Analytical reference points for age-structured models: application to data-poor fisheries

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Analytical solutions for biological reference points are derived in terms of maximum lifetime reproductive rate. This rate can be calculated directly from biological parameters of maturity, fecundity, and natural mortality or a distribution for this rate can be derived from appropriate metadata. Minimal data needs and assumptions for determining stock status are discussed. The derivations lead to a re-parameterization of the common stock–recruit relationships, Beverton–Holt and Ricker, in terms of spawning potential ratio. Often, parameters in stock–recruit relationships are restricted by tight prior distributions or are fixed based on a hypothesized level of stock resilience. Fixing those parameters is equivalent to specifying the biological reference points. An ability to directly calculate reference points from biological data, or a meta-analysis, without need of a full assessment model or fisheries data, makes the method an attractive option for data-poor fisheries. The derivations reveal an explicit link between the biological characteristics of a species and appropriate management. Predicted stock status for a suite of shark species was compared with recent stock assessment results, and the method successfully identified whether each stock was overfished.

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Introduction

Fish stocks for which there are limited or no data available from a fishery pose a serious challenge for stock assessment. Under current US fisheries management policy (MSFCMRA, 2006), the status of a fish stock, reference points that delineate overfished and overfishing limits, and sustainable annual catch limits must be specified. Resource surveys can typically inform about the resource trend on a relative scale (depletion levels, for example). However, determining stock status from resource surveys alone requires a decision about what the level of depletion was at the start of the survey, where the optimal depletion occurs (the MSY level), and how far below the optimal depletion level the overfished limit should be set. Catches provide the magnitude of abundance, and without information on the scale of abundance, estimating sustainable catch levels will likely be difficult or impossible.

In a data-rich case, stock status is determined by estimating current levels of fishing mortality and spawning-stock biomass (or egg production) and comparing these with reference points, which are typically associated with maximum sustainable yield (MSY). However, even in cases when data are plentiful, estimating MSY levels can still be difficult. For example, MSY is a function of the underlying stock–recruit relationship, which can be difficult to estimate, and some analyses would suggest that recruitment appears to be independent of stock size (Sissenwine and Shepherd, 1987; Hilborn and Walters, 1992; Myers, 2001). In some cases, the resource may have been depleted for much of the time-series, so there is little contrast in the spawning biomass. In other cases, recruitment variability or recruitment measurement error may mask the underlying relationship with the level of spawners. When these situations arise, a proxy is often employed in place of the true, but inestimable, MSY level (Restrepo and Powers, 1999). Common proxies are based on productivity such as a percentage of spawning potential ratio (SPR) or average biomass level, although sometimes proxies based on the rates of fishing mortality $F_{0.1}$, F_{max}, or $F = M$ (where M is the rate of natural mortality), or some multiple of these may be used. SPR is the ratio between the number of spawners (or eggs) produced over a recruit's lifetime (given fishing mortality, F) divided by the number of spawners produced without fishing; as such, it measures the proportional reduction in total potential productivity attributable to fishing.

After specifying an appropriate %SPR, the fishing mortality that achieves that SPR ($F_{\%SPR}$) can be calculated, given fishery selectivity. This proxy for F_{MSY}, $F_{\%SPR}$, can form the basis of F-based reference points (to define overfishing), and the corresponding spawning biomass is associated with the overfished definition.

The key for this type of proxy reference point is specifying an appropriate %SPR; this could depend on whether the proxy is referring to limits, targets, or other management objectives. In a data-poor situation, that specification can be difficult indeed.

SPR has its roots in an insightful paper by Goodyear (1977) in which the concept of compensation ratio (CR) was introduced. The theory underlying the CR is based on consideration of a density-dependent population that is exposed to an exogenous mortality source (fishing, for example). In an unexploited state, the population is in equilibrium. With the addition of exploitation, the vital rates need to adjust by a factor that compensates for the additional source of mortality in order for the population to re-stabilize and persist at a non-zero level. This adjustment factor is calculated by taking the ratio of spawners produced over the lifetime of a recruit without fishing and dividing by the number of spawners produced with fishing. In this ratio, the denominator is always less than the numerator (because it includes more mortality), so the resulting CR value is always ≥ 1. This value is the factor by which vital rates must increase for population persistence. As noted by Goodyear (1977, 1993), the adjustment could be in any of the vital rates (survival, maturity, fecundity), and at any age, or in a combination of vital rates at different ages. However, it is generally assumed that compensation occurs in pre-recruit survival because it is the age class with the greatest abundance and therefore the most likely rate to respond to density effects (Ricker, 1954; Goodyear, 1977, 1993). We adopt that assumption here.

In the 1980s, assessment scientists began examining the change in potential resource productivity caused by fishing (Gabriel *et al.*, 1989; Mace and Sissenwine, 1993). This was estimated by comparing the number of spawners produced with fishing against the number produced without fishing, in other words, the new quantity being calculated was the inverse of Goodyear's (1977) CR. It represented a fractional reduction of the maximum (unexploited) productivity. The term "spawning-stock biomass (SSB) per recruit" was coined, and calculations analogous to yield-per-recruit (YPR) were performed to determine an F that did not reduce the capacity of a resource's productivity below a point that severely compromised future recruitment. These SSB considerations were related to management requirements for defining limits that avoided recruitment-overfishing (Sissenwine and Shepherd, 1987; Clark, 1991; Mace and Sissenwine, 1993; Mace, 1994). The connection between these analyses and CR was noted by Goodyear (1993), who first applied the term SPR to this calculation. Often, the egg-production relationship is unknown and the SSB is used as a surrogate, which implicitly assumes that weight-at-age is proportional to the quantity of eggs that would be produced at age (Goodyear, 1993; Murawski *et al.*, 2001; Marshall *et al.*, 2006).

The application of SPR-based reference points has evolved in response to changes in management issues. In the 1980s, management of US marine fisheries was concerned with avoiding stock levels and fishing rates that would lead to reductions in recruitment (Myers *et al.*, 1994). Therefore, SPR-related recommendations addressed recruitment-overfishing. In the 1990s, management emphasis shifted to maintaining stocks above levels that would produce MSY, and defining depleted stock levels as being overfished (MSFCMA, 1996). Therefore, SPR-related benchmarks were utilized as proxies for F_{MSY}. Currently, US management policy requires specification of both targets and limits for management, with explicit regulatory actions if limits are exceeded

(MSFCMRA, 2006). Both targets and limits are often based upon the stock's MSY and, hence, the SPR. However, when determining appropriate levels of SPR, one must be clear whether a management target or limit is being addressed. Here, we focus on the current US policy that defines F_{MSY} as a limit of overfishing, and on SPR benchmarks that relate to F_{MSY}. Additionally, we address the overfished reference point by deriving the SSB at MSY in terms of depletion from the unexploited level.

By definition, %SPR is constrained between zero (resource fully depleted) and 100% (resource unexploited). When specifying an appropriate fishing level ($F_{\%SPR}$), the closer %SPR is to 100%, the less exploitation is permitted. Clark (1991) evaluated Alaskan groundfish stocks through extensive simulation, and recommended $F_{35\%}$ as an appropriate proxy for F_{MSY}. Mace and Sissenwine (1993) recommended $F_{20\%}$ as a recruitment-overfishing limit for stocks with average resilience, but noted that elasmobranchs (sharks, skates, and rays) would be expected to require a higher SPR. Mace (1994) expanded the earlier analysis and suggested $F_{40\%}$ as a default F_{MSY} proxy when the stock–recruit relationship was unknown. Clark (1993) revisited his first analysis (Clark, 1991) by incorporating recruitment variability, and revised his recommended F_{MSY} proxy to $F_{40\%}$. More recently, Clark (2002) expanded the analyses to consider lower values of slope at the origin, as might be expected for long-lived rockfish, but his focus was still on recommending a single level of SPR that would be sustainable for most fish without causing too much yield to be foregone in the more resilient stocks. He concluded that an SPR $>40\%$ should meet current management needs ($F_{43\%}$ for the examples in Clark, 1991), but noted that for very low values of slope at the origin, the appropriate fishing level could be $F_{60\%}$ or even $F_{70\%}$ (Clark, 2002). Therefore, there has been recognition all along that SPR levels are related to the slope at the origin of stock–recruit curves, and that life history is an important consideration. However, the analytical relationship between SPR and the underlying stock–recruit curve has not been explored fully.

