

A perspective on steepness, reference points, and stock assessment

Marc Mangel, Alec D. MacCall, Jon Brodziak, E.J. Dick, Robyn E. Forrest, Roxanna Pourzand, and Stephen Ralston

Abstract: We provide a perspective on steepness, reference points for fishery management, and stock assessment. We first review published data and give new results showing that key reference points are fixed when steepness and other life history parameters are fixed in stock assessments using a Beverton–Holt stock–recruitment relationship. We use both production and age-structured models to explore these patterns. For the production model, we derive explicit relationships for steepness and life history parameters and then for steepness and major reference points. For the age-structured model, we are required to generally use numerical computation, and so we provide an example that complements the analytical results of the production model. We discuss what it means to set steepness equal to 1 and how to construct a prior for steepness. Ways out of the difficult situation raised by fixing steepness and life history parameters include not fixing them, using a more complicated stock–recruitment relationship, and being more explicit about the information content of the data and what that means for policy makers. We discuss the strengths and limitations of each approach.

Résumé : Nous offrons une perspective sur l'inclinaison, les points de référence pour la gestion des pêches et l'évaluation des stocks. Nous passons d'abord en revue les résultats publiés et présentons de nouveaux résultats qui démontrent que des points de référence clés sont fixés quand l'inclinaison et d'autres paramètres du cycle biologique sont fixés dans les évaluations des stocks reposant sur une relation stock–recrutement de type Beverton–Holt. Nous utilisons des modèles de production et structurés par âge pour explorer ces situations. En ce qui concerne le modèle de production, nous obtenons des relations explicites pour l'inclinaison et les paramètres du cycle biologique, puis pour l'inclinaison et les principaux points de référence. Pour le modèle structuré par âge, nous devons généralement utiliser une approche numérique et présentons un exemple qui complémente les résultats analytiques du modèle de production. Nous discutons de ce que signifie le fait de fixer la valeur de l'inclinaison à 1 et de la manière d'établir un a priori pour l'inclinaison. Parmi les moyens pour contourner la difficulté soulevée par la fixation de l'inclinaison et des paramètres du cycle biologique figurent le fait de ne pas fixer ces valeurs, l'utilisation d'une relation stock–recrutement plus complexe et une approche plus explicite en ce qui concerne le contenu en information des données et ce que cela signifie pour les responsables de l'élaboration de politiques. Nous abordons les forces et les limites de chacune de ces approches. [Traduit par la Rédaction]

Introduction

Models for the stock–recruitment relationship (SRR) involving two parameters almost entirely dominate in age-structured stock assessments. These SRRs can be written in the form $R(B) = \alpha B f(B, \beta)$, where $R(B)$ is a measure of the recruitment produced by spawning biomass B , α is maximum productivity per unit spawning biomass, and $f(B, \beta)$ characterizes the form of density dependence, with the parameter β measuring the intensity of the density dependence in the prerecruit phase (Walters and Martell 2004; Mangel 2006) and $f(B, \beta) \rightarrow 1$ as B declines. Two of the most commonly used SRRs are the Beverton–Holt SRR (BH-SRR; Beverton and Holt 1957)

$$(1) \quad R(B) = \frac{\alpha B}{1 + \beta B}$$

for which recruitment increases asymptotically to its maximum value α/β , and the Ricker SRR (R-SRR; Ricker 1954)

$$(2) \quad R(B) = \alpha B \exp(-\beta B)$$

for which there is a possibility of a decline in recruitment at high spawning stock abundance. When B is very small, so that the denominator in eq. 1 or the exp in eq. 2 are well approximated by 1, both of these SRRs are of the form $R(B) \approx \alpha B$ (see Sissenwine and Shepherd 1987); when $\beta B \ll 1$ so that the denominator or exponential can be Taylor-expanded, they are of the form $R(B) \approx \alpha B(1 - \beta B)$, giving the familiar logistic equation.

Although the shape of the SRR is important, it is often ambiguous what the appropriate SSR is given the available stock assessment information. For example, Dorn (2002) concluded in a meta-analysis of rockfish (*Sebastes* spp.) stock and recruitment data that neither the R-SRR nor the BH-SRR can be distinguished as a preferred model on the basis of statistical goodness of fit. Brodziak (2002) reached a similar conclusion in an analysis of USA west coast groundfish stock–recruitment data. Alternatively, in a meta-analysis of 128 diverse fish stocks, Punt et al. (2005) concluded that as a general model, the BH-SRR is strongly preferred over the R-SRR, but that “there are also indications that other (more complicated) forms may provide better representations of the existing data” (p. 76). This conclusion is not unexpected because models with more parameters can approximate variability in the observations used to estimate the SRR more accurately than

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M. Mangel. Center for Stock Assessment Research MS E-2, University of California, Santa Cruz, CA 95064, USA. Department of Biology, University of Bergen, Bergen 5020, Norway.

