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# Variability of Fishing Mortality by Age: Consequences for Maximum Sustainable Yield

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*Abstract.*—The influence of variation in age-specific vulnerability to fishing on maximum sustainable yield (MSY) in numbers and weight was evaluated with simulation techniques that incorporated biological characteristics of red snapper *Lutjanus campechanus* and an arbitrary stock–recruitment relation. I evaluated MSY for 10 arbitrary selectivity ogives that systematically varied from greater vulnerability to fishing mortality among the oldest ages to greater vulnerability among the youngest ages. The values of MSY in numbers and weight varied by factors of 2.6 and 4.5, respectively, for the range of selectivity schedules examined. Because selectivity schedules often are not constant through time, values estimated from catch data should be viewed with caution when they are applied in current management settings. Further, setting MSY as a management objective will often be insufficient for developing management advice unless the desired long-term age composition of the catch or some other qualifying factor is also specified. This is particularly true for the situation in which fisheries with inherently different selectivities compete for a resource, as is often the case when recreational and commercial interests are involved.

Nearly two decades have passed since Larkin presented "an epitaph for the concept of maximum sustained yield" (MSY) as the keynote address at the 1976 annual meeting of the American Fisheries Society (Larkin 1977). His commentary described how the many difficulties associated with the implementation of MSY make this biological reference point too dangerous to be adopted as a management objective. Although little has changed to lessen the wisdom of his remarks, MSY continues to play an important role in fisheries management, both as a biological reference point and as a management goal (Barber 1988), and the surplus production methods which provide most estimates of MSY are constantly being improved (Prager 1994). The simplicity of the MSY concept often endears it to both managers and fishermen who continue to promote its use. However, this apparent simplicity belies a more complicated reality in which the term can represent quantities that depend on one's background or perception. In particular, estimates of MSY from surplus production methods (e.g., Graham 1935; Schaefer 1957; Pella and Tomlinson 1969) may be far different from similar estimates drawn from stock–recruit methods (Beverton and Holt 1957; Ricker 1973), both in magnitude and in units, although both approaches involve similar assumptions about the existence of compensatory population processes that result in an equilibrium maximum productivity at some intermediate stock level.

Ricker (1975) defined MSY as "the largest average catch or yield that can be continuously taken from a stock under existing environmental conditions." Conceptually, MSY can be defined in units of weight or numbers. In units of weight, MSY would be achieved if one simultaneously maximized yield per recruit (YPR) from the yield-per-recruit curve and maximum excess recruitment (MER) from the relation of stock and recruitment. The MER in this context is the difference between recruitment and spawners at MSY (Ricker 1975: Appendix III, page 347). This maximization could theoretically be accomplished by harvesting *all* of the excess recruits at the instant natural mortality and growth were equal and the recruits achieved their maximum bulk (Ricker 1975). In this special case, the fishing mortality that maximizes yield per recruit ($F_{MAX}$) and the mortality that maximizes excess recruitment ($F_{MER}$) would be equal, only one age would be harvested, and all of the harvest would occur in the same instant. This strategy cannot generally be accomplished in fisheries on wild stocks, which catch many different ages because of gear limitations or other factors, and $F_{MAX}$ and $F_{MER}$ would be the same only by chance.

The array of fishing mortalities by age is often referred to as the schedule of fishing mortalities, and the relative susceptibilities of each age to fishing are denoted as the selectivity schedule. When used to determine the best minimum size or age to begin harvest in a particular fishery, yield-per-recruit analyses use the fact that changes in the selectivity schedule affect yield per recruit. All of





TABLE 1.—Red snapper relative mean fecundities, mean weights, and 10 arbitrary selectivities at age assumed in this analysis. The selectivity schedule refers to the relative susceptibilities of each age to fishing.