We derive an analytical method to calculate appropriate levels of SPR, which can be used to define an $F_{\%SPR}$ proxy for F_{MSY}. We begin by briefly reviewing the concept of maximum excess recruitment (MER; Goodyear, 1980). Next, we revisit the analytical solution for SPR_{MER} for both the Beverton–Holt and Ricker stock–recruit functions (Brooks and Powers, 2007), then formulate these solutions in terms of maximum lifetime reproductive rate and steepness. We then derive analytical reference points for depletion at MER (i.e. proportional reduction from unexploited level, S_{MER}/S_0) and discuss how stock status can be estimated by comparing relative indices of abundance with the analytical MER depletion level. We also suggest alternative parameterizations of these same stock–recruit functions that explicitly reflect hypotheses about stock resilience. Finally, through simulation, we demonstrate the relationship between SPR_{MSY} and SPR_{MER}. The methodology is illustrated with application to dusky shark (*Carcharhinus obscurus*) and validated by comparing analytical predictions to a summary of results from recent stock assessments of several species of shark.

Material and methods
Maximum excess recruitment
Harvesting theory is based on the assumption that an adult stock can produce recruits in numbers that exceed replacement. Given a

stock–recruit function, it is possible to determine the point where the excess recruitment in number of individuals is at a maximum (i.e. MER; Ricker, 1975; Goodyear, 1980). MER differs from MSY in two respects. First, MER is derived by solving for a maximum in numbers, whereas MSY is the maximum in weight. Second, MER is a property of the stock–recruit function, whereas MSY considers the combined effect of a given fishing mortality on YPR and the extent of excess recruitment. We present derivations for reference points based on MER below, then explore extensions for MSY.

SPR$_{MER}$ for the Beverton–Holt function

The Beverton–Holt stock–recruit relationship is a monotonically increasing function that approaches an asymptotic level of recruitment. It has several parameterizations, one of which is

$$R = \frac{bS}{1 + aS}, \tag{1}$$

where R is the recruitment, S a measure of stock fecundity, a a density-dependent term, and b the slope at the origin. When R and S have the same units, then b is the maximum density-independent survival. For example, in many species of shark, S is often a measure of the number of pups born to a female per year, and R is the number of pups surviving the recruitment interval. For teleosts, it is more common that S is measured in units of biomass, whereas R has units in number of recruits. Therefore, in the teleost case, b is the product of density-independent survival and a scaling factor to translate biomass units into the number of recruits.

Equilibrium values for R_0 and S_0 (recruits and spawners, or eggs, when the stock is unexploited) and the corresponding levels where excess replacement is maximized (R_{MER} and S_{MER}) can be derived analytically. Define φ_0 as the unexploited spawners produced per recruit (Brooks and Powers, 2007):

$$\phi_0 \equiv \frac{S_0}{R_0} = \sum_{age=r}^{MaxAge} \mu_{age} E_{age} \prod_{j=r}^{age-1} e^{-M_j}, \tag{2}$$

where μ_{age} is the proportion mature at age, E_{age} the fecundity at age, r the age of recruitment, and M_j the age-specific natural mortality. When age $= r$, the product term in Equation (2) is defined to have a value of 1.0. From Equations (1) and (2), unexploited and MER levels of spawners and recruits, respectively, are (Brooks and Powers, 2007)

$$S_0 = \frac{b\phi_0 - 1}{a}, \quad R_0 = \frac{b\phi_0 - 1}{a\phi_0}, \tag{3}$$

$$S_{MER} = \frac{\sqrt{b\phi_0} - 1}{a}, \quad R_{MER} = \frac{b}{a}\left[1 - \frac{1}{\sqrt{b\phi_0}}\right]. \tag{4}$$

From this, an estimate of SPR$_{MER}$ can be obtained (Brooks and Powers, 2007):

$$SPR_{MER} = \frac{S_{MER}/R_{MER}}{\phi_0} = \frac{1}{\sqrt{b\phi_0}}. \tag{5}$$

The denominator in the final term, which is the root of the product of unexploited spawners per recruit (ϕ_0) and the slope at the origin (b), is equivalent to the root of the maximum lifetime reproductive rate at low density, $\hat{\alpha}$ (Myers *et al.*, 1997, 1999). In

other words,

$$SPR_{MER} = \frac{1}{\sqrt{\hat{\alpha}}}. \tag{6}$$

Therefore, if life history data are available, SPR$_{MER}$ can be obtained analytically, without the need for an assessment model or fishery catch or effort data. Although similar equilibrium derivations can be found in Appendix III of Ricker (1975), his equations applied to semelparous fish and assumed a slope of the replacement line equal to 1. For iteroparous fish, the slope of the replacement line is $1/\phi_0$, which we include in the derivations above.

Maximum lifetime reproductive rate, $\hat{\alpha}$, is the number of recruits produced by a recruit over its lifetime, in the absence of fishing. The quantity $\hat{\alpha}$ is also related to steepness, h, which is defined as the ratio of $R_{0.2S_0}/R_0$ (Mace and Doonan, 1988). The relationship between $\hat{\alpha}$ and h is derived in Myers *et al.* (1999):

$$\hat{\alpha} = \frac{4h}{1-h}. \tag{7}$$

Substituting the right side of Equation (7) into Equation (6) gives a relationship between SPR$_{MER}$ and steepness:

$$SPR_{MER}^2 = \frac{1-h}{4h} \Rightarrow SPR_{MER} = \frac{\sqrt{1-h}}{2\sqrt{h}}. \tag{8}$$

Equations (6) and (8) provide an analytical result for determining SPR$_{MER}$ and demonstrate that the appropriate level for a given stock depends on life-history characteristics (Table 1, Figure 1).

SPR$_{crash}$ for the Beverton–Holt function

Another reference point that follows from these derivations is SPR$_{crash}$, which is defined as the SPR as the level of spawners approaches the origin. It was originally derived in Goodyear (1977) as the maximum possible population compensation, denoted CR$_{crit}$, beyond which the population would become extinct. As noted above, SPR and CR are inversely related. Here, we define SPR$_{crash}$ as $1/CR_{crit}$. The maximum population compensation is given by the ratio of the slope of the replacement line with no exploitation ($1/\phi_0$) to the slope at the origin (b). This ratio, $1/(b\phi_0)$, is exactly $\hat{\alpha}^{-1}$. In other words, SPR$_{crash} = \hat{\alpha}^{-1}$.

Table 1. Levels of SPR$_{MER}$ and the minimum level of steepness (h) and maximum lifetime reproductive rate ($\hat{\alpha}$) for which SPR$_{MER}$ is appropriate assuming either a Beverton–Holt or Ricker stock–recruit function.

	Beverton–Holt		Ricker	
SPR$_{MER}$	Minimum $\hat{\alpha}$	Minimum h	Minimum $\hat{\alpha}$	Minimum h
0.1	100.0	0.96	21.9	0.85
0.2	25.0	0.86	9.9	0.71
0.3	11.1	0.74	6.0	0.60
0.4	6.3	0.61	4.2	0.51
0.5	4.0	0.50	3.1	0.43
0.6	2.8	0.41	2.4	0.37
0.7	2.0	0.34	1.9	0.32
0.8	1.6	0.28	1.5	0.27
0.9	1.2	0.24	1.2	0.23
1.0	1.0	0.20	1.0	0.20

