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Scientific Review of Definitions of Overfishing in U.S. Fishery Management Plans

Supplemental Report

Prepared for the National
Marine Fisheries Service by

P. Mace, L. Botsford
J. Collie, W. Gabriel, P. Goodyear,
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U.S. Department of Commerce
National Oceanic and Atmospheric Administration
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NOAA Technical Memorandum NMFS-F/SPO-21
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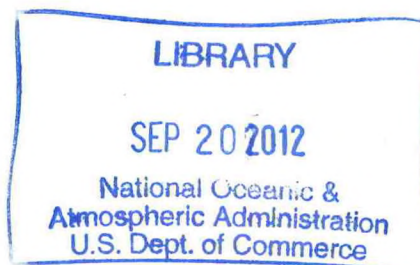
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U.S. Department of Commerce
Michael Kantor, Secretary

National Oceanic and Atmospheric Administration
D. James Baker, Under Secretary for Oceans and Atmosphere

National Marine Fisheries Service
Rolland E. Schmitten, Assistant Administrator for Fisheries



A. Introduction

This Supplemental Report extends the original report of the NMFS "Scientific Review of Definitions of Overfishing in U.S. Fishery Management Plans." Conclusions reported here are the result of an additional three day meeting involving many of the original Review Panel members, held in February 1996. The purpose of the supplemental meeting was to review a class of biological reference points, often referred to as non-equilibrium measures of spawning potential ratio, that have been proposed and used to measure current stock status with respect to overfishing. These measures, described below, are commonly used as reference points for fisheries in the southeastern U.S. (e.g. for red snapper and mackerel), but were inadvertently omitted from the original review of definitions of overfishing.

The Review Panel investigated several measures which index the condition of the resource in terms of relative spawning potential. The next section discusses terminology and describes the measures considered. This is followed by example calculations for simulated and real fish stocks. The report concludes with a series of conclusions and recommendations pertaining to the utility of the measures.

B. Definitions and Terminology

The acronym, SPR, has been used to represent both Spawning Potential Ratio and Spawning (biomass) Per Recruit. As implied by its name, the spawning potential ratio is a relative measure. It expresses the spawning production of a fished population relative to the spawning production of an unfished population with otherwise similar characteristics. By contrast, spawning per recruit is an absolute measure (usually expressed in units of weight or numbers of eggs), intended to be analogous to yield per recruit (YPR). Spawning per recruit is converted to a relative measure by dividing by the maximum spawning per recruit, which occurs under conditions of no fishing, and expressing the result as a percentage. Relative spawning per recruit is commonly abbreviated as %SPR. Thus, spawning potential ratio is usually measured on a scale of 0 to 1 while % spawning per recruit is expressed as a percentage. Use of proportions or percentages in FMP overfishing definitions, in the scientific literature, and even in this report may not be consistent, but it is usually clear which one is being used because %SPR levels less than 1% are rarely considered.

A much more fundamental point of departure between the two SPR measures is that % spawning per recruit is a static measure while spawning potential ratio is a transitional measure. Although the conceptual foundation for the two measures is similar, there are differences in methods of calculation and in the interpretation of results. For spawning per recruit (static measure), the reference points are calculated from a standard (Beverton-Holt) "spawning per recruit analysis" which is analogous to the familiar yield per recruit analysis, and uses exactly the same inputs (e.g. constant weights at age, a constant natural mortality vector, and a constant fishing mortality vector), with the addition of a constant maturity ogive. For the spawning potential ratio (transitional measure), the reference points are

calculated from empirical estimates of population numbers and fishing mortalities by age and year derived from age-structured stock assessments. With the exception of some of the work conducted by Goodyear (1980, 1993; see original report of the NMFS Overfishing Definition Review Panel), virtually all of the theoretical development and empirical analyses of SPR reference points relate to the static approach, for which each level of SPR (or %SPR) corresponds directly to a unique level of fishing mortality (for a given selectivity ogive).

In this supplemental report, the acronym "SPR" is always preceded by the terms "static," "static %," or "transitional," to differentiate between the alternative interpretations.

The Review Panel considered two primary measures of transitional SPR: the spawning production in year t relative to that which would have been produced in year t if there had been no fishing on the cohorts that exist in year t ; and the spawning production per recruit in year t relative to that which would have been produced in year t if there had been no fishing on the cohorts that exist in year t (called SPR1 and SPR2, respectively, by Powers MS). These measures have been variously referred to as "non-equilibrium," "dynamic," and "transitional." The Review Panel preferred the latter terminology and has used it consistently from here on. SPR1 is referred to as the weighted transitional SPR (where the weighting is by year class strength); while SPR2 is referred to as the unweighted transitional SPR, or simply transitional SPR. Similarly, "static %SPR" has frequently been referred to as "equilibrium %SPR," but since equilibrium conditions are not essential for the measure to be valid, the Review Panel preferred the term "static." The word "static" refers to the underlying assumption that growth rates, maturity schedules, natural mortality, fishing mortality, and selectivity patterns are constant; however, recruitment itself need not be constant.

Equations for static and transitional SPR are given below, using the following notation:

- t = year
- r = age of recruitment into the fishery
- G = maximum age of fish in the stock
- $N_{i,t}$ = number of fish of age i at the beginning of year t
- $P_{i,t}$ = per capita reproductive output of fish of age i at the beginning of year t
(measured in egg mass per female or suitable proxy; most commonly expressed as average weight of fish of age i in year t multiplied by average proportion mature of age i in year t)
- $M_{i,t}$ = natural mortality rate of fish of age i during year t
- $F_{i,t}$ = fishing mortality rate of fish of age i during year t
- $Z_{i,t}$ = total mortality rate of fish of age i during year t ($= F_{i,t} + M_{i,t}$).