| Age | Relative fecundity | Weight (kg) | Selectivity schedule 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1 | 0.0000 | 0.03 | 0.008 | 0.042 | 0.097 | 0.097 | 0.179 | 0.269 | 0.424 | 0.730 | 0.942 | 1.000 |
| 2 | 0.0000 | 0.19 | 0.010 | 0.047 | 0.123 | 0.152 | 0.227 | 0.339 | 0.531 | 0.865 | 1.000 | 0.958 |
| 3 | 0.0047 | 0.54 | 0.015 | 0.058 | 0.138 | 0.178 | 0.269 | 0.463 | 0.695 | 0.973 | 0.947 | 0.878 |
| 4 | 0.0204 | 1.13 | 0.025 | 0.073 | 0.169 | 0.210 | 0.317 | 0.555 | 0.836 | 1.000 | 0.681 | 0.624 |
| 5 | 0.0468 | 1.87 | 0.026 | 0.105 | 0.215 | 0.257 | 0.381 | 0.672 | 0.938 | 0.941 | 0.425 | 0.354 |
| 6 | 0.0783 | 2.82 | 0.026 | 0.190 | 0.303 | 0.341 | 0.481 | 0.831 | 1.000 | 0.735 | 0.228 | 0.169 |
| 7 | 0.1257 | 3.85 | 0.032 | 0.296 | 0.407 | 0.432 | 0.624 | 0.926 | 0.996 | 0.459 | 0.116 | 0.084 |
| 8 | 0.1876 | 5.00 | 0.047 | 0.407 | 0.555 | 0.583 | 0.751 | 0.984 | 0.916 | 0.281 | 0.069 | 0.042 |
| 9 | 0.3190 | 6.17 | 0.074 | 0.534 | 0.602 | 0.715 | 0.868 | 1.000 | 0.743 | 0.189 | 0.042 | 0.021 |
| 10 | 0.4960 | 7.44 | 0.128 | 0.651 | 0.798 | 0.810 | 0.948 | 0.942 | 0.562 | 0.118 | 0.031 | 0.010 |
| 11 | 0.7222 | 8.63 | 0.192 | 0.757 | 0.872 | 0.894 | 0.989 | 0.815 | 0.407 | 0.086 | 0.021 | 0.010 |
| 12 | 0.8569 | 9.85 | 0.288 | 0.841 | 0.911 | 0.946 | 1.000 | 0.677 | 0.336 | 0.086 | 0.015 | 0.010 |
| 13 | 0.9216 | 11.01 | 0.374 | 0.905 | 0.973 | 0.978 | 0.984 | 0.571 | 0.283 | 0.086 | 0.015 | 0.010 |
| 14 | 0.9401 | 12.15 | 0.460 | 0.947 | 0.995 | 1.000 | 0.942 | 0.508 | 0.243 | 0.086 | 0.021 | 0.010 |
| 15 | 0.9539 | 13.16 | 0.529 | 0.979 | 1.000 | 0.973 | 0.862 | 0.444 | 0.216 | 0.086 | 0.021 | 0.010 |
| 16 | 0.9585 | 14.22 | 0.588 | 0.984 | 0.983 | 0.914 | 0.762 | 0.396 | 0.194 | 0.080 | 0.021 | 0.010 |
| 17 | 0.9631 | 15.11 | 0.652 | 0.989 | 0.973 | 0.832 | 0.682 | 0.375 | 0.185 | 0.075 | 0.015 | 0.010 |
| 18 | 0.9677 | 16.03 | 0.711 | 0.995 | 0.957 | 0.765 | 0.613 | 0.349 | 0.172 | 0.075 | 0.015 | 0.010 |
| 19 | 0.9723 | 16.88 | 0.770 | 0.995 | 0.946 | 0.709 | 0.555 | 0.328 | 0.168 | 0.075 | 0.015 | 0.010 |
| 20 | 0.9723 | 17.62 | 0.813 | 0.995 | 0.936 | 0.674 | 0.508 | 0.317 | 0.159 | 0.075 | 0.015 | 0.010 |
| 21 | 0.9769 | 18.26 | 0.850 | 0.995 | 0.920 | 0.627 | 0.481 | 0.306 | 0.150 | 0.075 | 0.015 | 0.010 |
| 22 | 0.9816 | 18.91 | 0.886 | 0.995 | 0.914 | 0.607 | 0.455 | 0.291 | 0.146 | 0.070 | 0.015 | 0.010 |
| 23 | 0.9862 | 19.44 | 0.920 | 0.995 | 0.909 | 0.587 | 0.444 | 0.280 | 0.146 | 0.070 | 0.015 | 0.010 |
| 24 | 0.9862 | 19.98 | 0.947 | 0.995 | 0.904 | 0.571 | 0.433 | 0.269 | 0.143 | 0.070 | 0.015 | 0.010 |
| 25 | 0.9862 | 20.53 | 0.962 | 0.995 | 0.899 | 0.556 | 0.428 | 0.254 | 0.141 | 0.070 | 0.015 | 0.010 |
| 26 | 0.9908 | 20.95 | 0.968 | 0.995 | 0.888 | 0.541 | 0.418 | 0.243 | 0.141 | 0.070 | 0.015 | 0.010 |
| 27 | 0.9954 | 21.38 | 0.973 | 1.000 | 0.883 | 0.530 | 0.412 | 0.238 | 0.137 | 0.070 | 0.015 | 0.010 |
| 28 | 0.9954 | 21.67 | 0.984 | 1.000 | 0.877 | 0.510 | 0.407 | 0.227 | 0.137 | 0.070 | 0.015 | 0.010 |
| 29 | 0.9954 | 22.10 | 0.989 | 1.000 | 0.872 | 0.510 | 0.396 | 0.227 | 0.132 | 0.064 | 0.015 | 0.010 |
| 30 | 1.0000 | 22.40 | 1.000 | 1.000 | 0.872 | 0.500 | 0.391 | 0.227 | 0.128 | 0.064 | 0.015 | 0.010 |