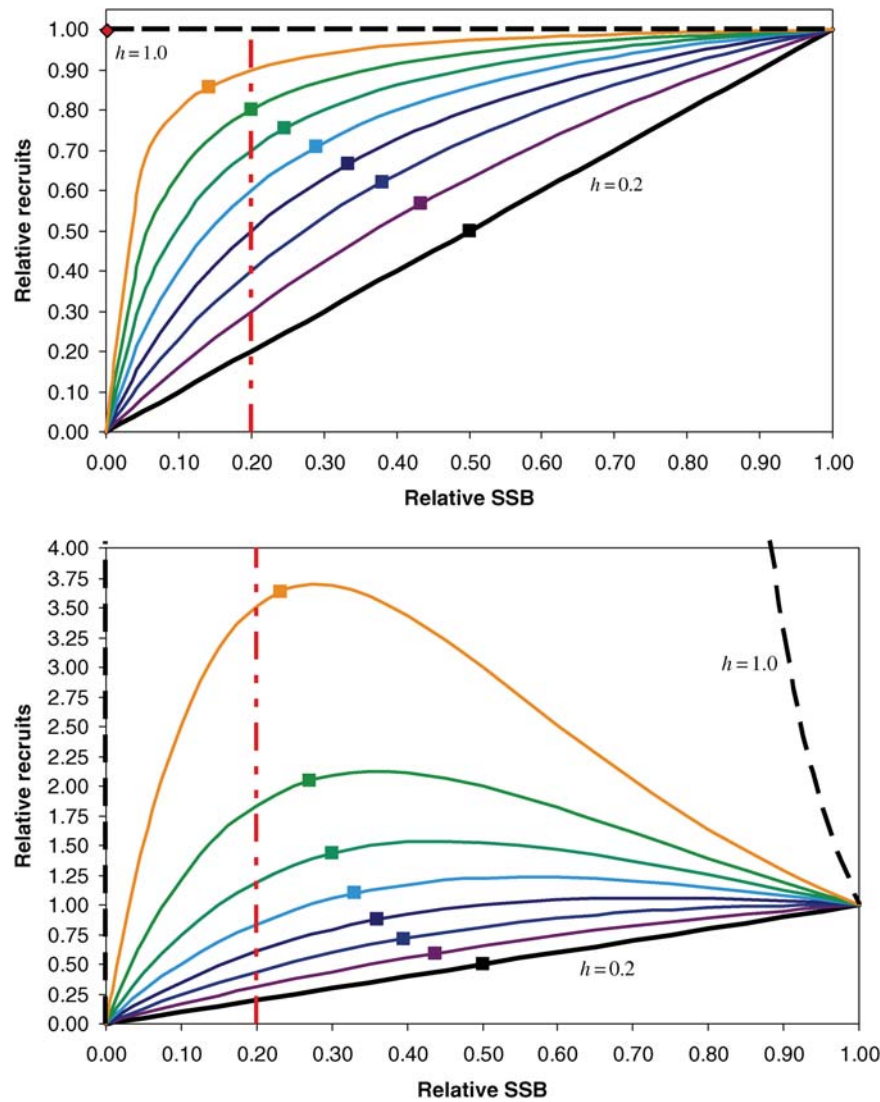Values are derived from Equations (6)–(8) and (11).

Figure 1. Depletion of relative spawners (SSB) and relative recruits at MER for the Beverton–Holt model (top) and the Ricker model (bottom) for steepness values (h) ranging from 0.2 to 1.0 in increments of 0.1 [Equations (12) and (13)]. The solid squares indicate the point of MER depletion for each steepness level. In the Ricker model, $h = 1.0$ is out of the plotted area for SSB less than $\sim$0.9. The vertical line at 0.2 indicates where relative recruitment is equal to steepness. A parameterization of the Ricker function in terms of steepness is derived in Brooks and Powers (2007).

SPR$_{MER}$ for the Ricker function

The Ricker stock–recruit relationship is a domed curve that exhibits overcompensation at high stock sizes by producing fewer recruits than at intermediate stock sizes. It can be parameterized as $R = bS \exp(-aS)$, where a is density-dependent mortality and b is density-independent mortality. At unexploited conditions, the equilibrium number of recruits and spawners is given by (Brooks and Powers, 2007)

$$S_0 = \frac{\ln(b\phi_0)}{a} = \frac{\ln(\hat{\alpha})}{a}, \quad R_0 = \frac{\ln(b\phi_0)}{a\phi_0} = \frac{\ln(\hat{\alpha})}{a\phi_0}. \quad (9)$$

The Ricker function is transcendental (i.e. it cannot be expressed as a finite combination of algebraic operations), so a closed form solution for MER cannot be obtained. Brooks and Powers (2007) derived a first-order approximation, which is

given by

$$S_{MER} \cong \frac{1 - \sqrt{1/\hat{\alpha}}}{a},$$

$$R_{MER} \cong \frac{b}{a}\left[1 - \sqrt{\frac{1}{\hat{\alpha}}}\right] \exp\left(\sqrt{\frac{1}{\hat{\alpha}}} - 1\right). \quad (10)$$

For a numerically exact solution, see Appendix 1. From Equations (9) and (10), we can derive an approximation for SPR$_{MER}$:

$$\text{SPR}_{MER} \cong \frac{S_{MER}/R_{MER}}{\phi_0} = \frac{\exp(1 - \sqrt{1/\hat{\alpha}})}{\hat{\alpha}}. \quad (11)$$

As was shown for the Beverton–Holt function, SPR$_{MER}$ is also a function simply of $\hat{\alpha}$ for the Ricker stock–recruit model. Although the concept of steepness, h, is more useful in a Beverton–Holt

context than in a Ricker format, SPR_{MER} may still be expressed as a function of h by substituting Equation (7) into Equation (11).

SPR_{crash} for the Ricker function

As was derived for the Beverton–Holt function, SPR_{crash} for the Ricker function is defined in terms of the ratio of the slope of the unexploited replacement line to the slope at the origin. Therefore, SPR_{crash} is also given by $\hat{\alpha}^{-1}$.

Determination of stock status

A requirement of stock assessments is to determine the status of the resource, i.e. whether a given stock is overfished and whether overfishing is occurring. Overfishing occurs when the current fishing mortality, F, exceeds the overfishing reference point F_{MSY}, with $F_{\%SPR}$ often being used as a proxy. If overfishing is occurring, then under US policy, managers must act to end overfishing within 2 years (MSFCMRA, 2006). The overfished status is determined by comparing current abundance with an overfished threshold, which is some proportion, p, of the stock size expected to produce maximum yield. Although many data-rich assessment methods can determine the optimal depletion level, the proportion, p, is principally a management decision that should reflect a balance between scientific advice and risk tolerance.

The depletion of spawners and recruits corresponding to MER in the Beverton–Holt model is a direct result of Equations (3) and (4):

$$\frac{S_{MER}}{S_0} = \frac{\sqrt{\hat{\alpha}} - 1}{\hat{\alpha} - 1} \quad \text{and} \quad \frac{R_{MER}}{R_0} = \frac{\hat{\alpha}}{\hat{\alpha} - 1}\left[1 - \frac{1}{\sqrt{\hat{\alpha}}}\right]. \quad (12)$$

Similarly, Equations (9) and (10) can be used to derive MER depletion for spawners and recruits in the Ricker model:

$$\frac{S_{MER}}{S_0} = \frac{1 - \sqrt{1/\hat{\alpha}}}{\ln(\hat{\alpha})} \quad \text{and}$$

$$\frac{R_{MER}}{R_0} = \frac{\hat{\alpha}}{\ln(\hat{\alpha})}\left[1 - \sqrt{\frac{1}{\hat{\alpha}}}\right]\exp\left(\sqrt{\frac{1}{\hat{\alpha}}} - 1\right). \quad (13)$$

Unsurprisingly, the optimal level of depletion also depends on life-history traits, the combined effect of which is reflected in the maximum lifetime reproductive rate, $\hat{\alpha}$. The more productive a stock, the more it can be exploited (Figure 1). The parameter $\hat{\alpha}$ is defined on the range of $[1, \infty)$, and simple application of L'Hôpital's rule demonstrates that at the limits of $\hat{\alpha}$, the MER level of spawning-stock depletion ranges from 0.5 to 0.0, respectively. Recruitment depletion at MER ranges from 0.5 to 1.0 for the Beverton–Holt function and from 0.5 to ∞ for the Ricker function.

Given an estimate of optimal depletion (S_{MER}/S_0) from Equation (12) or (13), the overfished threshold would be some proportion, p, of that level. Restrepo et al. (1998) recommended that p be the greater of $(1 - M)$ or 0.5. In practice, the proportion utilized varies between stocks and management plans, but never should it be <0.5 (NOAA, 2009). In the context of reference points suggested herein, a stock would be considered overfished if the current $S/S_0 < p(S_{MER}/S_0)$, and managers would be required to develop a rebuilding plan.

