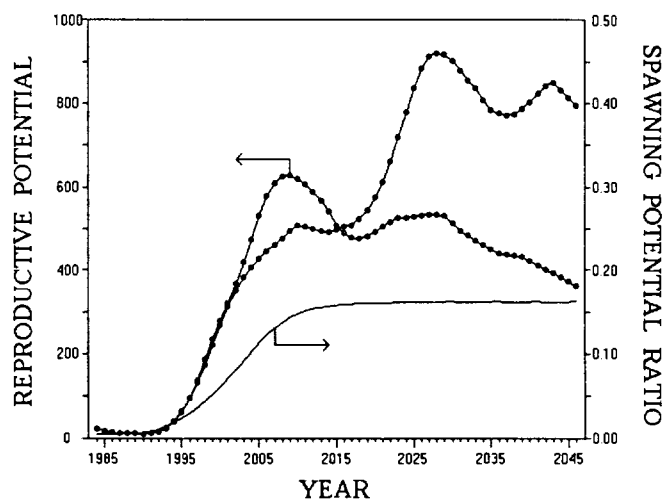


Fig. 13. Spawning stock biomass and SPR subsequent to management intervention for two cases where the stock is regulated by an asymptotic SR curve subject to significant annual environmental modification.

surface of the relationship in Fig. 9 would decline with increasing  $F$  for all length. An example is presented in Fig. 10 where sublegal fish were assumed to be caught with the same frequency as fish above the minimum size and suffered a 10% mortality as a result of the experience.

#### Analyses of Temporal Variation in SPR

If information on temporal trends in fishing mortality is available, then both the historical levels of SPR and its transient behavior resulting from changes in fishing mortality can be evaluated and/or forecast. Computations of past, present, and future trends in spawning stock and SPR were performed for hypothetical red snapper populations using computer simulation. Fishing mortality rates and initial cohort abundances

by age were taken from values for the U.S. Gulf of Mexico stock estimated by VPA analysis for 1984–1988 (Goodyear and Phares 1990). SPR for 1984 was estimated from the age distribution of the initial year's estimates of fishing mortality assuming these values applied to all prior years. This assumption allows estimates of the initial recruitment to all year classes comprising the population. Estimates in subsequent years gradually replace these initial equilibrium values with realized recruitment for years where data are available; these are replaced by forecasts for future years.

I simulated future population trends for three arbitrary stock-recruitment options to highlight the difference between SPR and the actual spawning potential of the stock: 1) a deterministic Beverton-Holt curve (Fig. 11); 2) a deterministic



Ricker curve (Fig. 12); and 3) two stochastically driven cases with a Beverton-Holt curve where year-class strength was strongly impacted by random environmental events (Figure 13).

Fishing mortality rates for each of these scenarios were adjusted from the historic levels beginning in 1991 so that the equilibrium SPR would be about 0.2. Note that the time trends of SPR in Figures 11–13 are independent of the time trend in the spawning potential of the stock. They are also independent of the particular stock-recruitment relation postulated.

This point highlights two important characteristics of SPR. First, setting spawning stock goals using this criterion assumes that the particular critical level chosen is sufficiently high that the size of the stock will be limited in part by density-dependent growth or mortality when SPR is at or above the critical value. In such circumstances the stock will be able to rebound from environmental perturbations. Viewed from a different context, at  $SPR = 0.1$  the slope of the stock-recruit (escapement) curve is 10% of its unfished level. Since the escapement curve must be greater than 1.0 to permit persistence, the slope of the unfished stock-recruitment curve of a stable fishery must have been greater than 10 to prevent a stock collapse and perhaps greater than 20 to accommodate the fishery.

The second consideration is a consequence of the fact that SPR does not measure the actual spawning potential of the stock. Management of the spawning potential of a stock using SPR proceeds from the conceptual notion that the fishing mortality should never be so severe that the average female recruit will be unable to replace herself (and her mate) in the next generation. To accomplish this goal, the reproductive potential of her average offspring (egg) must be limited by density-dependent reductions in survival or fecundity.

If such a population were to be depressed by some temporary environmental perturbation, the consequent reduction in the density dependence would permit the population to increase. This growth would continue until the population is eventually suppressed by density-dependent factors. The actual size of the spawning stock at this equilibrium point is primarily established by some factor related to the scale of the environment (often referred to as its carrying capacity). Thus while the estimate of SPR does not consider the actual size of the spawning stock, it anticipates an average mean spawning stock size. For constant recruitment, the percentage effect of fishing on SPR and the spawning potential of the stock are the same. However, if recruitment responds to the reduced abundance of the adults caused by fishing mortality, the two measures of the reproductive potential of the stock are potentially quite different.