A.D. MacCall, E.J. Dick, and S. Ralston. National Marine Fisheries Service, Southwest Fisheries Science Center, 110 Shaffer Road, Santa Cruz, CA 95060, USA.

J. Brodziak. National Marine Fisheries Service, Pacific Islands Fisheries Science Center, 2570 Dole Street, Honolulu, HI, 96822.

R.E. Forrest. Fisheries and Oceans Canada Pacific Biological Station, 3190 Hammond Bay Road, Nanaimo, BC V9T 6N7, Canada.

R. Pourzand.* Center for Stock Assessment Research, MS E-2, University of California, Santa Cruz, CA 95064, USA.

Corresponding author: Marc Mangel (e-mail: msmangel@soe.ucsc.edu).

*Present address: Oracle Corporation, 475 Sansome St., San Francisco, CA 94101, USA.

Table 1. Recent stock assessments in which steepness and natural mortality were fixed (see Monk 2013 for additional examples).

Common Name	Scientific Name	Citation
Cabazon	<i>Scorpaenichthys marmoratus</i>	Cope and Key 2009
Blackgill rockfish	<i>Sebastes melanostomus</i>	Field and Pearson 2011
Canary rockfish	<i>Sebastes pinniger</i>	Stewart 2009
Cowcod	<i>Sebastes levis</i>	Dick et al. 2009
Darkblotched rockfish	<i>Sebastes crameri</i>	Stephens et al. 2011
Greenspotted rockfish	<i>Sebastes chlorostictus</i>	Dick et al. 2011
Greenstriped rockfish	<i>Sebastes elongatus</i>	Hicks et al. 2009
Lingcod	<i>Ophiodon elongatus</i>	Hamel et al. 2009
Splitnose rockfish	<i>Sebastes diploproa</i>	Gertseva et al. 2009
Arrowtooth flounder	<i>Atheresthes stomias</i>	Kaplan and Helser 2007
Black rockfish, north	<i>Sebastes melanops</i>	Wallace et al. 2007
Black rockfish, south	<i>Sebastes melanops</i>	Sampson 2007
Blue rockfish	<i>Sebastes mystinus</i>	Key et al. 2008
Chilipepper rockfish	<i>Sebastes goodei</i>	Field 2008
Longnose skate	<i>Raja rhina</i>	Gertseva and Schirripa 2008
Shortbelly rockfish	<i>Sebastes jordani</i>	Field et al. 2007
Spotted spiny dogfish	<i>Squalus suckleyi</i>	Gertseva and Taylor 2011

models with fewer parameters. On the other hand, Sissenwine and Shepherd (1987) noted that in many cases one could not reject the hypothesis of a single parameter, as in the linear limit described above.

It has become common in the last 20 years to discuss SRRs in the context of stock resilience using an alternative parameter named steepness, usually denoted by h . The BH-SRR parameterization of steepness was developed by Mace and Doonan (1988), who defined steepness as the fraction of recruitment from an unfished population when the spawning stock biomass declines to 20% of its unfished level, and was popularized by Hilborn and Walters (1992; also see Walters and Martell 2004). Antecedents for steepness can be found in Goodyear (1977, 1980) and Kimura (1988); Jensen et al. (2012) also provide a recent review. Steepness must be firmly rooted in the evolutionary ecology of the species (e.g., He et al. 2006; Mangel et al. 2010), and the reproductive biology of a stock must surely be important for its management. However, we currently lack a full explanatory theory to predict steepness based on the evolutionary ecology and life history of a species, although methods to quantify the likely values of steepness from reproductive biology are being developed (Mangel et al. 2010; Brodziak and Mangel 2012).

Given that the data to which a stock assessment model is being fitted often have little or no information about steepness or natural mortality, setting both steepness and the adult natural mortality rate to assumed fixed values is not uncommon in stock assessments (Table 1; Monk 2013). The validity of this assumption was the focus of a pair of recent simulation studies based on assessments of 12 west coast US groundfish stocks. Lee et al. (2011) concluded that in many cases natural mortality could be estimated within the stock assessment model, assuming that the data were sufficient and the assessment model was correctly specified (see Francis 2012). Alternatively, natural mortality can be at least approximated from meta-analyses or life history parameters (Hoenig 1983; Brodziak et al. 2011), but about steepness we have less intuition. Lee et al. (2012) found support for fixing steepness in that there is often little information in stock assessment data concerning steepness.