Although we have derived reference points to delineate over-fishing and overfished conditions, the evaluation of stock status requires estimates of current F and S. In some cases, simple mean length models (e.g. Gedamke and Hoenig, 2006) or short-term tagging studies might provide an estimate of F. Current stock abundance could be inferred from an index of abundance that is scaled by unexploited stock size S_0. This approach has been a useful starting method in data-poor stock assessments for many years (Gulland, 1969). Hilborn (2001) and Goodyear (2003) introduced similar methods, requiring that an index be available that spans the entire period of fishery exploitation and that total removals be known accurately or that biomass in a given year be known. In data-poor situations, these conditions will rarely hold. However, if an index of abundance, $I(t)$, exists but does not extend back in time to unfished conditions, then the index could be scaled as follows. First, normalize I by the value in the first year: $I'(t) = I(t)/I(t = 1)$. Then, alternative hypotheses could be formulated as to the level of depletion at time $t = 1$. For example, let d be the hypothesized level of depletion at the start of the index: $d = I(t = 1)/I(\text{unfished})$. Given d, the index I' can be rescaled to obtain a relative index of depletion, D, such that $D(t) = dI'(t) = \frac{I(t)}{I(t=1)}\frac{I(t=1)}{I(\text{unfished})}$. Of course, because d is merely a constant, the trend of the annual mean is preserved, $\text{var}\{D(t)\} = d^2\text{var}\{I(t)\}$, and $CV\{D(t)\} = CV\{I(t)\}$. The value of $D(t)$ for the current year could then be compared with the level of depletion at MER to determine stock status relative to the overfished criterion. Specifically, a stock would be considered overfished if

$$\frac{D(t = \text{current})}{S_{MER}/S_0} = \frac{I(t = \text{current})/I(\text{unfished})}{S_{MER}/S_0} < p. \quad (14)$$

This approach implicitly assumes that all mature age classes (spawners) are fully selected by the index, I. In the absence of standardized indices, anecdotal information and expert perceptions could be used to derive an index of relative depletion (see Porch et al., 2006, for an example).

Alternative parameterization of stock–recruit functions

The relationship between SPR_{MER} and $\hat{\alpha}$ (or h) suggests an additional parameterization for the Beverton–Holt stock–recruit function:

$$R = \frac{4hR_0S}{R_0\phi_0(1-h) + (5h-1)S} = \frac{R_0S\hat{\alpha}}{S_0 + (\hat{\alpha}-1)S}$$

$$= \frac{R_0S/S_0}{SPR_{MER}^2 + (1 - SPR_{MER}^2)S/S_0}. \quad (15)$$

For the Ricker model, the relationship between SPR_{MER} and $\hat{\alpha}$ [Equation (11)] is another transcendental function, so we cannot directly solve for $\hat{\alpha}$ in terms of SPR_{MER}. Rather than reparameterizing the Ricker model, the $\hat{\alpha}$ corresponding to a given SPR_{MER} could be solved for numerically in Equation (11), then substituted into one of the following forms:

$$R = bS\exp(-aS) = \frac{S}{\phi_0}\left(\frac{4h}{1-h}\right)^{(1-S/S_0)} = \frac{S}{\phi_0}\hat{\alpha}^{(1-S/S_0)}. \quad (16)$$

In a typical stock assessment, the parameters in a stock–recruit function can be difficult to estimate because of lack of contrast and noise in the data. For these reasons, one often develops Bayesian priors for $\hat{\alpha}$ (or h). Those priors typically reflect values from similar species, e.g. using metadata from Myers and Mertz (1998), in combination with the life-history categories delineated in Winemiller and Rose (1992). Alternatively, preconceptions about a stock's resilience to fishing may be supplied by experts.
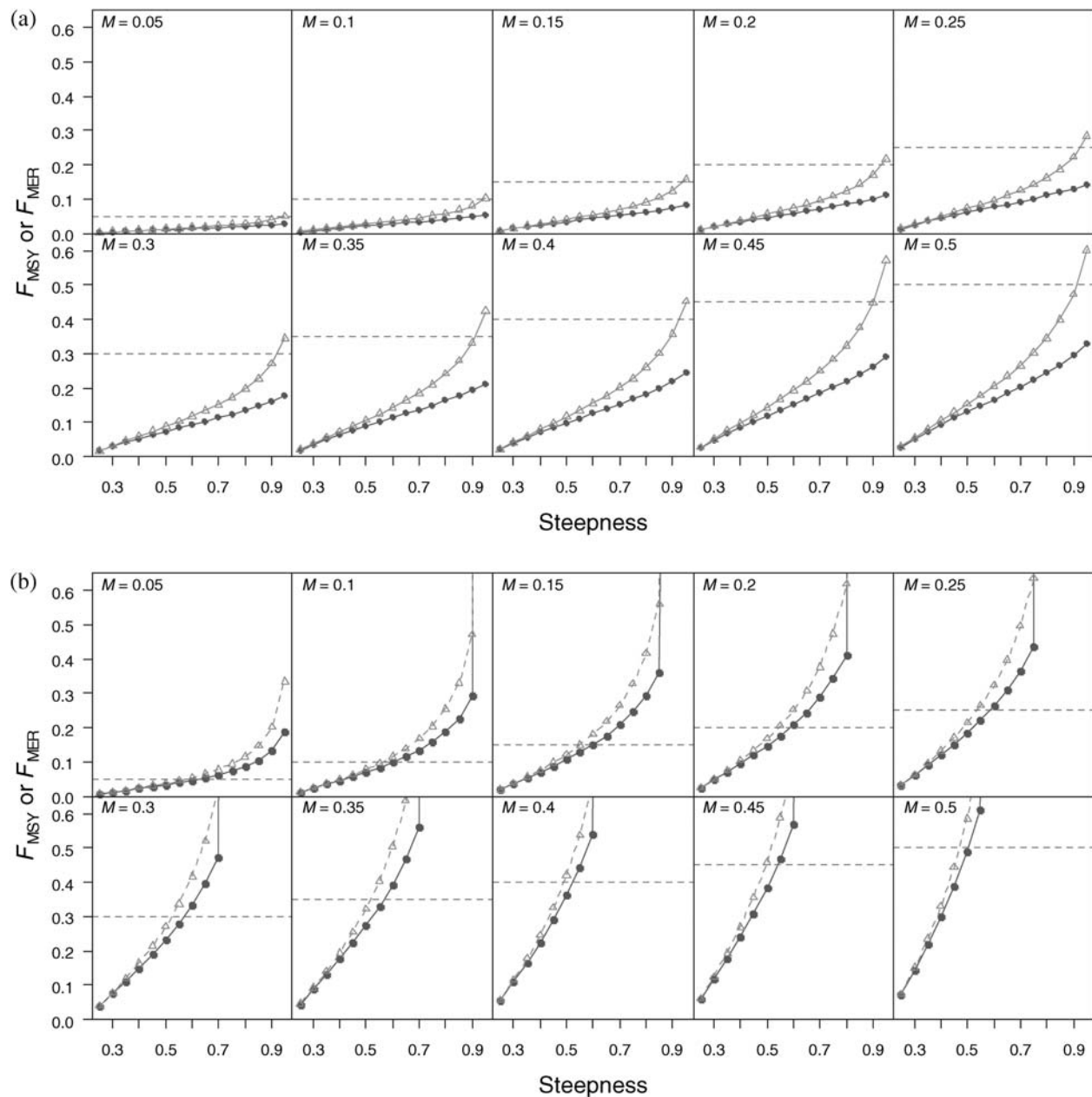
Figure 2. Results of a simulation to compare F_{MSY} (dots) with F_{MER} (open triangles) for steepness values in the range [0.25, 0.95] in increments of 0.05 and for M values in the range 0.05 to 0.50. Cases considered included the base case where all ages were fully selected (top) and a sensitivity case where the selectivity ogive was equal to the maturity ogive (bottom). The horizontal dashed line indicates the level of M.

Parameterizing the stock–recruitment function in terms of SPR_{MER} makes those preconceptions more direct and more transparent.

Simulation to evaluate SPR_{MSY} vs. SPR_{MER}

Our analyses have focused on MER, which maximizes harvest in numbers. We conducted a simulation study to evaluate how analytical values of SPR_{MER} compared with numerical estimation of SPR_{MSY}, where MSY reflects maximizing yield in biomass.

A standard age-structured population dynamics model (Appendix 2) was constructed and MSY was estimated across a range of age-constant rates of natural mortality ($M = 0.05, 0.1, 0.15, 0.2, ..., 0.5$) and steepness levels ($h = 0.25, 0.3, 0.35, ...,$

0.95). A Beverton–Holt stock–recruit relationship was assumed, with recruitment-at-age 1. Full vulnerability to the gear was assumed for all ages. Several sensitivity runs were explored where the age at 50% selectivity was a scalar multiple of the age at 50% maturity.