The actual size of the spawning stock in a sustainable fishery retains the scaling effect of the carrying capacity of the environment. This factor provides no information related to the capacity of the stock to sustain further increases in fishing mortality beyond that measured by SPR. In order to employ the estimated size of the spawning stock in management, it is

first necessary to develop a time series of stock and recruitment for that particular stock. This information is needed to judge the significance of the magnitude of any particular realization of the spawning stock size. Absent such knowledge, SPR can be very informative. However, without knowledge of stock trends there is no basis for judging the adequacy of any conservation measure. Consequently, conservation standards based upon SPR must be augmented by monitoring trends in the actual size of the spawning stock. In most situations this should not be a significant impediment, since collection of annual statistics that lead to estimates of SPR also provide information on the size of the spawning stock.

## Selection of Critical Minima for SPR

### Requirements

Obviously, there is a limit to the degree density-dependent processes can relax to permit increased survival. Once fishing causes the required increase in compensation to pass that limit, the population will begin to decline toward extinction. For most stocks that limit is probably variable in time and space due to variable environmental factors. Recruitment could be maintained relatively high (on average) until the limit is exceeded by increased fishing or its own random variation. The population and the fishery it supports could then suddenly collapse without warning.

Goodyear (1977) designated the upper limit on the compensatory capacity of a stock as  $CR_{crit}$  to represent the upper (critical) threshold beyond which additional mortality would drive the population to extinction. He further suggested that for management purposes  $CR_{crit}$  should be set at a value to protect against serious stock depletion. The analogous level of SPR,  $SPR_{crit}$ , is the reciprocal of  $CR_{crit}$ . The relationship between SPR and the increase in pre-recruit survival probability required for population persistence is given in Fig. 14. This relationship is independent of the particular species, but some (or all) of the required compensatory change may be the result of increases in age-specific maturities or fecundities depending on the specific characteristics of the species. Assuming a 50/50 sex ratio of eggs, the theoretical lower limit to the value of  $SPR_{crit}$  is the value  $2/P_{unfished}$ . The realized level is the reciprocal of the product of  $P_{unfished}$  and the mean annual density-independent natural survival probability. In species that produce large numbers of eggs, the density-independent survival probability is very low. This situation is typical of pelagic spawners (see, for example, the many papers in Blaxter 1974). This low density-independent survival probability causes  $P_{unfished}$  to have no predictive value for  $SPR_{crit}$ . Several potential approaches to establishing guidelines for selection of  $SPR_{crit}$  are available: 1) the relative magnitude of the compensatory change in survival per unit change in SPR; 2) observations of declines in recruitment in stocks where SPR has been estimated; and 3) information derived from spawner-recruit relations that have been fitted to other fish populations.

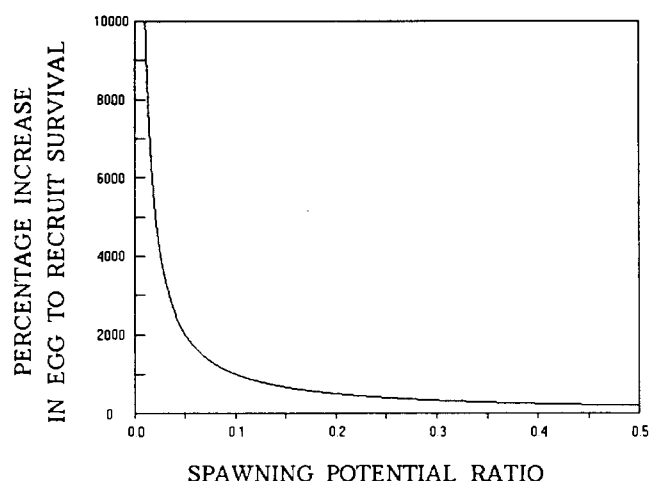


Fig. 14. Relationship between SPR and the proportional increase in egg to recruit survival required for population persistence.

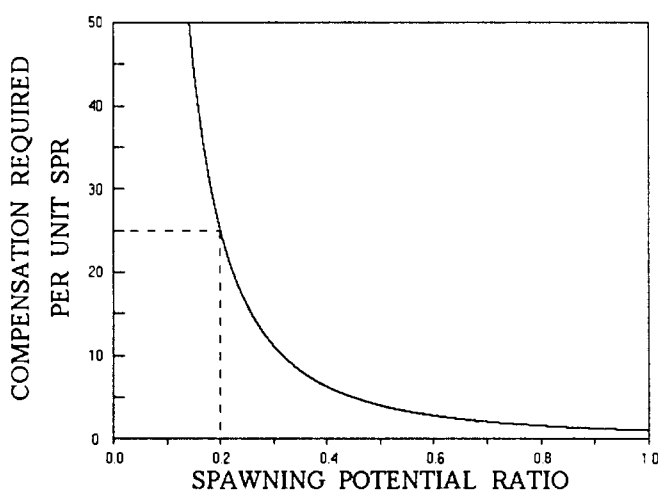


Fig. 15. Increase in magnitude of compensation required for persistence as SPR declines. Ordinate values are ratios of the compensatory change in mortality required to offset a reduction in SPR relative to that required at  $SPR=1.0$ .