Static %SPR

$$\text{Static \%SPR}_t = \frac{\sum_{i=r}^G \left\{ P_{i,t} \prod_{\substack{j=r \\ i \neq r}}^{i-1} [\exp(-Z_{j,t})] \right\} \cdot 100\%}{\sum_{i=r}^G \left\{ P_{i,t} \prod_{\substack{j=r \\ i \neq r}}^{i-1} [\exp(-Z_{j,t})] \right\}}$$

Unweighted transitional SPR

$$\text{SPR2}_t = \frac{\sum_{i=r}^G \left\{ P_{i,t} \prod_{\substack{j=r \\ i \neq r}}^{i-1} [\exp(-Z_{j,t+i+j})] \right\}}{\sum_{i=r}^G \left\{ P_{i,t} \prod_{\substack{j=r \\ i \neq r}}^{i-1} [\exp(-Z_{j,t+i+j})] \right\}}$$

Weighted transitional SPR

$$\text{SPR1}_t = \frac{\sum_{i=r}^G \left\{ N_{r,t+i+r} P_{i,t} \prod_{\substack{j=r \\ i \neq r}}^{i-1} [\exp(-Z_{j,t+i+j})] \right\}}{\sum_{i=r}^G \left\{ N_{r,t+i+r} P_{i,t} \prod_{\substack{j=r \\ i \neq r}}^{i-1} [\exp(-Z_{j,t+i+j})] \right\}}$$

During Review Panel deliberations, several other measures that are related to transitional SPR to varying degrees were developed. The only one of these discussed in detail was the spawning exploitation rate (SER), which expresses the amount of fishing on the spawning population in a given year, on a consistent scale from year to year (Thompson MS). Specifically, SER is the relative amount of spawning that is foregone during the next spawning cycle as a result of fishing; i.e. 1 minus the amount of spawning that will take place during the next spawning cycle divided by the amount of spawning that would take place if there were no fishing at all. SER and several other related measures are described in the Appendix, using the common currency of foregone reproduction.

C. Simulation Models

Several hypothetical numerical simulations were conducted to examine the dynamics of the weighted and unweighted transitional SPRs in relation to the static %SPR and in relation to spawning biomass and recruitment. The first set considered deterministic results for the hypothetical population used by Powers (MS), which was patterned after king mackerel populations. The population consisted of 30 ages with the youngest partial recruitment into the fishery at age 1. Natural mortality rate was assumed equal to 0.2, growth was governed by a von Bertalanffy equation, age of maturity was set at 5 years, and recruitment was modeled using a Beverton-Holt relationship. Partial recruitment for ages 1-6+ was assumed to be 0.1, 0.3, 0.2, 0.5, 0.7 and 1.0, respectively. Fully-recruited fishing mortality was assumed to be $F=0.07$ for 1940-59, $F=0.15$ for 1960-79, $F=0.35$ for 1970-79, $F=0.65$ for 1980-86, $F=0.2$ for 1987-91, $F=0.25$ for 1992-1999, and $F=0.3$ for 2000-2010.

Trajectories of spawning biomass, recruitment, and static and transitional SPR are presented for two periods: a phase of declining recruitment, occurring over the earlier period when fishing mortality was increasing, thus resulting in decreased spawning biomass (Figure S1); and a phase of increasing recruitment, occurring over the later period when fishing mortality declined, thus allowing the spawning stock to rebuild (Figure S2). In both cases, the unweighted and weighted SPR converged to the static %SPR. The differences between the weighted and unweighted SPR were not large, except that the weighted would usually take longer to converge to the static %SPR. Similar conclusions were drawn from deterministic simulations using red snapper-like data ($M=0.2$, relatively long-lived) presented at the supplemental overfishing review panel meeting, but not included here.

Another simulation was conducted for a hypothetical highly variable population (Figure S3). The population was characterized by stochastic recruitment with a CV of 50%, a high natural mortality rate ($M=0.6$), and low age of first maturity (2 years). The stochastic realization indicated that the unweighted transitional SPR converged to the static %SPR very quickly (1 or 2 years for fished populations). The weighted transitional SPR converged stochastically (the mean value was approximately the same as the static %SPR), but there were often large fluctuations in the weighted SPR from one year to the next due to the recruitment fluctuations.

The implications of these results is that the transitional SPRs may indeed reflect the transition from one fishing mortality regime to another, and that they measure the foregone reproduction as it passes through the age structure. However, fluctuations in the weighted transitional SPR caused by variations in recruitment may make it more difficult to interpret and to implement as a measure of the status of the stock relative to an overfishing definition. In addition, the models used above incorporate environmental effects only as random variation around a specified stock-recruitment relationship. Even without large inter-annual fluctuations in recruitment, certain systematic trends related to environmental effects not incorporated in stock-recruitment relationships (e.g. recruitment declining even while fishing

pressure is being reduced) can lead to situations where the unweighted and weighted transitional SPR are not as strongly correlated with spawning biomass as they were for the simulations summarized in Figures S1 and S2. For example, if recruitment declines even while fishing pressure is being simultaneously reduced, it is possible to obtain an inverse correlation between spawning biomass and the unweighted or weighted transitional SPR. This is illustrated in Figure S4 for a simulated population with $M=0.3$; weights at age calculated from a von Bertalanffy growth function with a Brody growth coefficient of 0.2 and an exponent of 3; partial recruitment (combined effect of selectivity and fish availability) at age of 0.2, 0.5, 0.8 and 1 for ages 1, 2, 3 and 4+, respectively; proportion mature at age of 0, 0.5, 0.8 and 1 for ages 1, 2, 3 and 4+, respectively; and the recruitment and fishing mortality time series given with the figure (note that while the size of the spawning stock depends on the sizes of relevant recruitments, the reverse was not assumed; i.e. the recruitment time series was not generated from a stock-recruitment relationship). Of course, the static %SPR does not correlate well with spawning biomass either; however, this is to be expected since static %SPR is purely a measure of fishing mortality.