For the base-case simulation, where all ages were fully selected, $F_{MER} > F_{MSY}$, although the disparity was greatly reduced at lower levels of steepness (Figure 2). One would expect this result because weight increases with age, so maximizing yield in weight would require allowing more fish to survive to older (heavier) ages. It is worth noting that the rule of thumb that $F_{MSY} \approx M$ (Clark, 1991, for example) never held in the base case, and $F_{MER} \approx M$ was only true at the highest levels of steepness ($h > 0.9$). This is

because the maturity ogive is shifted to the right of the selectivity ogive in the base simulations. In sensitivity runs where the selectivity ogive was equal to the maturity ogive, there were more cases where F_{MSY} (or F_{MER}) exceeded M, but again this was for higher values of steepness, especially for $M > 0.4$ (Figure 2). When selectivity occurred at 75% of the age of maturity, results were similar to the base case, except that F_{MSY} and F_{MER} only exceed M for $h > 0.75$. In a few cases, F_{MSY} (and F_{MER}) had no upper bound beyond a given steepness. We note, however, that simulations explored all combinations of steepness and M, which would be expected to produce some unrealistic life histories. For example, it would be unlikely to observe very low natural mortality rates (typical of slow-growing species with late, protracted maturation) in association with very high steepness. These unrealistic combinations explain some of the cases where F_{MSY} or F_{MER} were extremely high, because mortality and reproduction would be such that the species could be exploited without consequence for subsequent recruitment. This was equally true when the selectivity ogive was shifted to the right of the maturity ogive, in which case only the lowest levels of steepness ($h < 0.5$) had F_{MSY} or F_{MER} less than M.

Example: application to dusky shark (*C. obscurus*)

Dusky sharks are a common coastal pelagic shark ranging from the surf zone to depths of 400 m (Compagno, 1984). They have a very late age at reproduction (20 years), are long-lived (>40 years), produce few pups (mean = 7.1, s.d. = 2.05, range = 2–12), and are believed to have a gestation period of 2–3 years (Natanson *et al.*, 1995; Branstetter and Burgess, 1996; Romine, 2004). These life-history traits make the species highly vulnerable to exploitation, yet dusky sharks were regularly landed by both recreational and commercial fisheries before being classified as a prohibited species in the United States in 1999 (NMFS, 1999). Before 1992, the magnitude of annual landings and discards was uncertain because landing statistics were species-aggregated and weight-converted. After 1999, landings were prohibited, and discards were presumably larger but not well recorded. Despite the uncertainty in total catches, fisheries-independent and fisheries-dependent indices suggested declining abundance and average size. Several complementary methods used to assess the status of the western North Atlantic stock of dusky sharks coincided in indicating overfished and overfishing conditions (Cortés *et al.*, 2006).

Although the quality of the catch time-series made traditional stock assessment of the species difficult, biological information was available that was amenable to deriving SPR-based reference points. There was also a fisheries-independent index of abundance that provides information on relative depletion.

Using the life-history parameters listed in Cortés *et al.* (2006, their Table 3.1), we estimated $\hat{\alpha}$ directly by calculating unexploited spawners per recruit (ϕ_0), and an estimate of the slope at the origin [b in Equation (1)], which effectively is a measure of first-year survival (pup survival, s_{pup}). As a starting point, we can select the low estimate of pup survival (0.78). Then from Equation (2) and values in Table 2, we obtain $\hat{\alpha} = s_{pup}\phi_0 = (0.78 \times 1.72 = 1.34)$. Therefore, the expected SPR_{MER} for the Beverton–Holt function for dusky sharks is $1/\sqrt{\hat{\alpha}} = (0.86)$, and $S_{MER}/S_0 = (0.46)$.

A fisheries-independent index of abundance (1974 to present) exists from a longline survey conducted by the Virginia Institute of Marine Science (VIMS; Cortés *et al.*, 2006; see their Table 4.3). Dusky sharks were not believed to be at unexploited levels in 1974, but a working hypothesis was that the stock might have been depleted to 80% of virgin levels. We therefore rescaled the

Table 2. Biological parameters for dusky shark, extracted from information presented in Cortés *et al.* (2006).

Age	μ	Survivorship (e^{-M})	Age	μ	Survivorship (e^{-M})
0	0	0.78			
1	0	0.865	21	0.687	0.93
2	0	0.875	22	0.803	0.932
3	0	0.883	23	0.881	0.933
4	0	0.889	24	0.929	0.934
5	0	0.894	25	0.958	0.934
6	0	0.899	26	0.975	0.935
7	0	0.903	27	0.985	0.935
8	0	0.907	28	0.991	0.936
9	0	0.91	29	0.994	0.937
10	0	0.913	30	0.996	0.937
11	0.001	0.915	31	0.998	0.938
12	0.002	0.918	32	0.998	0.939
13	0.006	0.919	33	0.999	0.939
14	0.013	0.922	34	0.999	0.939
15	0.03	0.923	35	1	0.94
16	0.062	0.925	36	1	0.94
17	0.124	0.926	37	1	0.94
18	0.226	0.927	38	1	0.94
19	0.37	0.928	39	1	0.941
20	0.535	0.93	40	1	0.942

μ is the proportion mature at age, and survivorship is the probability of survival at the beginning of each age. Age-specific fecundity (number of female pups per year) was 2.84 for ages 21 and older, and zero for younger ages.
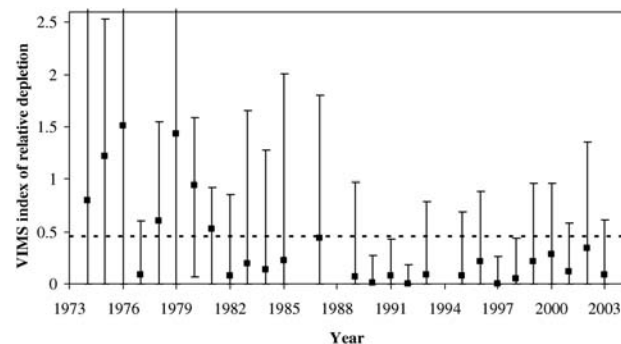

Figure 3. VIMS longline index for dusky shark with 95% confidence intervals, after dividing all points by the first index value, then multiplying by 0.8 (the hypothesized level of depletion in the first year). The dashed horizontal line is the MER level of spawner depletion [Equation (12)].

VIMS longline index by I_{1974}, and multiplied all the scaled points by 0.8 (Figure 3). The 2003 value (0.240) divided by the 1974 value (2.197) is 0.109, and the relative index of depletion in 2003 becomes 0.087 (0.109 × 0.8). This index provides a hypothesis about likely levels of current stock depletion, which when compared with the reference depletion at MER (0.087/0.46 = 0.19) suggests that the current stock level is overfished. This conclusion is in agreement with the results of the multiple stock assessment methodologies used in Cortés *et al.* (2006). However, even if no depletion were assumed for the VIMS index in 1974 (i.e. $d = 1.0$), the index in 2003 would be 0.109, which still implies an overfished stock. We note that all ages are assumed to be fully vulnerable to the gear, which is supported by the lack of an ascending limb in the catch curve applied to data from an at-sea bottom longline observer programme

Table 3. Comparison of recent stock assessment results for overfished status, analytically predicted depletion (S_{MER}/S_0), and the depletion in the final year (D_t) based on a scaled index of abundance.

Scientific name	Common name	Geographic area[a]	Overfished? (assessment results)	SPR_{MER}	S_{MER}/S_0	D_t	Ratio	Overfished? (analytical prediction)	Reference
Carcharhinus obscurus	Dusky shark	NWA	Yes	0.86	0.46	0.09	0.19	Yes	Cortés et al. (2006)
Carcharhinus plumbeus	Sandbar shark	NWA	Yes	0.64	0.39	0.22	0.56	Yes	NMFS (2006)
Carcharhinus limbatus	Blacktip shark	EGM	No	0.61	0.38	1.55	4.12	No	NMFS (2006)
Carcharhinus limbatus	Blacktip shark	NWA	NC	0.57	0.36	4.93	13.56	No	NMFS (2006)
Prionace glauca	Blue shark	NWA/NA	No	0.26	0.21	0.80	3.86	No	ICCAT (2008)
Isurus oxyrinchus	Shortfin mako	NWA	NC	0.89	0.47	0.67	1.43	No	ICCAT (2008)
Sphyrna tiburo	Bonnethead	EGM	No	0.59	0.37	2.24	6.06	No	NMFS (2007)
Rhizoprionodon terraenovae	Atlantic sharpnose	GM	No[b]	0.71	0.42	0.72	1.72	No	NMFS (2007)
Rhizoprionodon terraenovae	Atlantic sharpnose	NWA	No	0.73	0.42	8.29	19.63	No	NMFS (2007)
Carcharhinus acronotus	Blacknose shark	GM	Yes	0.54	0.35	0.08	0.23	Yes	NMFS (2007)
Carcharhinus isodon	Finetooth shark	EGM	No	0.78	0.44	0.42	0.96	No	NMFS (2007)

Overfished status was determined based on whether the ratio, calculated as $D_t/(S_{MER}/S_0)$, was less than p, which we took to be the greater of $(1 - M)$ and 0.5. M was estimated always as the mean of age-specific values from age 1 to the maximum age. NC indicates no conclusion.
[a]Geographic areas are: NWA, Northwest Atlantic; EGM, Eastern Gulf of Mexico; NA, North Atlantic; GM, Gulf of Mexico.
[b]Only one common stock was assessed (GM + NWA), but because there was area-specific biological and relative abundance information, we used our analytical method to predict depletion for stocks in the two areas.