#### Force of Exogenous Mortality

The relation between SPR and the required mean (equilibrium) increase in pre-recruit survival rates for population persistence presented in Fig. 15 provides information relative to the first of these approaches. The slope of the curve rises rapidly below about  $SPR = 0.20$ , suggesting that the compensatory reduction in mortality required for population persistence becomes disproportionately larger than the change in the SPR as SPR declines. The rate of increase in the amount of compensation required per unit reduction in SPR is presented in Fig. 15. The values on the ordinate are the ratios of the change in compensatory mortality for a unit reduction in SPR relative to the first unit reduction from the unfished stock. Thus, for population persistence, a unit reduction in SPR at

$SPR=0.2$  requires a compensatory increase in survival which is about 25 times greater than the change required at  $SPR=1$ . Although there is no discontinuity in the curve which signals a transition from safe to unsafe levels, simple inspection of its shape suggests that the threshold level for the SPR should probably not be set much below 20% without considerable justification and that 30% might be a more reasonable first choice.

#### Observed Recruitment Patterns

The ICES working group on methods of fish stock assessment (Anon. 1983) outlined a method for the examination of SSBR using scattergrams of stock and recruitment to define levels of fishing mortality ( $F_{high}$ ,  $F_{med}$ , and  $F_{low}$ ) that correspond to high, moderate, and low risks of stock collapse. Gabriel et al. (1989) and Gabriel (1985) applied these concepts in an evaluation of SPR and recruitment for several demersal finfish species of the Northwest Atlantic. They noted declines in recruitment at levels of SPR below 20% in several species. Their results led to recommended conservation targets for SPR of no less than 20% for cod, 28–30% for haddock, 25–30% for yellowtail, and 20% for other species (Anon. 1987). More recently, Mace and Sissenwine (1993) used this approach to examine data for 91 fished stocks of 27 species and found that SPR averaged about 0.19 overall with variations according to taxonomic affinity and life history characteristics.

#### Analysis of Fitted Stock-Recruitment Curves

A third method of evaluating possible critical limits for SPR in stocks where knowledge is limited is through analyses of the frequency distributions of fitted stock-recruitment curves from the literature. Note that the limiting SPR for a population's persistence is the reciprocal of the slope of its stock-recruitment curve at the origin (Goodyear 1977, 1980; Anon. 1988a). Thus, one alternative would be to construct a cumulative frequency distribution (CDF) of fitted stock-recruitment curves (perhaps by groupings of similar life histories). The critical levels could then be based on some agreed-upon criterion, for example the value corresponding to the 20th percentile of the distributions. Assuming the fitted slopes had been accurately estimated, this procedure would establish a limit that would protect 80% of the stocks from complete collapse (extinction). However, criteria based on the minimum values of SPR consistent with population persistence would probably be too dangerous to employ.

A somewhat better approach might be to establish a minimum conservation standard for SPR based on a safer criterion. One approach would be to adopt a standard for SPR consistent with average recruitment rates that would produce some agreed upon fraction of recruitment required for Maximum Sustainable Yield (MSY). These levels should be somewhat higher than the minimum consistent with population persistence and would therefore be more protective of the stock. In deterministic stock-recruitment relationships there is a level

of parental stock that produces a maximum of excess recruitment. By analogy, in the real (stochastic) world, there is an average parental stock level that produces on average a maximum excess in recruitment. Fishing at an exploitation rate that results in such a parental stock and also maximizes the biomass yield for each recruit to the population produces MSY.

Note that this theoretical MSY requires: 1) a stock size that produces maximum excess recruitment, and 2) exploitation of the excess recruits in a manner which maximizes yield for each harvested recruit. Theoretically, this would require harvesting all of the excess recruits at the time of their maximum biomass. Fisheries on wild stocks cannot generally be prosecuted in this manner. Consequently, there exists a separate value of MSY that would be realized for any particular ogive of age-specific selectivities of a population to fishing mortality. Consequently, from a practical point of view, MSY and  $F_{MSY}$  are not unique parameters because the maximum yield attainable from a stock involves both the production of recruits and their exploitation. However, on the production side, there is a unique value of spawning stock in deterministic stock-recruitment models that produces maximum excess recruitment. Since equilibrium requires harvesting all of the excess recruits, there is a unique fishing mortality rate  $F_{MSY}$  that accomplishes this constraint.

I evaluated the behavior of the SPR required for recruitment rates that produce MSY and 50% of MSY for the standard Ricker and Beverton-Holt stock-recruitment model of the forms previously employed. For both models, the recruitment at MSY is given where the slope of the stock recruitment curve is unity (Ricker 1973). Recruitment at MSY and 50% of MSY was evaluated numerically over a large range of possible parameter sets for both models. The absolute level of recruitment for both of these models was a function of the parental stock size and model parameters. However, the level of SPR associated with recruitment rates that produced MSY and 50% of MSY were solely a function of the slope of the stock-recruitment curve at its origin (Figures 16 and 17). The SPR required for 50% of MSY recruitment also is remarkably similar for the two models (Fig. 17).