the biological reference points estimated for a stock with yield-per-recruit analysis (e.g., $F_{0.1}$ [the value of $F$ at which the slope of the yield-per-recruit is 10% of the slope at the origin] and $F_{MAX}$) are schedule-specific. This paper explores the relation between MSY and the underlying selectivity schedule with simulation techniques.

## Methods

The age-structured population model used in this analysis is of the form I used to characterize YPR for striped bass *Morone saxatilis* (Goodyear 1984), and it is described in detail elsewhere (Goodyear 1989). In the present analyses, I used biological characteristics estimated for Gulf of Mexico red snapper *Lutjanus campechanus* (Goodyear 1992) and an arbitrary Ricker stock–recruit relation in which recruitment is a function of population fecundity:

$$R = \alpha P \cdot \exp(-\beta P);$$

$R$ is recruitment in numbers of survivors at age 1, and $P$ is parental fecundity.

Natural mortality was 0.20 for all 30 ages represented in the model, and growth and fecundity were constant functions of age (Table 1). The slope at the origin of the stock–recruitment curve ($\alpha$, representing an unfinished stock) and the level of recruitment at MSY predicted from the stock–recruitment relation were arbitrarily set at 5 and 10, respectively. The size of the parental stock at MSY ($P_{MSY}$) that produced the recruitment at MSY ($R_{MSY}$) was estimated iteratively to within a tolerance of 0.01%, and the associated value of $\beta$ was calculated as

$$\beta = -\log_e(R_{MSY}/\alpha P_{MSY})/P_{MSY}.$$

When fishing mortality spans the spawning lifetime, actual recruitment at MSY depends on the outcome of the interaction between YPR and equilibrium recruitment in which some harvested fish have previously contributed to reproduction. In this situation, true $R_{MSY}$ would equal the value of $R_{MSY}$ calculated directly from the stock–recruitment relation only by chance. I numerically evaluated the actual $R_{MSY}$ by exploiting the ability to compute the equilibrium parental stock from the spawner–recruit relation, given knowledge of the

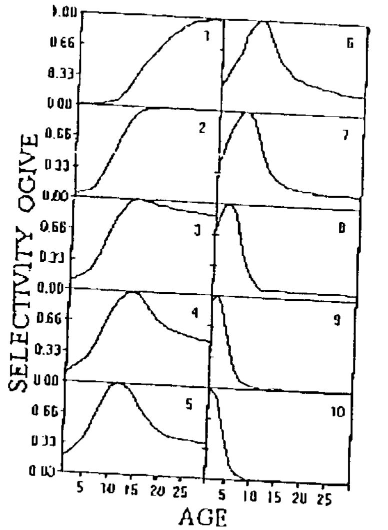


FIGURE 1.—Selectivity schedules for each of the 10 evaluations of maximum sustainable yield.