(Cortés et al., 2006). Although the overfished status could be evaluated for this species, no current measure of F is possible given that capture of the species is currently prohibited.

As further validation of the methodology derived herein, the results from other recently assessed shark stocks were compared with analytically predicted spawner depletions. Always, the longest fishery-independent time-series of abundance was scaled by the first year's observation, and assessment decisions reflecting historical depletion (d) were used. To determine whether the stock status was overfished, a decision regarding p, the fraction below MER depletion, was needed. As the species examined are elasmobranchs, and their life history makes them more vulnerable than teleosts, we chose p to be the greater of $(1 - M)$ and 0.5. Of the 11 shark stocks, including dusky shark, examined where the stock assessments reached a conclusion (nine cases: three overfished, six not overfished), predictions from our methodology consistently matched the results from the stock assessments (Table 3). We note, however, that some of the abundance indices we used showed high interannual variation that is not biologically consistent with real fluctuations in abundance, and more likely reflects noise. In such cases, smoothing the abundance trend, or averaging over several years, might be a more conservative approach to determine stock status. We did not attempt a similar determination of overfishing status, because selectivity in these fisheries would need to be determined to calculate $F_{\%SPR}$.

Discussion

The question has been asked, "How much spawning per recruit is enough?" (Mace and Sissenwine, 1993). This was asked in the context of trying to determine a minimum amount of spawning biomass that would avoid recruitment-overfishing. As a result of revisions to the Magnuson–Stevens Act (MSFCMA, 1996; MSFCMRA, 2006), US fishery management now focuses on preventing overfishing and maintaining sufficient spawning biomass while at the same time achieving MSY. In this revised context, reference points are required to evaluate current levels of stock abundance and fishing mortality. An SPR level is often used as a proxy for MSY reference points to define overfishing and overfished reference points; usually that level is determined by a

committee. The analytical results herein indicate that there is not a single level that is optimal or even sufficient for all stocks and that overfishing specifications need to be related to life history.

Early in the development of searching for a single default SPR level as a proxy for recruitment-overfishing, values ranging from 20 to 40% or more were proposed (Clark, 1991, 1993; Mace and Sissenwine, 1993; Mace, 1994; Clark, 2002). These default SPR levels were seen as a compromise between achieving sustainability and avoiding large foregone yield for highly productive stocks. Our derivations indicate that only the most resilient stocks would be assured of fishing not exceeding F_{MSY} when using a reference point based on 30% SPR. Very long-lived, slow-maturing species would require much higher levels of SPR to ensure that $F < F_{MSY}$. For example, it has been suggested that several large species of coastal shark may have steepness in the range of 0.2–0.4 (SEDAR, 2006). For those species, an SPR of at least 60% would be required, and because $SPR_{MSY} > SPR_{MER}$, the appropriate SPR level could be higher if management focuses on yield in biomass rather than in number.

We demonstrated analytically (for Beverton–Holt and Ricker relationships) that the optimal depletion of spawners (S_{MER}/S_0) had an upper bound of 0.5, i.e. spawners would always be depleted by at least 50% of unexploited levels (see also Figure 1). As summarized by Au et al. (2008), a likely range for spawner depletion is 0.2–0.5, with the range for sharks probably lying at the upper end of that interval, perhaps 0.4–0.5. The computations from these previous studies corroborate our analytical finding. We emphasize, however, that this depletion refers to mature biomass (i.e. SSB) in an age-structured model. This differs from surplus production models, where depletion refers to total population biomass (all ages combined), and the point of inflection of the population growth function could lie on either side of 0.5.

Using our analytical result for SPR_{MER} in place of SPR_{MSY} would produce reference points that are biased low. To some extent, this might be counterbalanced by the fact that SPR calculations based on a maximum age that is too young introduces positive bias (Goodyear, 1993). As most observations of maximum age come from fished stocks, underestimating the maximum age is a real possibility. Nevertheless, SPR_{MER} provides

a relevant starting point because it is associated with the life history of the species under consideration, and the direction of bias is known. Alternatively, rather than using the analytical SPR$_{MER}$, SPR$_{MSY}$ could be calculated by exploring a range of plausible selectivity ogives and/or rates of natural mortality.

Our results confirm and explain those obtained by Galucci *et al.* (2006) and Goodwin *et al.* (2006), who found that the reproductive potential and CR, respectively, were the most significant factors in sustainable harvest and were most strongly correlated with density-dependence. For Galucci *et al.* (2006), the fraction of reproductive potential removed from density-independent populations (effectively, SPR) was shown to be directly linked to the probability of population depletion and susceptibility to overfishing. Goodwin *et al.* (2006) found a strong positive correlation between unexploited spawners per recruit and the CR, and a negative correlation between unexploited spawners per recruit and the slope at the origin. As we have shown, the correlation pattern results directly by definition of $\hat{\alpha}$ and the reference points that can be derived from it.

An overfished reference point in terms of depletion of spawners, S_{MER}/S_0, was derived as a corollary to the development of SPR$_{MER}$. Gauging whether the current level of stock depletion was greater or less than the overfished reference point would require an index of spawners, perhaps from a research survey, and a management specification about the proportion, p, below optimal depletion where the stock is considered to be overfished. To determine whether overfishing is occurring, a measure of current fishing mortality would need to be compared with $F_{\%SPR}$.

The SPR proxies that we have derived are equally relevant to more data-rich stocks, where one is more likely to have information to evaluate current status relative to the reference points. Although we illustrated our methodology exclusively with sharks, the method is not restricted to elasmobranchs. The small number of offspring, and the large size at birth among elasmobranchs, makes empirical observation and measurement possible. We expect that the biological parameters needed for this method could also be obtained for marine mammals, because their life-history strategy is similar to that of elasmobranchs. One could perform similar MER or MSY calculations for teleosts, but the slope at the origin is typically very difficult to measure, let alone to estimate, because recruitment variation can span several orders of magnitude. In fact, it is this estimation difficulty for teleosts that has prompted the application of reference point proxies based on $F_{\%SPR}$.

Our derivations tacitly assume that all age classes beyond recruitment are fully selected. Shifting the selectivity ogive to coincide with or to exceed the maturity ogive leads to lower SPR$_{MER}$ (and SPR$_{MSY}$), because the population can sustain more exploitation. Bias in any of the life-history parameter estimates could have a small effect on SPR. Williams and Shertzer (2003) explored MSY reference points over a wide variety of selectivity and life-history parameter combinations and concluded that SPR was a robust reference point because it had very low sensitivity to parameter misspecification. Although it is expected that SPR will be robust to selectivity, the corresponding $F_{\%SPR}$ is sensitive to the selectivity vector, because the same SPR (or equilibrium stock depletion) can be attained with a high F on only the oldest ages or a low F on all ages.

Our derived values of SPR$_{MER}$ are deterministic, but many of the biological parameters that go into it are expected to have a variability associated with them, perhaps through individual variation or uncertainty in vital rates (Cortés, 2002), intraspecific variation by area (Cope, 2006), or measurement uncertainty. Parameters that have the greatest influence on SPR$_{MER}$ (or SPR$_{MSY}$) could be identified through sensitivity analysis. It would then be most important to characterize uncertainty in that set of parameters, through Monte Carlo simulation or specification of prior distributions.

The mapping between SPR$_{MER}$, $\hat{\alpha}$, and h reveals the importance of prior distributions, for they strongly determine the management reference points for a stock. For example, when an assessment model is not able to estimate steepness (h), it is sometimes fixed at one or more values based on prior knowledge. Then management advice is based on output from models run at those fixed values. What has not been universally recognized is that those prescribed levels of steepness actually are the management reference points because they directly determine SPR.

A related issue concerns the implications of those fixed steepness levels for the underlying life-history parameters. As demonstrated by Brooks and Cortés (2006), the best scientific advice about the individual components of maturity, fecundity, and survival can sometimes produce implausible values for steepness. Brandon *et al.* (2007) attempted to overcome this situation by specifying a joint prior on parameters that constrained their combined effects to a biologically plausible subset.