The value of SPR associated with MSY recruitment might be considered a management goal while the lower values associated with declines to 50% of MSY may represent a lower critical threshold. SPR levels for MSY recruitment vary over a range of 15–90% over the parameter space evaluated. Clark (1991) found that a large fraction of MSY for several groundfish stocks could be obtained by harvesting at about 35% SSBR over the likely range of density dependence for these stocks (initial SR slopes of 4–16). Given the general shape of the curves of Fig. 17 and the knowledge that near maximum yields are obtained in the regions just above the isopleths, it is evident that his results are in close agreement with the present analyses and are a consequence of his selection of reasonable slopes for the spawner-recruit curves.

To compare the SPR for 50% of MSY recruitment to estimates of the slopes of stock recruitment curves at their origin, I

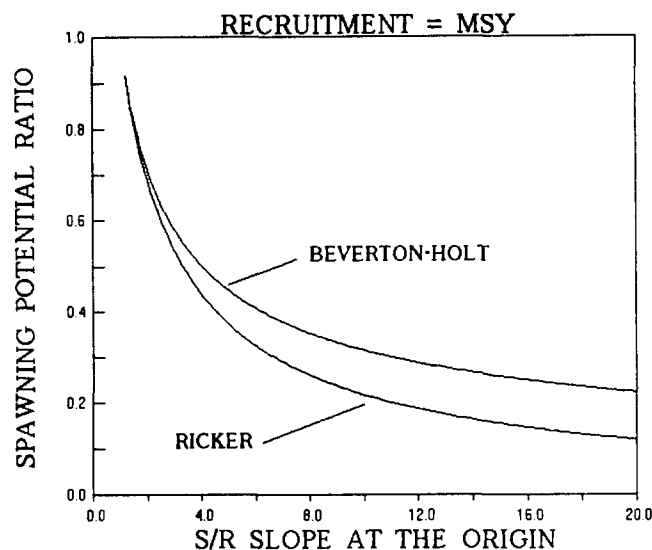


Fig. 16. SPR at MSY recruitment as a function of slope at the origin for two spawner-recruit curves.

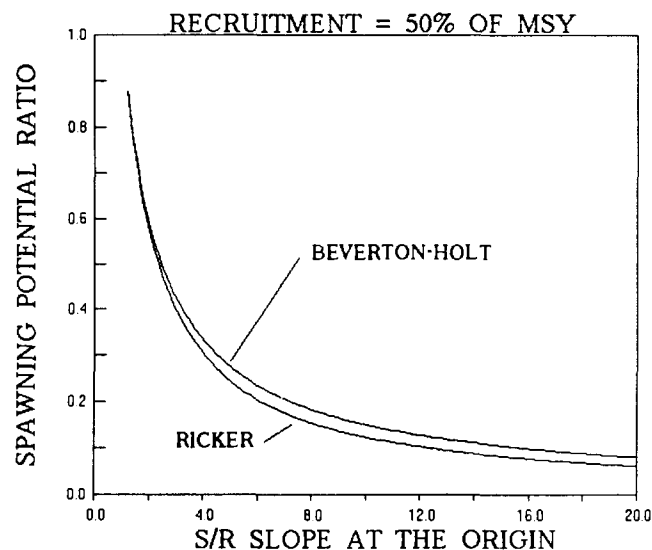


Fig. 17. SPR below which recruitment will fall below 50% of recruitment at MSY as a function of slope at the origin for two spawner-recruit curves.

overlaid the Ricker model estimates for 33 exploited stocks of marine and anadromous fishes derived by Cushing and Harris (1973) on the data of Fig. 17. The results are shown in Fig. 18. The 20th and 50th percentiles of the cumulative distribution were slopes of about 1.55 and 2.4 respectively. These levels suggest that the limiting SPR for 50% of MSY recruitment is 0.5 at the 50th percentile and 0.65 at the 20th percentile of the distribution. Both values are considerably more conservative than the 0.2 value derived from both inspection of the shape of the relationship of Fig. 15 and from the behavior of demersal stocks of the northwest Atlantic.