Deterministic Bev-Holt S-R, decreasing recruitment

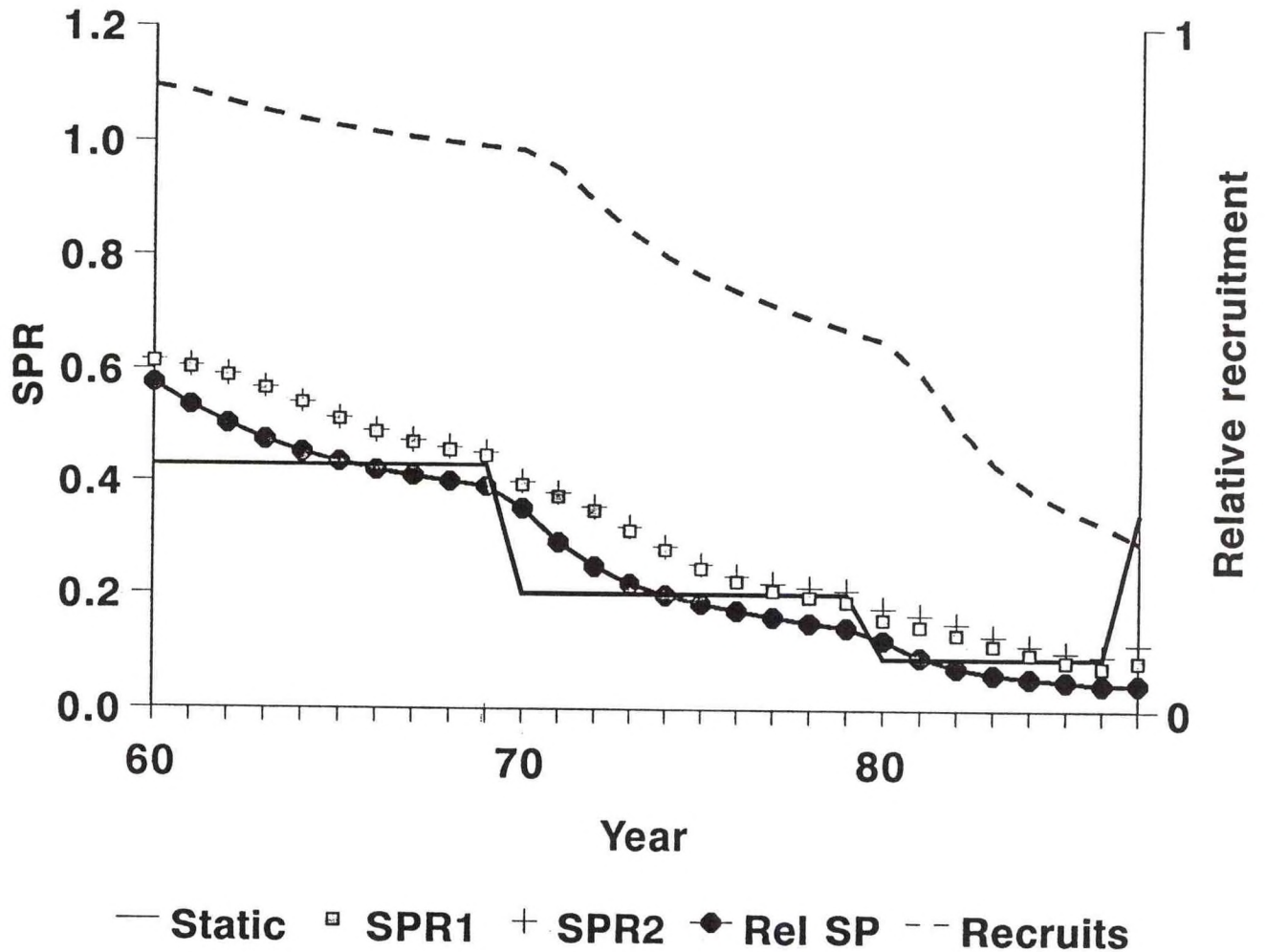


Figure S1. Comparisons of static %SPR, weighted transitional SPR, unweighted transitional SPR, relative spawning biomass, and relative recruitment for a simulated deterministic population experiencing increasing fishing mortality, which in turn resulted in declining spawning biomass and declining recruitment (see text for simulation inputs).

Deterministic Bev-Holt S-R, increasing recruitment

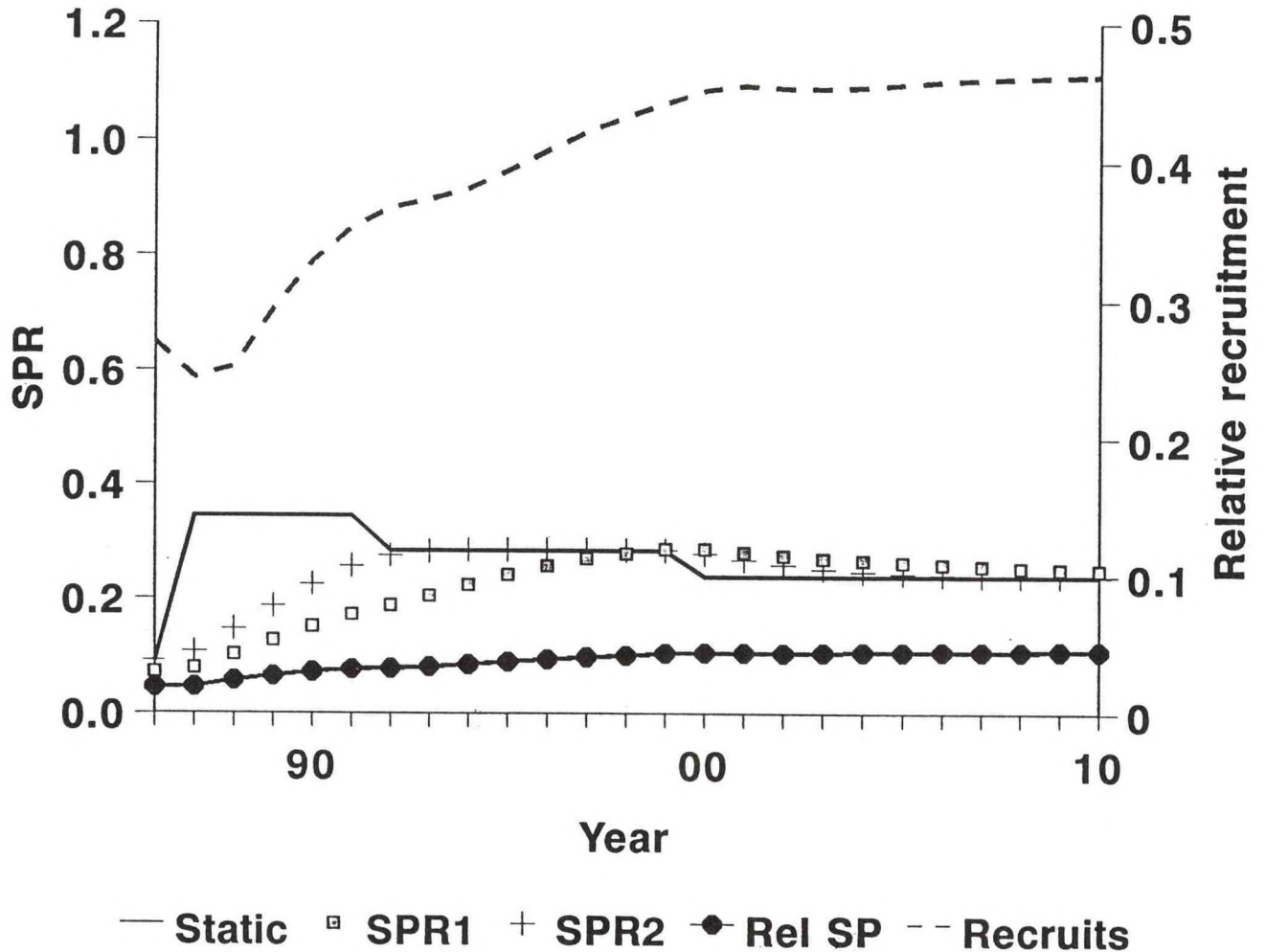


Figure S2. Comparisons of static %SPR, weighted transitional SPR, unweighted transitional SPR, relative spawning biomass, and relative recruitment for a simulated deterministic population that has recently experienced increasing fishing mortality, which in turn resulted in increasing spawning biomass and increasing recruitment (see text for simulation inputs).