Stock assessment and management for data-poor fisheries is extremely challenging. Often, time-series of catches are short, if indeed they exist, and may reflect landings of an aggregate species complex. Developing standardized fishery-dependent indices may not be possible if infrastructure does not exist to collect information on effort or to sample landed catches directly. With this derivation of SPR$_{MER}$, it would be possible to establish reference points for data-poor species based solely on biological information. Moreover, as the default management advice for data-poor species is sometimes applied to an aggregate complex, this methodology could provide a rationale for determining species groupings. One of the existing approaches for species groupings relies on Productivity and Susceptibility Analysis (PSA; see Hobday *et al.*, 2007; Rosenberg *et al.*, 2007, and references therein), where decisions are made based on the same biological inputs required for our methodology. Although the PSA approach allows identification of species potentially most at risk of becoming overfished or experiencing overfishing, it is not possible to make stock status determinations based on PSA criteria. In contrast, our approach produces quantitative reference points that can be used directly to determine stock status.

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References

Au, D. W., Smith, S. E., and Show, C. 2008. Shark productivity and reproductive protection, and a comparison with teleosts. *In* Sharks of the Open Ocean, pp. 298–308. Ed. by M. D. Camhi, E. K. Pikitch, and E. A. Babcock. Blackwell Publishing, Oxford, UK.

Beverton, R. J. H. 1992. Patterns of reproductive strategy parameters in some marine teleost fishes. Journal of Fish Biology, 41: 137–160.

Brandon, J. R., Breiwick, J. M., Punt, A. E., and Wade, P. R. 2007. Constructing a coherent joint prior while respecting biological

realism: application to marine mammal stock assessments. ICES Journal of Marine Science, 64: 1085–1100.

Branstetter, S., and Burgess, G. H. 1996. Commercial shark fishery observer program. Characterization and comparisons of the directed commercial shark fishery in the eastern Gulf of Mexico and off North Carolina through an observer program. Final Report, MARFIN Award NA47FF0008. 33 pp.

Brooks, E. N., and Cortés, E. 2006. Issues related to biological inputs to blacktip and sandbar shark assessments. Southeast Data Assessment Review 11–10, Assessment Workshop, Southeast Fisheries Science Center, Miami, FL.

Brooks, E. N., and Powers, J. E. 2007. Generalized compensation in stock–recruit functions: properties and implications for management. ICES Journal of Marine Science, 64: 413–424.

Charnov, E. L. 1993. Life History Invariants: Some Explorations of Symmetry in Evolutionary Ecology. Oxford University Press, Oxford.

Clark, W. G. 1991. Groundfish exploitation rates based on life history parameters. Canadian Journal of Fisheries and Aquatic Sciences, 48: 734–750.

Clark, W. G. 1993. The effect of recruitment variability on the choice of a target level of spawning biomass per recruit. *In* Proceedings of the International Symposium on Management Strategies for Exploited Fish Populations, University of Alaska, pp. 233–246. Ed. by G. Kruse, R. J. Marasco, C. Pautzke, and T. J. Quinn. Alaska Sea Grant College Program Report, 93-02.

Clark, W. G. 2002. $F_{35\%}$ revisited ten years later. North American Journal of Fisheries Management, 22: 251–257.

Compagno, L. J. V. 1984. Sharks of the world. An annotated and illustrated catalogue of shark species known to date. FAO Species Catalogue, 4, Parts 1 and 2. FAO Fisheries Synopsis, 125.

Cope, J. M. 2006. Exploring intraspecific life history patterns in sharks. Fishery Bulletin US, 104: 311–320.

Cortés, E. 2002. Incorporating uncertainty into demographic modelling: application to shark populations and their conservation. Conservation Biology, 16: 1048–1062.

Cortés, E., Brooks, E. N., Apostolaki, P., and Brown, C. A. 2006. Stock assessment of dusky shark in the US Atlantic and Gulf of Mexico. Sustainable Fisheries Division Contribution SFD-2006-014, NOAA Fisheries, Miami, FL. 155 pp. https://grunt.sefsc.noaa.gov/P_QryLDS/download/SFD283_SFD-2006-014.pdf?id=LDS.

Gabriel, W. L., Sissenwine, M. P., and Overholtz, W. J. 1989. Analysis of spawning stock biomass per recruit: an example for Georges Bank haddock. North American Journal of Fisheries Management, 9: 383–391.

Galucci, V. F., Taylor, I. G., and Erzini, K. 2006. Conservation and management of exploited shark populations based on reproductive value. Canadian Journal of Fisheries and Aquatic Sciences, 63: 931–942.

Gedamke, T., and Hoenig, J. M. 2006. Estimating mortality from mean length data in non-equilibrium situations, with application to the assessment of goosefish (*Lophius americanus*). Transactions of the American Fisheries Society, 135: 476–487.

Goodwin, N. B., Grant, A., Perry, A. L., Dulvy, N. K., and Reynolds, J. D. 2006. Life history correlates of density-dependent recruitment in marine fishes. Canadian Journal of Fisheries and Aquatic Sciences, 63: 494–509.

Goodyear, C. P. 1977. Assessing the impact of power plant mortality on the compensatory reserve of fish populations. *In* Proceedings of the Conference on Assessing the Effects of Power Plant Induced Mortality on Fish Populations, Gatlinburg, Tennessee, 3–6 May 1997, pp. 186–195. Ed. by W. van Winkle. Pergamon Press, New York.

Goodyear, C. P. 1980. Compensation in fish populations. *In* Biological Monitoring of Fish, pp. 253–280. Ed. by C. H. Hocutt, and J. R. Stauffer. Lexington Books, D. C. Heath and Co, Lexington, MA.

Goodyear, C. P. 1993. Spawning stock biomass per recruit in fisheries management: foundation and current use. *In* Risk Evaluation and Biological Reference Points for Fisheries Management, pp. 67–81. Ed. by S. J. Smith, J. J. Hunt, and D. Rivard. Canadian Special Publication in Fisheries and Aquatic Sciences, 120.

Goodyear, C. P. 2003. Biological reference points without models. Collected Volume of Scientific Papers ICCAT, 55: 633–648.

Gulland, J. A. 1969. Manual of Methods for Fish Stock Assessment. 1. Fish Population Analysis. FAO, Rome. 154 pp.

Hilborn, R. 2001. Calculation of biomass trend, exploitation rate, and surplus production from survey and catch data. Canadian Journal of Fisheries and Aquatic Sciences, 58: 579–584.

Hilborn, R., and Walters, C. J. 1992. Quantitative Fisheries Assessment. Choice, Dynamics and Uncertainty. Chapman and Hall, London. 570 pp.

Hobday, A. J., Smith, A., Webb, H., Daley, R., Wayte, S., Bulman, C., Dowdney, J., et al. 2007. Ecological Risk Assessment for the Effects of Fishing: Methodology. Report R04/1072 for the Australian Fisheries Management Authority, Canberra. 173 pp.

ICCAT. 2008. Report of the 2008 Shark Stock Assessment Meeting, SCRS/2008/017. ICCAT, Madrid.

Mace, P. M. 1994. Relationships between common biological reference points used as thresholds and targets of fisheries management strategies. Canadian Journal of Fisheries and Aquatic Sciences, 51: 110–122.

Mace, P. M., and Doonan, I. J. 1988. A generalized bioeconomic simulation model for fish population dynamics. New Zealand Fishery Assessment, Research Document, 88/4. 51 pp.

Mace, P. M., and Sissenwine, M. P. 1993. How much spawning per recruit is enough? *In* Risk Evaluation and Biological Reference Points for Fisheries Management, pp. 101–118. Ed. by S. J. Smith, J. J. Hunt, and D. Rivard. Canadian Special Publication in Fisheries and Aquatic Sciences, 120.

Marshall, C. T., Needle, C. L., Thorsen, A., Kjesbu, O. S., and Yaragina, N. A. 2006. Systematic bias in estimates of reproductive potential of an Atlantic cod (*Gadus morhua*) stock: implications for stock–recruit theory and management. Canadian Journal of Fisheries and Aquatic Sciences, 63: 980–994.

MSFCMA (Magnuson–Stevens Fishery Conservation and Management Act). 1996. NOAA Technical Memorandum, NMFS-F/SPO-23.

MSFCMRA (Magnuson–Stevens Fishery Conservation and Management Reauthorization Act). 2006. Public Law No. 109-479, 120 Stat. 3575.