Three factors influence the adequacy of the results of Cushing and Harris for the present purpose. First, these authors did not account for the influence of fishing in the construction of the estimates of recruitment. Hence, their estimates of density dependence in the fished stocks should

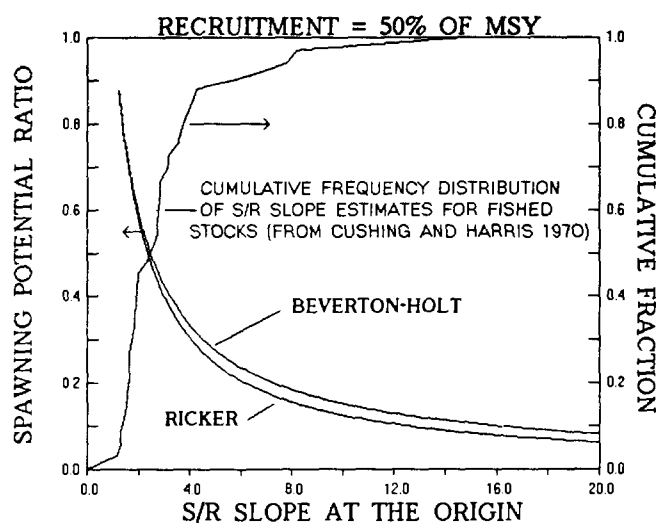


Fig. 18. Cumulative frequency distribution of estimated slopes at the origin of stock-recruit curves and limiting SPR below which recruitment will drop below 50% of recruitment at MSY for two spawner-recruit models.

already reflect the influence of some fishing mortality and, depending on the stock, are actually estimates of the slopes of the escapement curves. From this point of view the seemingly high critical values of SPR developed with this approach can be viewed as limitations on the expansion of the fisheries that existed for the various stocks over the levels existing when the stock and recruitment data were taken.

The second factor relates to the adequacy of the model representation for multiple age-class spawners. Christensen and Goodyear (1988) used simulation techniques to examine the robustness of statistical procedures to estimate the slope at the origin of an underlying Ricker stock-recruit relation in a multiple-age spawning population. Their results indicated that, if the stock-recruitment data do not correspond to parental stock fecundity and the lifetime egg production of the filial yearclass, regression techniques will commonly provide estimates of the slope at the origin that are biased high for low true values and low for high true values.

The third factor results from a statistical artifact encountered when fitting the Ricker model to random "observations" of stock and recruitment. The linearized form of the model involves regressing  $R/P$  as a function of  $P$ . This results in estimates of slopes at the origin of about 2.7 with correlation coefficients of 0.71 (see Kenney 1982). Unfortunately, non-linear fitting techniques such as those employed by Cushing and Harris (1973) do not remove the bias in estimates of the slope from such data (Christensen and Goodyear 1988). Thus, to the extent that random noise influences the estimates from Cushing and Harris, all of the slopes will be biased towards a median value of about 2.7. Given these uncertainties, it seems clear that the CDF obtained from the fits presented by Cushing and Harris cannot be used to establish limits for SPR without additional analysis. However, it is also clear that their results do not support selection of critical values lower than the 20% derived from the first two approaches.

Taken together with the findings of Mace and Sissenwine (1993), these observations suggest a working critical minimum for SPR of about 0.2 (20%) for stocks where the spawner-recruit relation is indeterminate or cannot be evaluated with existing data. An evaluation of the adequacy of this estimate should be considered an important research problem. This could be accomplished by compilations of additional empirical evidence of the relation between SPR and recruitment or of the distributions of slopes of stock-recruit curves at their origins.

## SPR Contrasted with Other Biological Reference Points

### Yield Per Recruit

Note that the size and mortality dimensions of Figures 9 and 10 conform to a common presentation of yield-per-recruit analyses. Consequently it is possible to calculate yield and SPR for each level of fishing mortality and minimum size. This permits evaluations of the location of isopleths of SPR on standard yield-per-recruit analyses and on the surface of yield as a function of fishing mortality and minimum size.

Analyses of yield per recruit are given in Fig. 19 assuming no fishing-induced mortality of fish below the minimum size and in Fig. 20 for a 10% mortality of released fish. Release mortality was incorporated in these calculations following the methods of Waters and Huntsman (1986). For comparison the isopleths of 5, 10, and 20% SPR are superimposed on the surface of yield per recruit for the same parameter space.

Two biological reference points related to yield per recruit are often discussed in relation to stock management:  $F_{\max}$  and  $F_{0.1}$ .  $F_{\max}$  is a value of fishing mortality that maximizes yield per recruit, and  $F_{0.1}$  is the value of fishing mortality at which the incremental gain in yield for an increase in fishing mortality is 10% of the yield per recruit produced at very low levels of  $F$  (Gulland and Boerema 1973). A typical analysis is presented in Fig. 21 for Gulf of Mexico red snapper along with SPR. In this example SPR is 30% at  $F_{0.1}$  and just under 20% at  $F_{\max}$ . These analyses assume age-1 snapper to be 0.02 and age-2 snapper to be 0.389 as vulnerable to fishing as all older ages in the population. Depending upon natural mortality and growth in a population,  $F_{\max}$  may approach infinity because yield per recruit increases monotonically with increasing fishing mortality. It is always greater than  $F_{0.1}$ , and for a wide class of models  $F_{\max}$  is also greater than  $F_{\text{MSY}}$  (Deriso 1982). Because  $F_{\max}$  may contemplate extremely high levels of fishing mortality that would reduce the spawning potential of the stock to near zero,  $F_{\max}$  is not a generally useful conservation standard. On the other hand,  $F_{0.1}$  is always less than infinity, and because of the nature of growth and mortality it is often at a level that provides substantial survival of recruits into the age classes contributing to the spawning potential of the stock. Thus, while this measure does not directly incorporate notions of the spawning stock, its adoption as a conservation standard