Stochastic Bev-Holt S-R, High M

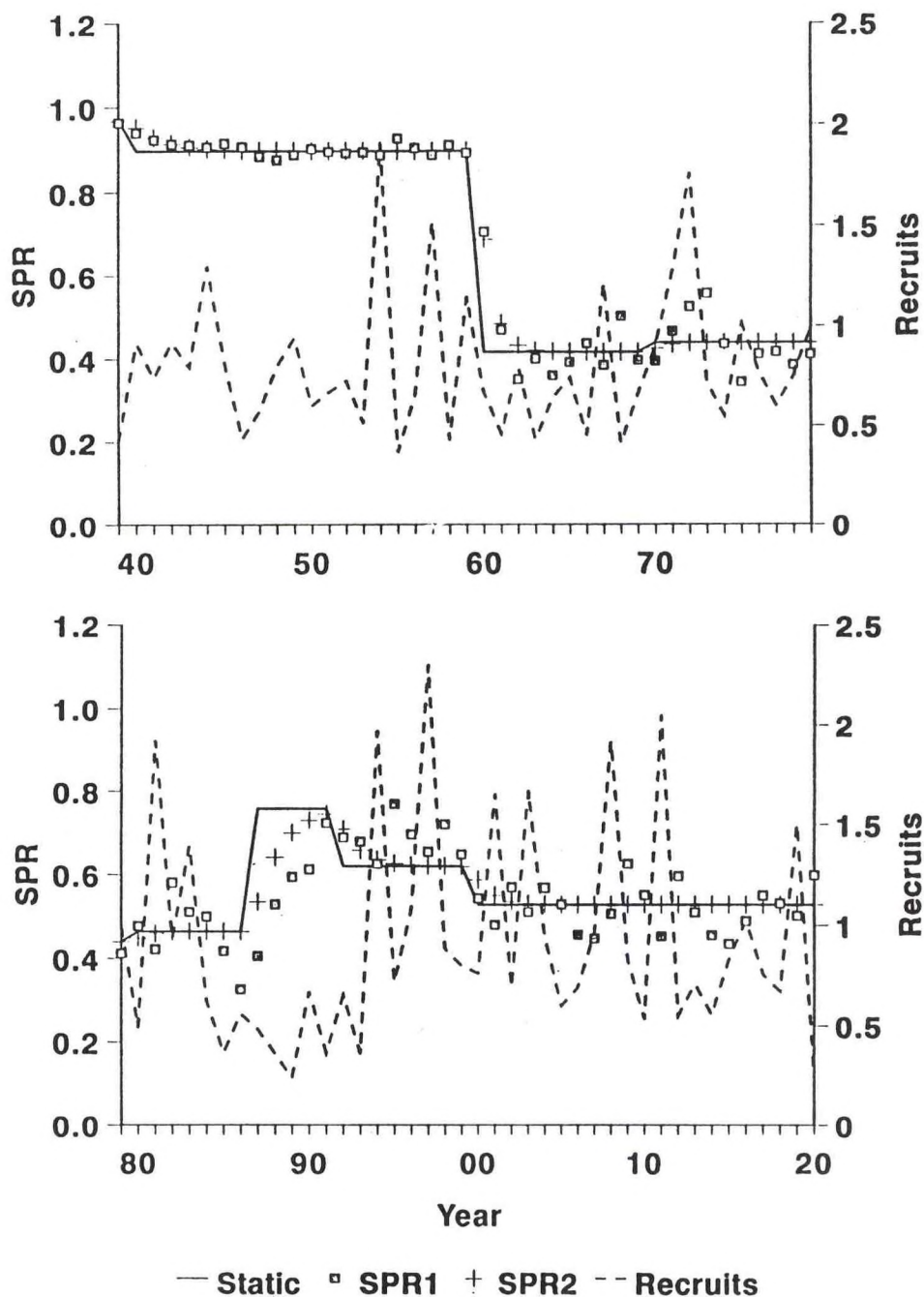


Figure S3. Comparisons of static %SPR, weighted transitional SPR, unweighted transitional SPR, and relative recruitment for a simulated population with stochastic recruitment with a CV of 50%, a high natural mortality rate ($M=0.6$), and low age of first maturity (2 years).

<u>Year</u>	<u>Recruitment</u>	<u>F</u>
1960	30,000	0.3
1961	30,000	0.3
1962	30,000	0.3
1963	30,000	0.3
1964	30,000	0.3
1965	30,000	0.3
1966	30,000	0.3
1967	30,000	0.3
1968	30,000	0.3
1969	30,000	0.3
1970	30,000	0.3
1971	30,000	0.3
1972	30,000	0.3
1973	30,000	0.5
1974	30,000	0.5
1975	30,000	0.5
1976	30,000	0.5
1977	30,000	0.5
1978	30,000	0.5
1979	25,000	0.5
1980	25,000	0.5
1981	20,000	0.1
1982	20,000	0.1
1983	15,000	0.1
1984	15,000	0.1
1985	12,000	0.1
1986	12,000	0.1
1987	10,000	0.1
1988	10,000	0.1
1989	8,000	0.1
1990	8,000	0.1
1991	6,000	0.1
1992	6,000	0.1
1993	6,000	0.1
1994	6,000	0.1
1995	6,000	0.1