exploitation rate. Equation (20) of Ricker's (1975) Appendix III gives the rate of exploitation at MSY, and his equation (16) gives the number of spawners required to sustain an equilibrium rate of exploitation. His equations presume that exploitation precedes reproduction and that the fraction of recruits surviving to spawn at any rate of exploitation ($\mu$) is $1 - \mu$. The spawning potential ratio (SPR) of Goodyear (1993) is the multiple-age equivalent of $1 - \mu$ in Ricker's Appendix III. The SPR, the ratio of lifetime reproductive potential per recruit in fished versus unfished stocks, was used to estimate equilibrium parental fecundity ($P$) for the exploited state as

$$P = \log_e(\alpha \cdot \mathrm{SPR})/\beta.$$

Equilibrium recruitment is calculated by substituting this value of $P$ into the stock–recruitment curve.

The MSYs in weight ($MSY_W$) and numbers ($MSY_N$) were evaluated for 10 arbitrary selectivity schedules that varied systematically from greater vulnerability to fishing mortality among the older ages to greater vulnerability at younger ages, a trend that might occur as a stock is depleted by fishing over a period of time (Figure 1). The first step in evaluating MSY was to select an arbitrary value of fishing mortality ($F$) for the most vulnerable age-group. Second, the schedule of fishing mortalities for all ages was then computed as the product of $F$ and the selectivity schedule. Third, the stable age distribution of the harvested population was computed, and the corresponding value of SPR was derived. Fourth, equilibrium parental fecundity was computed from SPR. Fifth, equilibrium recruitment was computed from equilibrium parental fecundity.

The equilibrium recruitment value, together with the stable age distribution for the given fishing mortality vector, permit estimation of the equilibrium yield for any sustainable level of fishing mortality. The equilibrium yield corresponding to $R_{MSY}$ calculated directly from the stock–recruit relation was taken as the starting point for estimating MSY for each of the selectivity schedules. Through trial and error, it became evident that the value of $F$ that produced this initial equilibrium yield estimate fell at or below the value that produced $MSY_N$ and above the value which produced $MSY_W$. Consequently, I estimated $MSY_N$ by incrementally increasing the value of $F$ until the maximum was found. Similarly, I estimated $MSY_W$ by incrementally reducing the value of $F$ until the maximum was encountered. Both determinations were made with precision sufficient to ensure that estimates of MSY fell within 0.5% of their true values. Values of $F_{MSY}$ for weight and number of fish ($F_{MSYW}$ and $F_{MSYN}$) were calculated simultaneously with their respective yield counterparts. The MSY values of SPR were also estimated for each selectivity schedule evaluated. The numerical values of $F$ at MSY represent the annual fishing mortalities for the age-class(es) most vulnerable to fishing. For comparison, $F_{0.1}$ and $F_{MAX}$ from the yield-per-recruit curve were also estimated for each selectivity schedule with the same convention.

## Results

As expected, MSY in numbers and weight differed for each of the selectivity schedules (Figure 2). As the age of maximum vulnerability to the fishery decreased, $MSY_W$ decreased. For the particular selectivities evaluated here, the decrease was about 78%, from 9.4 to 2.1 (units are arbitrary). In comparison, maximum yield per recruit declined 76%, from 0.69 to 0.23 kg over the same range of selectivities. In contrast, the values of $MSY_N$ increased as the age of maximum vulnerability to the fishery decreased (Figure 2). The increase was about 2.6-fold, from 1.6 to 4.1 (units arbitrary). However, the proportional change was somewhat less than that observed for the variation in $MSY_W$.