Murawski, S. A., Rago, P. J., and Trippel, E. A. 2001. Impacts of demographic variation in spawning characteristics on reference points for fishery management. ICES Journal of Marine Science, 58: 1002–1014.

Myers, R. A. 2001. Stock and recruitment: generalizations about maximum reproductive rate, density dependence, and variability using meta-analytic approaches. ICES Journal of Marine Science, 58: 937–951.

Myers, R. A., Bowen, K. G., and Barrowman, N. J. 1999. Maximum reproductive rate of fish at low population sizes. Canadian Journal of Fisheries and Aquatic Sciences, 56: 2404–2419.

Myers, R. A., and Mertz, G. 1998. Reducing the uncertainty in the biological basis of fisheries management by meta-analysis of data from many populations: a synthesis. Fisheries Research, 37: 51–60.

Myers, R. A., Mertz, G., and Fowlow, S. 1997. Maximum population growth rates and recovery times for Atlantic cod, *Gadus morhua*. Fishery Bulletin US, 95: 762–772.

Myers, R. A., Rosenberg, A. A., Mace, P. M., Barrowman, N., and Restrepo, V. R. 1994. In search of thresholds for recruitment overfishing. ICES Journal of Marine Science, 51: 191–205.

Natanson, L. J., Casey, J. G., and Kohler, N. E. 1995. Age and growth estimates of the dusky shark, *Carcharhinus obscurus*, in the western North Atlantic Ocean. Fishery Bulletin US, 93: 116–126.

NMFS (National Marine Fisheries Service). 1999. Final fishery management plan for Atlantic tunas, swordfish and sharks. NOAA, NMFS, Highly Migratory Species Division, Silver Spring, MD.

NMFS (National Marine Fisheries Service). 2006. SEDAR (Southeast Data Assessment and Review) 11. Large coastal shark complex, blacktip, and sandbar shark stock assessment report. NOAA/ NMFS Highly Migratory Species Division, Silver Spring, MD.

NMFS (National Marine Fisheries Service). 2007. SEDAR (Southeast Data Assessment and Review) 13. Small coastal shark complex, Atlantic sharpnose, blacknose, bonnethead, and finetooth shark stock assessment report. NOAA/NMFS Highly Migratory Species Division, Silver Spring, MD.

NOAA. 2009. National Standard 1 Guidelines 50 CFR 600. Federal Register, 16 January 2009, 74: 3178–3213.

Porch, C. E., Ecklund, A-M., and Scott, G. P. 2006. A catch-free stock assessment model with application to goliath grouper (*Epinephelus itajara*) off southern Florida. Fishery Bulletin US, 104: 89–101.

Restrepo, V. R., and Powers, J. E. 1999. Precautionary control rules in US fisheries management: specification and performance. ICES Journal of Marine Science, 56: 846–852.

Restrepo, V. R., Thompson, G. G., Mace, P. M., Gabriel, W. L., Low, L. L., MacCall, A. D., Methot, R. D., *et al.* 1998. Technical guidance on the use of precautionary approaches to implementing National Standard 1 of the Magnuson–Stevens Fishery Conservation and Management Act. NOAA Technical Memorandum, NMFS-F/ SPO. 54 pp.

Ricker, W. E. 1954. Stock and recruitment. Journal of the Fisheries Research Board of Canada, 11: 559–623.

Ricker, W. E. 1975. Computation and interpretation of biological statistics of fish populations. Bulletin of the Fisheries Research Board of Canada, 191.

Romine, J. G. 2004. Status and demographic analysis of the dusky shark, *Carcharhinus obscurus*, in the Northwest Atlantic. MS thesis, College of William and Mary. 88 pp.

Rosenberg, A. A., Agnew, D., Babcock, E., Cooper, A., Mogensen, C., O'Boyle, R., Powers, J. E., *et al.* 2007. Setting annual catch limits for US fisheries: an expert working group report. MRAG Americas, Washington, DC. 36 pp.

SEDAR (Southeast Data Assessment and Review) 11. 2006. Large coastal shark complex, blacktip and sandbar shark. NOAA/ NMFS Highly Migratory Species Division, Silver Spring, MD.

Sissenwine, M. P., and Shepherd, J. G. 1987. An alternative perspective on recruitment overfishing and biological reference points. Canadian Journal of Fisheries and Aquatic Sciences, 44: 913–918.

von Bertalanffy, L. 1938. A quantitative theory of organic growth (inquiries on growth laws II). Human Biology, 10: 181–213.

Williams, E. H., and Shertzer, K. W. 2003. Implications of life-history invariants for biological reference points used in fishery management. Canadian Journal of Fisheries and Aquatic Sciences, 60: 710–720.

Winemiller, K. O., and Rose, K. A. 1992. Patterns of life-history diversification in North American fishes: implications for population regulation. Canadian Journal of Fisheries and Aquatic Sciences, 49: 2196–2218.

Appendix 1
Numerical calculation of SPR_{MER}

As was demonstrated in Brooks and Powers (2007), a numerically exact value of SPR_{MER} may be calculated as a function of $\hat{\alpha}$, noting that

$$SPR_{MER} = \frac{S_{MER}}{\phi_0 R_{MER}} = \frac{\exp(aS_{MER})}{\hat{\alpha}}, \quad (A1)$$

and

$$\exp(-aS) \cong 1 - aS + \frac{(aS)^2}{2!} - \frac{(aS)^3}{3!} + \cdots + \frac{(aS)^n}{n!}(-1)^n. \quad (A2)$$

Then, aS is found from the solution to

$$\left[1 - aS + \frac{(aS)^2}{2!} - \frac{(aS)^3}{3!} + \cdots + \frac{(aS)^n}{n!}(-1)^n\right](1 - aS)$$
$$= \frac{1}{\hat{\alpha}}. \quad (A3)$$

Therefore, (A1) can be used to compute SPR_{MER} as a function of $\hat{\alpha}$.

Appendix 2
Population dynamics model for SPR_{MSY} simulation

The simulation to compare numerically estimated SPR_{MSY} with analytically estimated SPR_{MER} was carried out over several levels of M, h (steepness), and for different scalars on the age of 50% fishery selectivity. Given a level of M, life-history theory was employed to derive other biological inputs. For example, the age at 50% maturity (a_{50}) was obtained from the relationship $a_{50} = \ln((3K + M)/M)/K$ (Beverton, 1992). The maturity ogive was assumed to be knife-edged such that maturity-at-age, μ_a, is 1 for $a \geq a_{50}$ and 0 otherwise. A scalar of 0 (base case), 0.75, 1.0, or 1.25 was applied to a_{50} to calculate selectivity at age, s_a. The parameter K in the von Bertalanffy growth equation (von Bertalanffy, 1938) was derived as $K = M/1.65$ (Charnov, 1993). Arbitrary scalars in the simulation were unexploited recruitment ($R_0 = 1E+7$), mean asymptotic size ($L_\infty = 100$), the theoretical age at which length is zero ($t_0 = 0$), and parameters of the power function relating length-at-age (l_a) to weight-at-age, $w_a = \alpha\, l_a^\beta$, where $\alpha = 1E-3$, $\beta = 3$.

Given the specifications above, F_{MSY} was obtained by finding the value of F that maximized equilibrium yield (Y), calculated as $Y = YPR(F) \cdot S(F)/\phi(F)$, where

$$YPR(F) = \sum_{a=1}^{A-1} w_a F s_a \frac{(1 - \exp(-M - F s_a))}{(M + F s_a)} \prod_{j=1}^{a-1} \exp(-M - F s_j)$$
$$+ \frac{w_A F s_A}{(M + F s_A)} \prod_{j=1}^{A-1} \exp(-M - F s_j), \quad (A4)$$

$$\phi(F) = \sum_{a=1}^{A-1} \mu_a E_a \prod_{j=1}^{a-1} \exp(-M - F s_j)$$
$$+ \frac{g_A \mu_A}{(1 - \exp(-M - F s_A))} \prod_{j=1}^{A} \exp(-M - F s_j), \quad (A5)$$

$$\breve{S}(F) = \frac{R_0 \hat{\alpha}\, \phi(F) - R_0 \phi_0}{\hat{\alpha} - 1} = \frac{4h R_0 \phi(F) - R_0 \phi_0(1-h)}{5h - 1}. \quad (A6)$$

In Equations (A4) and (A5), A is the maximum age modelled, E_a the fecundity at age (eggs, pup production, or spawning biomass, for instance), $\breve{S}(F)$ the equilibrium spawning biomass for a given F, and $\phi(F)$ the lifetime production of spawners per recruit for a given F.