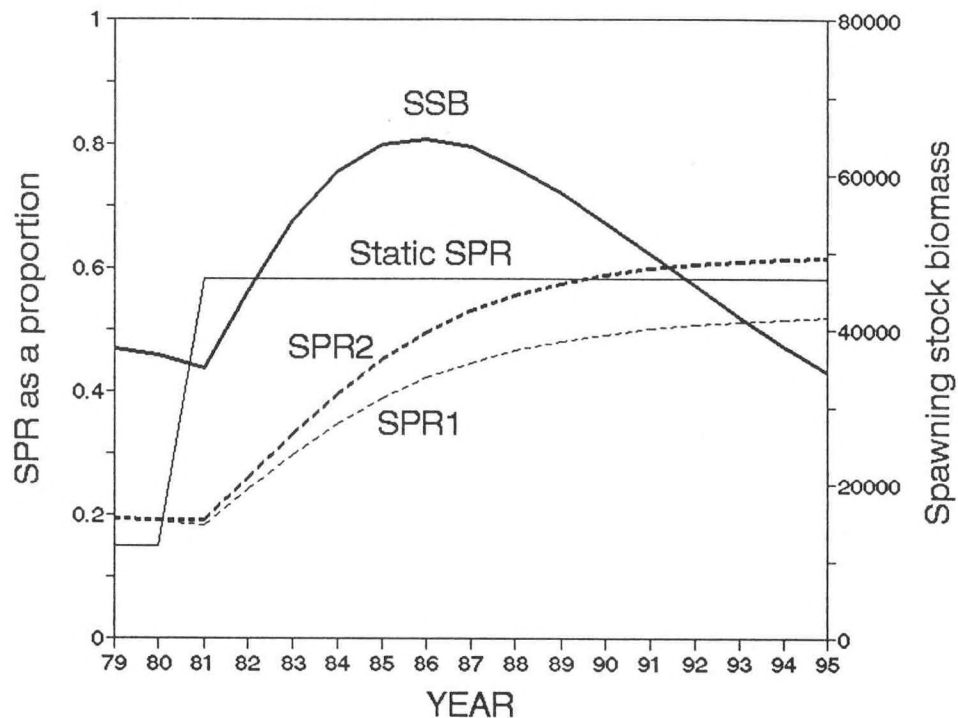


Figure S4. Relationship between static %SPR, unweighted transitional SPR (SPR2), weighted transitional SPR (SPR1) and spawning stock biomass (SSB), for the case where recruitment (R) and fishing mortality (F) are declining simultaneously (i.e. recruitment is (temporarily) not related to stock size by a traditional stock-recruitment relationship).

D. Empirical Examples

Weighted and unweighted transitional SPR measures were calculated for two empirical examples: southern New England yellowtail flounder and Georges Bank haddock. The data used were not necessarily derived from the most recent peer-reviewed assessment, and therefore may not correspond exactly with recent assessment results.

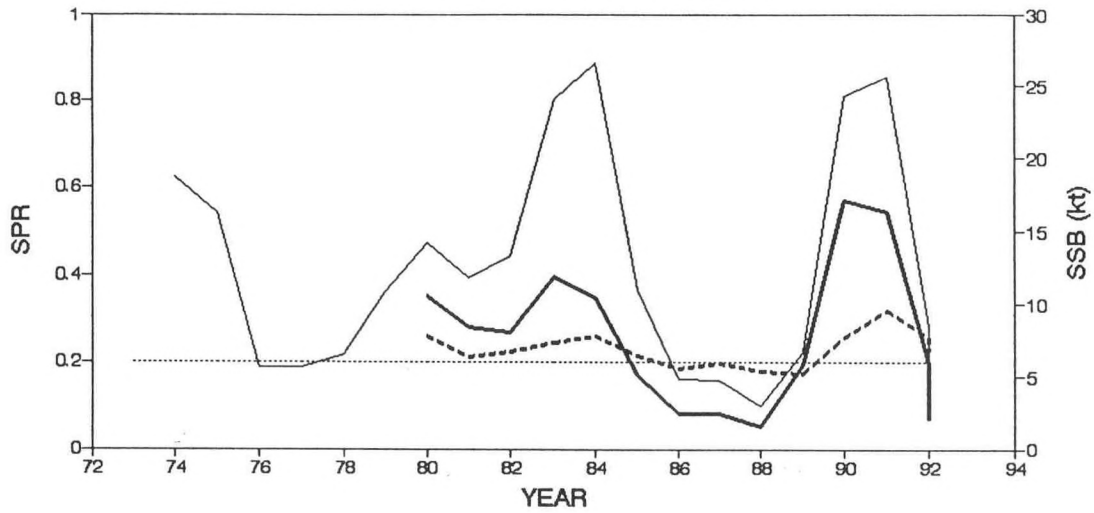
(i) Southern New England Yellowtail flounder

The weighted transitional SPR (SPR1), unweighted transitional SPR (SPR2), and spawning stock biomass (SSB) were calculated for southern New England yellowtail flounder using 7 or 15 age classes, with the oldest age (A_{\max}) comprising a plus group (Figure S5). This example illustrates two effects of the number of ages used: (i) the larger the number of ages, the fewer the number of years for which SPR1 and SPR2 can be calculated (because cohorts need to have been fished for at least [A_{\max} - age of recruitment + 1] years in order for all required cells to be filled), and (ii) increasing the number of ages results in substantial declines in the absolute values of SPR1 and SPR2 (because the denominators [zero fishing] increase with increasing numbers of ages, although they eventually converge at about $\log_e 100/M$). In this example, it also appears that SPR1 tracks biomass reasonably well. Absolute values of SPR1 and SPR2 can sometimes differ considerably.

(ii) Georges Bank haddock

The spawning exploitation ratio (SER), weighted transitional SPR (SPR1), unweighted transitional SPR (SPR2), and spawning stock biomass (SSB) were calculated for Georges Bank haddock using 15 age classes (Figure S6). This example illustrates that SPR1 is sensitive to biomass, while SPR2 is not. It also shows that the absolute values of the two indices can be quite different; for this particular example, SPR2 is almost invariably larger than SPR1, sometimes by as much as 2.5-fold. Relative to a particular overfishing threshold (e.g. $SPR = 0.3$), SPR2 would indicate that the stock was/is in much better condition than would SPR1. However, neither of the indices reflect the fact that spawning stock biomass is considered to be severely depleted relative to levels that existed from at least 1930 to 1960 (generally ranging between 100,000 and 150,000 mt). It is also interesting to note that sudden increases in spawning biomass (e.g. in 1965/66 and 1977-80) appear to have been accompanied by large increases in SER (annual exploitation rate for the spawning component of the population).