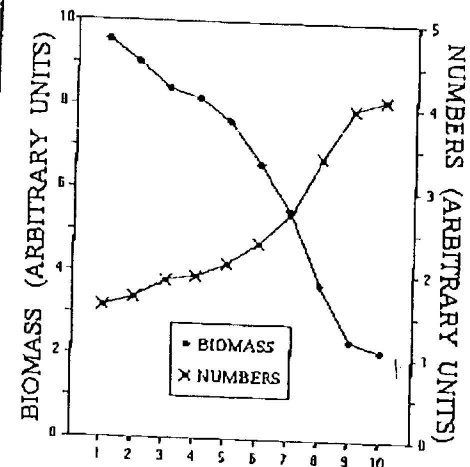


FIGURE 2.—Values of maximum sustainable yield in weight (biomass) and numbers for each of the 10 selectivity schedules in Figure 1.

Values of $F_{MSYW}$ and $F_{MSYN}$ for each of the selectivity curves are presented in Figure 3 and Table 2. For these simulations, $F_{MSYW}$ was always lower than $F_{MSYN}$, although for most of the selectivity schedules, the values were very similar. The trends in $F_{0.1}$ and $F_{MAX}$ with respect to the selectivity schedule were similar to those seen in $F_{MSYW}$ and $F_{MSYN}$ (Table 2). Indeed, each of these measures was highly correlated with each of the others (Table 2).

TABLE 2.—Instantaneous fishing mortality at selected biological reference points for each selectivity schedule included in the analysis and associated correlation matrix. The $F_{MSYN}$ is the value of $F$ that provides the maximum sustainable catch in numbers; $F_{MSYW}$ is the value of $F$ at maximum weight yield, $F_{0.1}$ is the value where the slope of the yield-per-recruit curve is 10% of that at the origin, and $F_{MAX}$ is the value of $F$ at which yield per recruit is maximum.

| Schedule or correlate | Sustainable yield | | Yield per recruit | |
|---|---|---|---|---|
| | $F_{MSYN}$ | $F_{MSYW}$ | $F_{0.1}$ | $F_{MAX}$ |
| | Instantaneous fishing mortality | | | |
| 1 | 1.743 | 1.142 | 0.481 | 2.783 |
| 2 | 0.329 | 0.259 | 0.234 | 0.597 |
| 3 | 0.235 | 0.198 | 0.193 | 0.385 |
| 4 | 0.219 | 0.181 | 0.197 | 0.359 |
| 5 | 0.173 | 0.147 | 0.174 | 0.285 |
| 6 | 0.140 | 0.124 | 0.163 | 0.244 |
| 7 | 0.134 | 0.121 | 0.166 | 0.235 |
| 8 | 0.162 | 0.146 | 0.194 | 0.261 |
| 9 | 0.226 | 0.203 | 0.262 | 0.352 |
| 10 | 0.241 | 0.220 | 0.281 | 0.380 |
| | Correlation matrix | | | |
| $F_{MSYN}$ | | 0.999 | 0.933 | 0.999 |
| $F_{MSYW}$ | | | 0.944 | 0.999 |
| $F_{0.1}$ | | | | 0.929 |

The SPR at $MSY_W$ tended to be slightly higher than the value that gave maximum excess recruitment from the stock–recruit curve (Figure 4). In contrast, SPR at $MSY_N$ tended to be slightly lower than either (Figure 4). However, inspection of the trend suggests (and experimentation confirmed) that if all of the exploitation occurs in prereproductive ages, the SPR at $MSY_N$ is equal to the value that gives $R_{MSY}$ estimated directly from the stock–recruit curve.

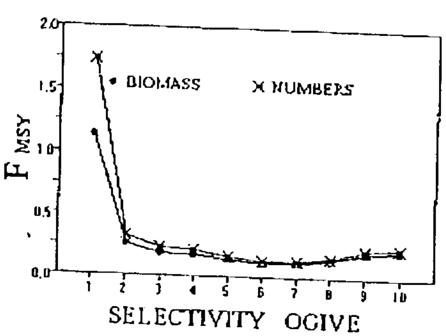


FIGURE 3.—Annual fishing mortality of the most vulnerable ages at maximum sustainable yield (MSY) in weight (biomass) and numbers for the 10 selectivity schedules of Figure 1.