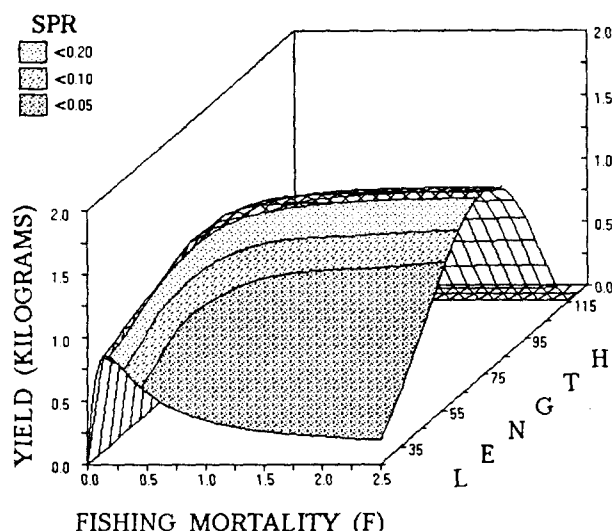


Fig. 19. Isopleths of SPR on the surface of yield per recruit as a function of length at recruitment and fishing mortality assuming no fishing-induced mortality of sublegal fish.

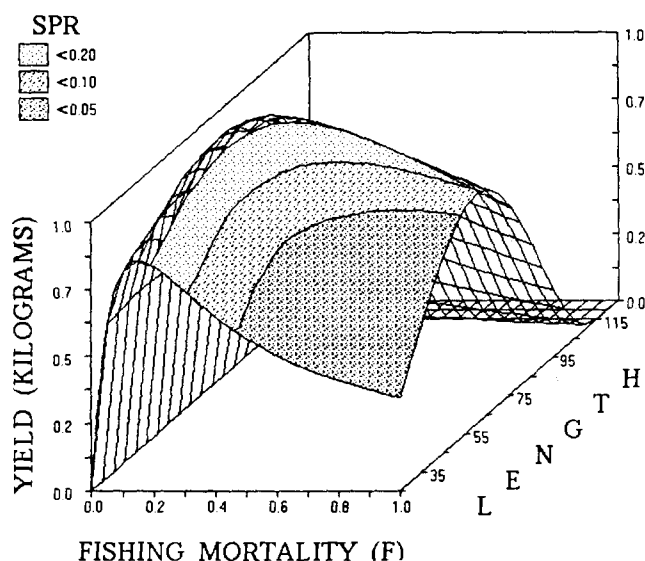


Fig. 20. Isopleths of SPR on the surface of yield per recruit as a function of length at recruitment and fishing mortality assuming 10% of released sublegal fish die as a result of the experience.

has profound implications for the expected lifetime reproductive contribution of a recruit. Because of these implications  $F_{0.1}$ , originally proposed as an economic consideration, has been widely adopted as management goal for fishery conservation. Because the contour for  $F_{0.1}$  lies on the far side of the contours of Figures 19 and 20, it cannot be plotted on the same perspective. However, a two-dimensional presentation of the same information permits simultaneous presentation of  $F_{0.1}$ ,  $F_{max}$ , and isopleths of yield and of SPR as a function of minimum size and fishing mortality. Examples of two-dimensional presentations of the data of Figures 19 and 20 and  $F_{0.1}$  and  $F_{max}$  are presented in Figures 22 and 23. The shaded contours represent levels of SPR that decrease from upper left to lower right in the order 0.3, 0.2, 0.1, 0.05, and 0.01. The yield contours for the Fig. 22 increase from left to

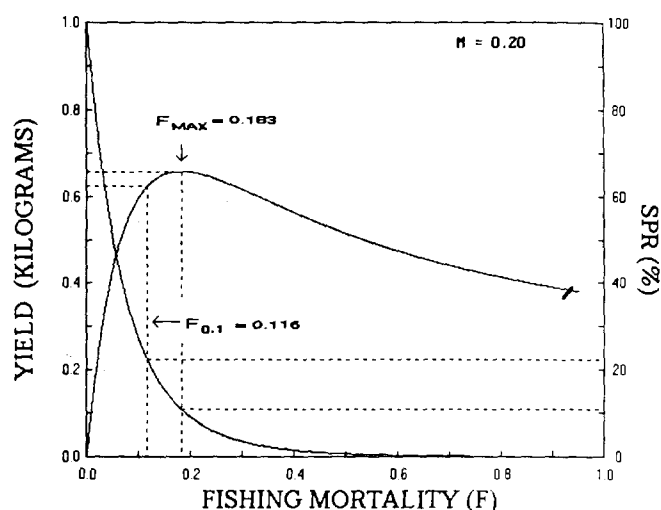


Fig. 21. Estimates of  $F_{max}$  and  $F_{0.1}$  for Gulf of Mexico red snapper and corresponding levels of SPR.

right and for Fig. 23 they increase toward the innermost concentric circle. For both figures the yield contours increase in the order 0.25, 0.50, 0.75, 0.9, 0.95 and 0.99 of the maximum yield attainable within the parameter space.