Southern New England Yellowtail Flounder (7 ages)



Southern New England Yellowtail Flounder (15 ages)

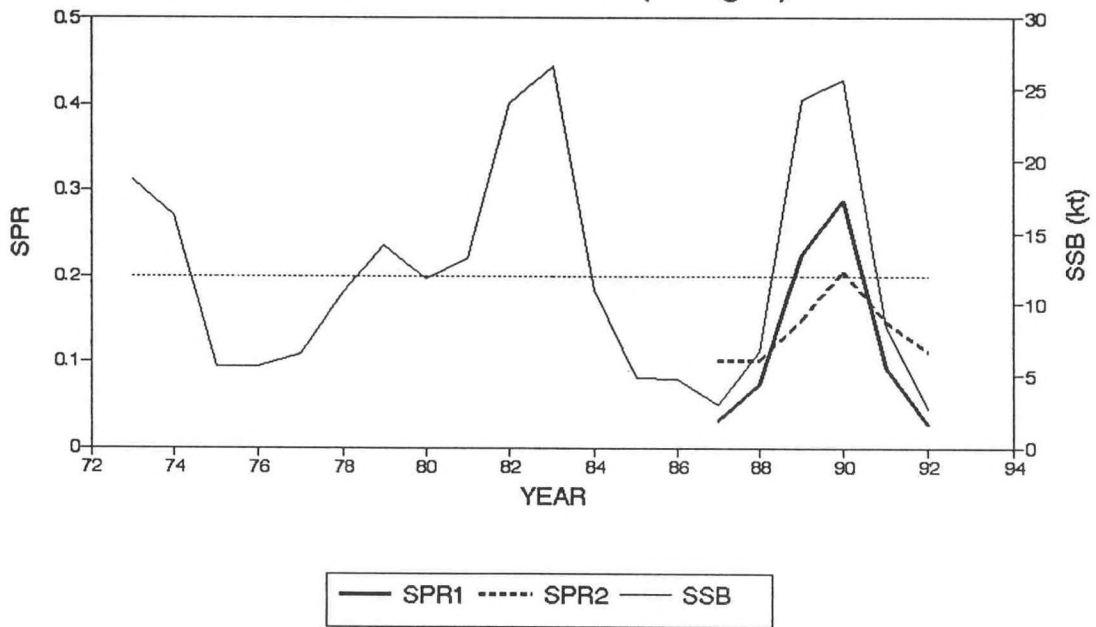


Figure S5. Comparisons between unweighted transitional SPR (SPR2), weighted transitional SPR (SPR1) and spawning stock biomass (SSB) for southern New England yellowtail flounder.

Georges Bank Haddock

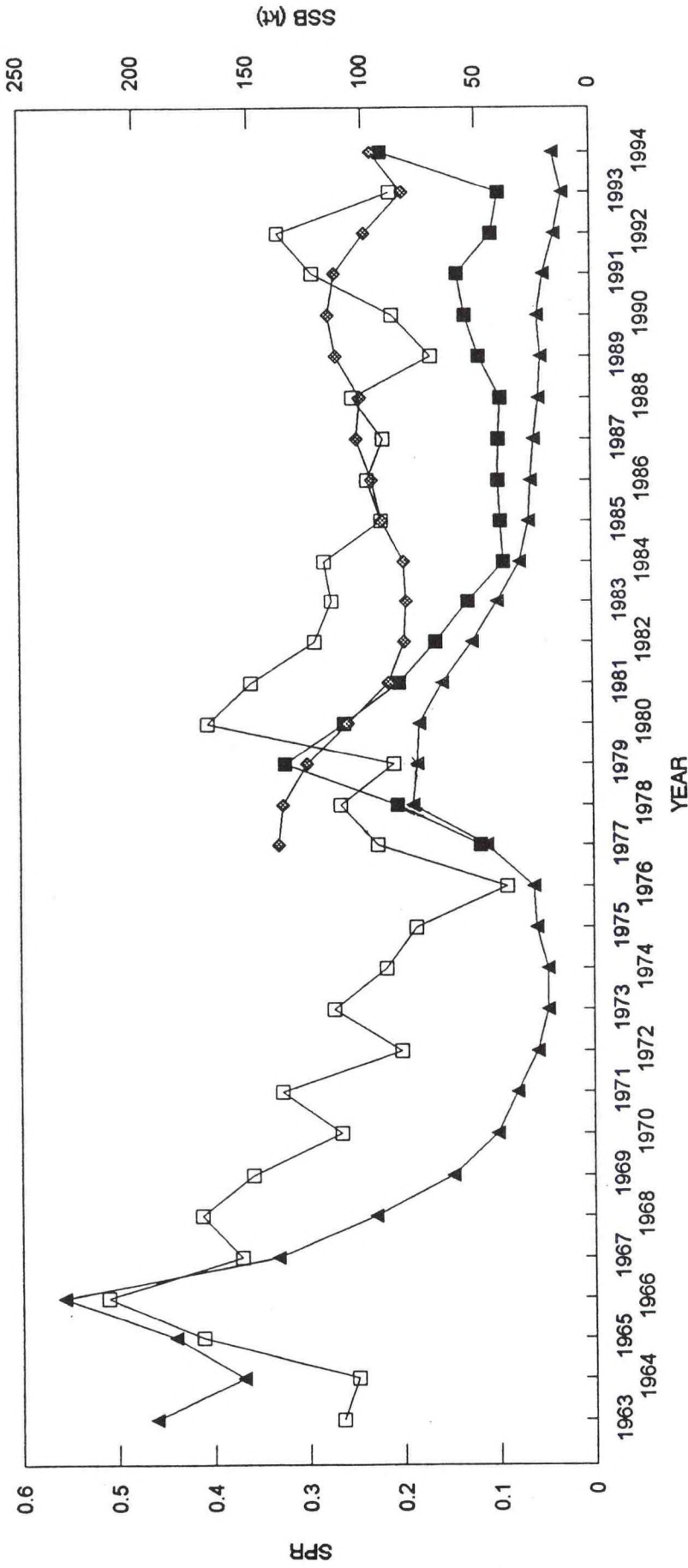


Figure S6. Comparisons between unweighted transitional SPR (SPR2), weighted transitional SPR (SPR1), spawning exploitation ratio (SER) and spawning stock biomass (SSB) for Georges Bank haddock.

E. Conclusions and Recommendations

(i) Spawning Exploitation Rate (SER)

The spawning exploitation rate (Thompson MS; equation also given in the Appendix) expresses the amount of fishing on the spawning population in a given year, on a consistent scale from year to year. As such, it is a useful alternative to quantities like fully-recruited fishing mortality or other reference levels of fishing mortality, which may not be strictly comparable from year to year due to changes in selectivity patterns. SER should be particularly useful for stocks with partial recruitment patterns that are not flat-topped. It is not directly related to static %SPR or transitional SPR because it compares the results of fishing this year to no fishing this year, not no fishing ever.