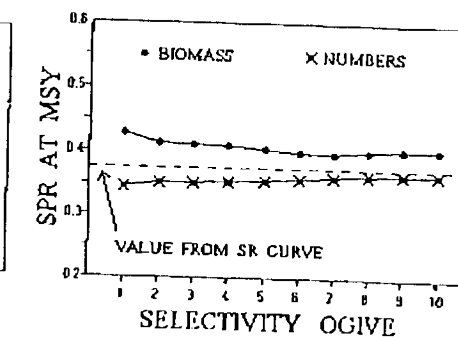


FIGURE 4.—Spawning potential ratio (SPR) at maximum sustainable yield (MSY) in weight (biomass) and numbers for each of the 10 selectivity schedules of Figure 1; SR is spawner–recruit.

## Discussion

The increase in $MSY_N$ that occurred with decreasing age of maximum susceptibility is a result of natural mortality. The absolute maximum yield in numbers would occur if it were possible to harvest all of the excess recruits at the instant they recruited to the fishery, before natural mortality could reduce their abundance. In contrast, $MSY_W$ involves both the number of fish harvested and their mean weight. Consequently, factors that favor increased yield per recruit also favor increased values of $MSY_W$. However, because $MSY_W$ is the maximization of the product of yield per recruit and recruitment, the level of fishing mortality that maximizes $MSY_W$ would be the same as $F_{MAX}$ only by chance. The high degree of correlation among the $F$ criteria in Table 2 is the result of the importance of the selectivity schedule to each of the measures. It suggests that $MSY_W$, $MSY_N$, $F_{MSYW}$, and $F_{MSYN}$ should be expected to be as variable as YPR, $F_{0.1}$, and $F_{MAX}$. These results suggest that the variability of $MSY_W$ for a given stock is largely a function of factors influencing yield per recruit, whereas the scale is largely a function of the stock–recruitment relation.

Estimates of MSY derived from yield and effort data with surplus production methods implicitly assume constant selectivities for the period of the data. Although it might be possible to construct proofs that such MSY estimates are robust if the selectivities exhibited some mean behavior or were functionally related to stock productivity, consideration of the robustness of MSY estimation is beyond the scope of this paper. However, such estimates are clearly unlikely to represent the absolute maximum sustainable yield that a stock could support but instead represent the maximum yields that can be sustained if the characteristics of the fishery continue unchanged from historical conditions. Consequently, the adoption of estimates derived from time series data for use in current management settings must be done with caution unless there is reason to believe that the selectivity patterns that existed in the historical fishery will continue to exist under all future conditions.

These results probably will not surprise analysts who have conducted investigations involving estimates of MSY. However, they should help clarify, for those who wish to promote the use of MSY, that the mere selection of MSY as a management goal will often be insufficient. Maximum sustainable yield is not a unique quantity but depends on how the stock is exploited. Size limits and gear, seasonal, areal, or other restrictions are all likely to change the age distribution of fish in the harvest and associated fishing mortalities. Likewise, changes in the relative abundances of harvestable ages in the population are likely to alter fishing practices to favor harvest of those cohorts of high abundance. Under each of these circumstances, MSY will be different.

One objective of the Magnuson Fishery Conservation and Management Act (U.S. Congress 1990) is to achieve "on a continuing basis, the optimum yield from each fishery for the United States fishing industry," or more simply, optimum sustainable yield (OSY). Although the intent of the language is clear, it provides little guidance for an operational definition to evaluate the performance of management or the condition of the fishery. The results of this analysis demonstrate that MSY is not a unique value, and the simple substitution of M for the O in OSY will often not provide a more precise operational definition of a management objective than is embodied in the concept of OSY itself. This is particularly true for situations like those that exist for Gulf of Mexico red snapper. The selectivity schedules for the commercial and recreational fisheries competing for this resource are widely disparate and continue to be modified by minimum size and other regulations and increasing abundances of once-depleted ages (Goodyear 1992). Indeed, from a practical standpoint, there may be no such thing as MSY for fisheries in which selectivities are randomly varying functions of human behavior. It is however, possible to evaluate the consequences of alternative selectivity schedules and select those that will maximize yield or other benefit. This will require that the management process clearly specify quantifiable objectives, particularly when inherently different fisheries are competing for the same resource.

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