Experimentation with parameters from a number of stocks suggest that the 20–30% SPR contours often lie very near or slightly above profiles of fishing mortality rates that produce  $F_{0.1}$ . Consequently, selection of critical levels for SPR within this range often produce maximum to near maximum yield per recruit, and little biomass yield for each recruit will be lost by adopting SPR goals in this range. Inspection of the behavior of  $F_{0.1}$  and  $F_{max}$  in Figures 22 and 23 reveals a sometimes overlooked feature of their definitions: neither is a constant for the population. The values taken by both measures are functions of the distribution of fishing mortality among ages in the population. If this distribution changes because the fishery changes to target younger fishes because of declining stock, or if it changes because of conservation actions, the value of the measure shifts. Although commonly employed,  $F_{0.1}$  is a “backdoor” approach to preservation of spawning potential since it does not directly consider the spawners. Further, since the actual value of  $F_{0.1}$  depends on the characteristics of the fishery, it is not uniquely related to any attribute of the spawning potential of the stock. Any changes resulting from modifications of the selectivity of gears employed or caused by the imposition of conservation measures that affect the age distribution of the harvest will cause a change in the value of  $F_{0.1}$ . These changes are independent of their effect on the spawning potential of the stock. Deriso (1987) defined an optimal  $F_{0.1}$  as a combination of the size or age at entry of fish into a fishable population that maximizes the yield obtained from fishing at  $F_{0.1}$ . This value is unique for the simple yield-per-recruit theory in Beverton and Holt (1957). However it is not well suited to the management of fish stocks exposed to competing fisheries with different ages at entry and different objectives.

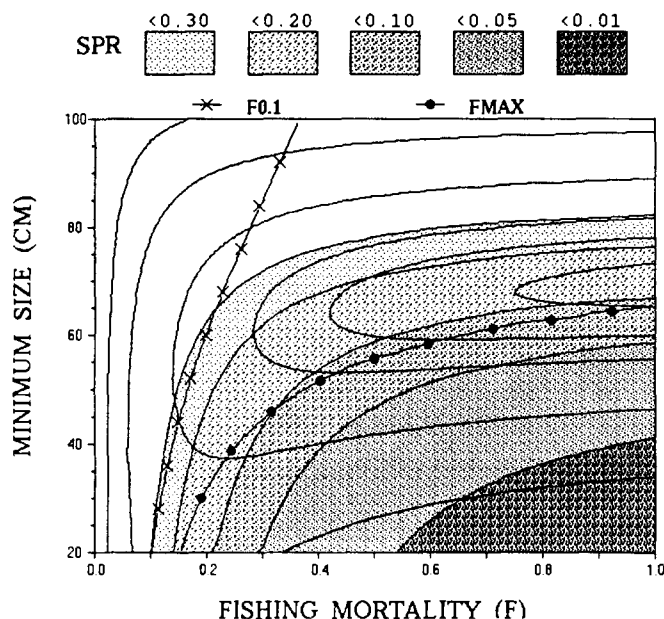


Fig. 22. SPR, yield per recruit,  $F_{\max}$  and  $F_{0.1}$  as a function of length at recruitment and fishing mortality for Gulf of Mexico red snapper assuming no fishing-induced mortality for sub-legal fish.

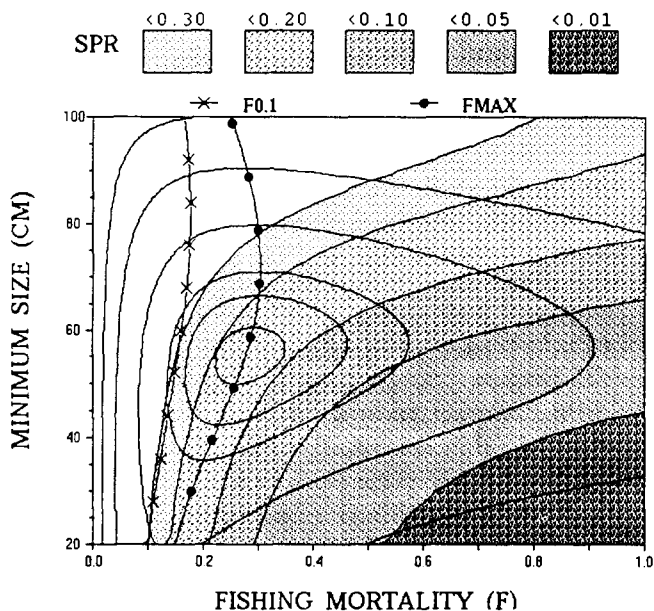


Fig. 23. SPR, yield per recruit,  $F_{\max}$  and  $F_{0.1}$  as a function of length at recruitment and fishing mortality for Gulf of Mexico red snapper assuming a 10% mortality for fish caught and released below the minimum size.