(ii) Static %SPR

The static %SPR (sometimes referred to as an equilibrium SPR, although its application need not be limited strictly to equilibrium conditions) was one of the focal points for discussion in the original Review Panel report. The interpretation of this measure is simple and unambiguous. It is the amount of spawning (measured as egg production or spawning biomass) per recruit for one or more cohorts fished using a constant fishing mortality pattern (constant selectivity combined with constant reference fishing mortality) throughout their lifespans, relative to the amount of spawning that would have occurred if there had been no fishing. While it assumes stationarity in terms of growth rates and mortality and maturity schedules, it does not require that recruitment be constant. For a given selectivity pattern, static %SPR maps 1:1 with fishing mortality. Thus, it can be used as a measure of the act of *overfishing*; i.e. it is a measure of the outcome obtained by repeatedly applying a particular fishing mortality rate.

(iii) Transitional SPR

Transitional SPR (SPR2 in Powers, MS; original derivation and discussion in Goodyear 1980, 1993) represents a straightforward extension of static %SPR that corresponds conceptually (although not mathematically) to a running average of fishing mortality rates. Transitional SPR is particularly useful in the context of rebuilding plans because it is tied to an implicit rebuilding target rather than an absolute biomass target which may be difficult to specify. If, for example, the rebuilding target was 20% SPR, then use of the static %SPR would imply that all that was necessary for "recovery" to have occurred would be for the fishing mortality to dip below $F_{20\%}$ in a single year, whereas use of the transitional SPR would imply that "recovery" will not have occurred until the negative effect of past high fishing mortality rates has been eliminated. Essentially, the aim is to rebuild the age structure of the stock.

In addition, if recruitment varies around a stock-recruitment relationship (i.e. does not exhibit systematic trend; independent of stock size), then a stock fished continuously at $F_{20\%}$

should eventually recover (or decline) to the biomass associated with $F_{20\%}$. Note, however, that when recruitment exhibits systematic trends independent of stock size, trends in transitional SPR do not necessarily reflect realized trends in spawning biomass (see Figure S4). In both cases, the transitional SPR indicates how close the age structure of the stock is to being rebuilt (even though the rebuilding target is expressed in relative rather than absolute terms). If fishing mortality is constant at $F_{20\%}$, then it will take one reproductive generation time (maximum age minus age of recruitment) to rebuild the age structure.

(iv) Weighted transitional SPR

The weighted transitional SPR (SPR1 in Powers, MS) is not strictly analogous to static %SPR or transitional SPR, since it is not measured on a per recruit basis (i.e. it is sensitive to year class size). It is essentially the realized reproduction in a given year as a fraction of the maximum reproduction which would have been realized if existing cohorts had never been fished. Although conceptually appealing, interpretation of this index is not straightforward. It is not simply an index of historical fishing mortalities, as is the (unweighted) transitional SPR, but neither does it index spawning biomass. It combines elements of both in a complex way, making the absolute value of the index difficult to interpret relative to a specified overfishing threshold.

While an upward trend in the index may be a positive sign that a stock rebuilding program is heading in the right direction, it does not necessarily mean that the stock biomass is increasing. Certain systematic trends related to environmental effects (e.g. recruitment declining even while fishing pressure is being reduced), can lead to an inverse correlation between spawning biomass and unweighted or weighted transitional SPR (Figure S4). Similarly, the fact that the absolute value of the index is above or below the overfishing threshold reference point may not always be a good indicator of stock status. Although both the unweighted and weighted transitional SPR may ultimately converge to the static %SPR, they can differ substantially in absolute value when a stock is in transition from one fishing mortality regime to another. The differences are most pronounced when recruitment is highly variable and/or natural mortality is high (i.e. the number of age classes in the population is low).

(v) Implementation of Transitional SPR Measures

If recruitment were constant, then the two transitional SPR measures would converge and both would be directly correlated with egg production (or spawning biomass if this is used as the proxy for egg production). Similar results can also be obtained for variable recruitment in the case where recruitment, fishing mortality, and spawning biomass are tightly linked by a stock-recruitment relationship. However, under conditions of highly variable or trending recruitment (particularly where recruitment is declining despite a concomitant decline in fishing mortality rate), neither index would necessarily be expected to correlate with biomass in any given year. This can be demonstrated by considering the extreme case of a stock that has not been fished for several years, yet continues to decline in

size due to adverse environmental conditions; even in the face of declining biomass, both transitional SPR measures would increase over time, resulting in an inverse correlation between spawning biomass and transitional SPR. Thus, neither measure is a good indicator of the extent of stock depletion *per se*, although both do in some way index the extent to which overfishing is responsible for the current stock condition: the unweighted transitional SPR reflects effects of historical fishing patterns on age structure, while the weighted transitional SPR reflects effects of both historical fishing patterns and recent recruitment on age structure.

In terms of the use of transitional SPR measures in control laws, the Review Panel believes that the unweighted transitional SPR can be considered an index of stock condition in terms of whether or not the stock is *overfished* (i.e. whether or not the age structure is distorted due to historical fishing patterns), but not necessarily in terms of whether or not the stock is *depleted* (with respect to total or spawning biomass). Thus, controls laws that specify lower thresholds beyond which fishing should cease probably need to consider explicit indices of biomass as well as or instead of the unweighted transitional SPR. Ideally, a control law (or series of control laws) would have axes corresponding to the act of *overfishing* (indexed by the static %SPR), the *overfished* condition (indexed by the unweighted transitional SPR), and the extent of stock *depletion* (indexed by absolute or relative estimates of biomass). This level of complexity is required because spawning or total biomass may be *depleted* due to adverse environmental effects, yet the stock may not be considered *overfished* based on estimates of transitional SPR. Similarly, a stock can be *overfished*, even though spawning or total biomass is high relative to optimum or historical levels. In effect, the term "*overfished*" can be thought of an index of the degree of distortion in the age structure due to historical fishing practices, whereas "*depleted*" simply implies low biomass. An *overfished* stock will often also have low biomass, but need not.

Both transitional measures suffer from a practical implementation problem. In order to calculate the denominators (i.e. amount of reproduction with zero fishing), it will often be necessary to expand the age classes well beyond the maximum age considered in the stock assessment, which in turn may result in the need to extend estimates of recruitment back in time (so that there are at least as many years as ages). The net effect is that the fishing mortalities for many of the older ages may be based on simplifying assumptions (e.g. constant recruitment) rather than empirical observations. Elements of the same problem apply for the static %SPR, except that the static %SPR explicitly assumes a stable age distribution, and so the expansion to older ages is more straightforward. Simulation models should be constructed to test the sensitivity of the transitional measures to assumptions about fishing mortalities on older ages.