#### Optimal Spawning Stock

One possible biological objective for management is to manage fishing mortality so that the spawning stock is maintained at some particular absolute (non-zero) level. This option has the advantage that (if successful) it directly preserves the stock at a level at least equal to the objective. The level of the objective itself may be based on surplus production models, spawner recruitment models, or similar considerations. Inadequate data are a principal impediment to the application

of this approach for many stocks. However, where sufficient information is available and the population renewal processes conform adequately to the assumptions of such models, the level of spawning stock can be set to achieve maximum surplus production, which leads to such things as maximum sustainable yield, or other similar goal. Because the objective involves maintaining spawning stock at a constant level, successful implementation ensures stock persistence. Whether the yield is the maximum (or optimum) attainable from the stock depends upon the adequacy of the model and estimates of its parameters. If the assumptions are met, then managing for a spawning stock that produces the maximum average recruitment will maximize long-term yield (Reed 1979). Thus, managing for a fixed, optimum spawning stock in some fisheries may permit higher average yields than could be attained though a management scheme based on SPR.

#### Fixed Rate Criteria

Although fixed escapement policies have been shown to maximize yield for a large number of population models (Reed 1979), they are less frequently employed in fisheries management than other schemes, in part because they can result in large annual variations in allowable harvest. In contrast, fixed harvest rate policies allow more stable harvests so long as the rate is low enough to permit population persistence. Management based primarily on  $F_{\text{MSY}}$ ,  $F_{\text{rep}}$ ,  $F_{\max}$ ,  $F_{0.1}$ , or  $F_{\text{mmy}}$  (Clark 1991) are fixed rate policies.

Management based on SPR also employs the concept of a fixed rate and shares the good (and bad) attributes of such policies. SPR, however, differs from the other fixed rate approaches in that it is not defined in units of fishing mortality or associated yield. This is of no disadvantage since SPR can be readily evaluated for any realized ogive of fishing mortalities. However, it provides the advantage of separating harvest objectives from conservation objectives. This characteristic allows a unique value of SPR to be employed as a conservation standard without the prejudice of the nature of harvesting strategy subsumed by the definitions of  $F_{\text{MSY}}$ ,  $F_{\text{rep}}$ ,  $F_{\max}$ ,  $F_{0.1}$ , and  $F_{\text{mmy}}$ . The advantage to decoupling the conservation standard from the harvesting strategy becomes immediately apparent if there are several distinct fisheries competing for a resource. This is a common problem when there is competition between recreational and commercial fisheries. These fisheries often seek the same species with different gears, at different places, and at different ages. Further, their objectives tend to be quite different. Given estimates of each component's contribution to fishing mortality by age, it is possible to apportion realized SPR among the fisheries. Similarly it is possible for management to allocate fractions of the allowable reduction of SPR among the fisheries according to any desired scheme. Within that framework, each fishery could be managed according to harvesting strategies designed for that fishery. This approach provides a mechanism to avoid undesirable reallocations of allowable harvest by imposing regulations which unintentionally change the relative availabilities of legally harvestable fish among the fisheries.

## Current and Future Usage

The 1990 amendments to the Magnuson Fishery Conservation and Management Act (U.S. Congress 1990) required definitions for overfishing for each fishery management plan administered under its Authority. This action was intended to be risk-averse to avoid depletion of stocks. Most of the overfishing definitions submitted to date have been based on SPR, usually in the context of a percentage of the unfished SSB (Mace and Sissenwine 1993). The critical values are intended to be minimum acceptable levels above which stocks maintain acceptable productivity and have typically been set in the range of 0.2 to 0.3 primarily based upon the experience in the Northwest Atlantic. This approach to management is too recent to evaluate its ultimate utility based on its empirical track record. However, there is reason to believe that it will protect against stock depletion as well as any other approach so long as the critical levels are set within acceptable ranges. It also provides a straightforward basis for the evaluation of persistent non-fishing anthropogenic sources of mortality against the spawning stock objectives for managed fisheries. Given the tendency for adoption of SPR minima in definitions of overfishing in U.S. FMP's and elsewhere, the strengths and weaknesses of this criterion for management should become readily apparent. Its ultimate utility will probably be assessed in some future historical retrospective of how it fares in the context of actual management activities: the restoration of now depleted stocks and the continued productivity of those now robust.

## Acknowledgements

I thank Drs. B. E. Brown, J. E. Powers, M. L. Parrack, M. H. Prager, and N. B. Thompson for their helpful comments and suggestions.

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