Another consequence of the need for extending the age distribution is that a number of years (equal to the number of assumed ages) will be incomplete and cannot be included in time series of calculations of the indices. For example, for $M=0.2$, there should probably be a minimum of 20 age classes, which means that even with 25 years of recruitment data, the calculations would not include a complete set of age classes for the first 20 years, leaving

only the most recent 5 years to examine trends in the indices (see yellowfin flounder example in Figure S5). Therefore, a long time series is required before estimates of transitional SPR can be calculated.

(vi) Other Measures

Other measures that could be considered to index some aspect of foregone reproduction, were discussed by the Review Panel, but not examined in detail (see Appendix). However, the Review Panel believes that the utility of such measures, particularly measures based on reproductive value, warrants further investigation.

(vii) Summary

All of the measures considered here relate primarily to fishing mortality, and do not index biomass *per se*, except in special circumstances (e.g. when most or all life history parameters are stationary, or tightly linked by a traditional stock-recruitment relationship). The Review Panel recommends the use of SER as a measure expressing the amount of fishing on the spawning population in a given year, on a consistent scale from year to year. The Panel also endorses continued use of static %SPR based on conclusions and guidelines set out in the original Review Panel report; i.e. as a measure expressing the ultimate consequences of continuing to fish at a particular rate with a particular selectivity pattern; therefore, as a measure of the act of *overfishing*. Finally, the Panel advocates more widespread utilization of (unweighted) transitional SPR as a straightforward extension of static %SPR that may be particularly useful in the context of rebuilding plans where a predetermined threshold transitional SPR can be specified as a recovery target; in this respect, transitional SPR can be considered a measure of the *overfished* condition. Other measures listed in Table S1 and discussed above warrant further investigation to determine their utility and interpretation in different situations.

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APPENDIX: Relative Foregone Reproduction

The measures examined in this report (SER, static %SPR, transitional SPR, and weighted transitional SPR) can be considered as part of a larger class of indices related by the common currency of "foregone reproduction." A continuum of measures expressing foregone reproduction due to fishing can be developed based on the effects of past, present, or future fishing practices. This section summarizes the spectrum of such measures (see also Table S1), all of which are expressed in relative units; i.e., none are measures of absolute reproductive losses. It should be noted that other measures are possible, and that the formulae in Table S1 can be tailored to specific situations, depending on the timing of spawning event(s) within the fishing year, and other relevant factors.

These measures (as with measures of static %SPR and transitional SPR) always have a quantity in the denominator which refers to reproduction in an unfished condition. In order to avoid erroneous estimates, it is important that this quantity reflects the number of age classes that would be expected in an *unfished* condition. For heavily exploited stocks, the necessary number of ages can be substantially higher than the oldest fish in the catches.

(a) Static Foregone Reproduction per Recruit (100-Static %SPR)/100

Foregone reproduction per recruit due to sustained fishing at a *constant rate* over time.

This measures the relative loss in reproduction due to fishing the population at a constant rate.

(b) Transitional Foregone Reproduction per Recruit (1-transitional SPR)

Foregone reproduction per recruit due to *previous* fishing at *observed rates*.

This measures the relative loss in reproduction that will occur this year due to past fishing if all extant cohorts had been of equal size.

(c) Transitional Foregone Reproduction (1-weighted transitional SPR)

Foregone reproduction due to *previous* fishing at *observed rates* on the *observed cohorts* in the population (i.e. considers actual recruitment levels).

This measures the relative loss in reproduction that will occur this year due to past fishing on the extant cohorts.

(d) Annual Foregone Reproduction (SER)

Foregone reproduction due to fishing in the *current year* on the *observed cohorts* in the population.

This measures how much reproduction is lost this year due to fishing at a given rate.

(e) Projected Foregone Reproduction

Foregone reproduction in the *future* at an *assumed* fishing mortality rate on the *observed cohorts* in the population.

This measures the future loss in reproduction due to fishing on the extant population with any given future F trajectory.

Table S1. Measures of foregone reproduction due to fishing.

Notation:

For ages r through G and time $t-G+r$ through t :

F_{obs} = age x time matrix of observed fishing mortality rates.

F_{con} = age x time matrix of hypothetical fishing mortality rates, where all columns are identical (i.e., fishing mortality at age is constant over time).

For ages r through G :

$S(F)$ = age vector of cumulative survival rates from recruitment age r through age a , given F .

P = age vector of annual per capita spawning rates.

f = age vector of hypothetical future fishing mortality rates.

$V(f)$ = age vector of future reproductive values, given f .

For ages r through G and time $t-G+r$ through t :

R = time vector of recruitment.

Quantities of Interest:

Quantity "a" (1 - static %SPR):

$$1 - \frac{\sum_{a=r}^G S_a(F_{con}) \cdot P_a}{\sum_{a=r}^G S_a(0) \cdot P_a}$$

Quantity "b" (1 - unweighted transitional SPR):

$$1 - \frac{\sum_{a=r}^G S_a(F_{obs}) \cdot P_a}{\sum_{a=r}^G S_a(0) \cdot P_a}$$

(continued on next page)

Table S1 cont.

Quantity "c" (1 - weighted transitional SPR):

Quantity "d" (SER):

$$1 - \frac{\sum_{a=r}^G R_{t-a} \cdot S_a(F_{obs}) \cdot P_a}{\sum_{a=r}^G R_{t-a} \cdot S_a(0) \cdot P_a}$$

$$1 - \frac{\sum_{a=r}^G R_{t-a} \cdot S_a(F_{obs}) \cdot P_a \cdot e^{-M-f_a}}{\sum_{a=r}^G R_{t-a} \cdot S_a(F_{obs}) \cdot P_a \cdot e^{-M}}$$

Quantity "e" (1 - reprod. value [ish]):

$$1 - \frac{\sum_{a=r}^G R_{t-a} \cdot S_a(F_{obs}) \cdot \sum_{j=a}^G P_j \exp \left[-M \cdot (j-a) - \sum_{k=a}^{j-1} f_k \right]}{\sum_{a=r}^G R_{t-a} \cdot S_a(F_{obs}) \cdot \sum_{j=a}^G P_j e^{-M \cdot (j-a)}}$$

Quantity "f"--any of the quantities "a" through "d" with P_a in the numerator replaced by

$$V_a(f) = \sum_{j=a}^G P_j \exp \left[-M \cdot (j-a) - \sum_{k=a}^{j-1} f_k \right]$$

and P_a in the denominator replaced by

$$V_a(0) = \sum_{j=a}^G P_j e^{-M \cdot (j-a)}$$