Reference points (RPs) are common outputs of stock assessments and are frequently used to help guide policy. Common RPs include unfished biomass, B_0 ; the biomass leading maximum sus-

tainable yield (MSY), B_{MSY} ; the biomass leading to maximum net production, B_{MNP} ; the rate of fishing mortality that gives MSY, F_{MSY} ; the ratio of spawning biomass per recruit when the population is fished at F_{MSY} to the spawning biomass per recruit of an unfished population, SPR_{MSY} ; maximum excess recruitment, MER; and the ratio of MER to recruitment in the unfished population, SPR_{MER} . Brooks et al. (2010) note that MER differs from MSY in that the former is based on population numbers and only depends on the SRR, while the latter is based on fishery yield in mass and also depends upon selectivity of the fishery. As a general feature, F_{MSY} is sensitive to the selectivity of fishing mortality and the biology of the species, while SPR_{MSY} is mainly sensitive to the biology of the species and thus provides a more robust RP.

The choice of SRR can have profound effects on the RPs that are an output of a stock assessment. For example, on the US west coast, the stock assessment of bocaccio (*Sebastes paucispinis*) in US waters used a BH-SRR and estimated $B_{MSY} = 0.39B_0$ (Field et al. 2009). On the other hand, Stanley et al. (2009) used a R-SRR (and ultimately a production model) for the assessment of bocaccio in Canadian waters and concluded $B_{MSY} = 0.5B_0$. Thus, alternative assessments for related stocks of the same species in the same biogeographic region can make quite different assumptions and reach quite different conclusions.

Work over the last decade has shown there are deep connections between RPs and steepness. For example, Williams 2002 (their fig. 1) showed that MSY increased with steepness in a theoretical model with varying ages of 50% selection and 50% maturity and that SPR_{MSY} was virtually the same function of steepness regardless of the combinations of age of 50% maturity and age of 50% selectivity. Similarly, Punt et al. (2008, their fig. 3c for a case study involving petrale sole, canary rockfish, sablefish, and Pacific whiting) and Brooks et al. (2010, their fig. 2 for a theoretical case study using a BH-SRR) showed that F_{MSY} is an increasing function of steepness, but that particular values depend upon the value of natural mortality and the shape of the maturity and selectivity ogives. Punt et al. (2008) also showed that in their case study B_{MSY}/B_0 and SPR_{MSY} are nearly perfectly predicted by steepness. Brooks et al. (2010) showed that

$$(3) \quad SPR_{MER} = \frac{1}{2} \sqrt{\frac{1-h}{h}}$$

Shertzer and Conn (2012) noted "[F]ixing steepness determines, in part, MSY-based management proxies" (p. 48).

In many stock assessments, a BH-SRR is used and natural mortality and steepness are fixed (Table 1 for west coast assessments; refer to Monk 2013 for a wide variety of others), thus causing one to wonder how much flexibility remains for learning about RPs from the data.

Outline of this perspective

We begin by showing additional cases of the patterns reported by Williams (2002), Brooks and Powers (2007), Punt et al. (2008), and Brooks et al. (2010), although we choose examples from actual stock assessments rather than theoretical models, to make the point that this is a general phenomenon. We show that key biological RPs of a number of recent stock assessments that used complicated models with a BH-SRR, but which fixed steepness and other life history parameters, can be predicted directly from simpler models with the same fixed values of steepness and natural mortality rate. We use both production models (PMs) and age-structured models (ASMs). PMs are still appropriately used in stock assessments, and in using a PM, the key ideas are easily explicated. We are thus able to develop intuition that is often buried in the details of an ASM. For the same reason, we use deterministic models and show that they predict with high accu-

Fig. 1. (a) Comparison of the posterior mean B_{MSY}/B_0 computed by Forrest et al. (2010) from a Bayesian hierarchical ASM and that predicted from steepness only and a PM (eq. 16). (b) SPR_{MSY} reported by Forrest et al. (2010) as a function of steepness (points) and that predicted only from steepness (line; Brooks et al. 2010 and this paper); (c) SPR_{MSY} as a function of steepness (points) and that for the stock assessments (line) listed in Table 1.

racy the RPs that are the result of stock assessments using complex age-structured demographic models.

We derive explicit formulas for steepness in terms of life history parameters and for the PM explicitly show the relationship among steepness, natural mortality, and F_{MSY} . For the ASM, we provide an example of the same relationships using numerical methods. We also show how steepness is connected to SPR for both PMs and ASMs, using analytical and numerical methods, respectively. We then discuss what it means to set $h = 1$ and how one could create appropriate priors for steepness.

We discuss research going forward and provide a perspective on using steepness to develop RPs for stock assessment. First, one may fix neither h nor M and estimate them within the stock assessment. Second, one may use a three-parameter SRR, which we show does not have the same limitations as the two-parameter BH-SRR or R-SRR. In this regard, we are preceded by Maunders (2003), who argued that the three-parameter Pella-Tomlinson production model should supplant the two-parameter Schaefer production model (Maunder 2003) as the default model (but see Prager 2003). Third, one may be more explicit about the information content of the data and what that means for policy makers by formulating an adaptive approach that accounts for uncertainties and risks (e.g., Brodziak et al. 2008). We discuss the strengths and limitations of each approach (and clearly, they are not mutually exclusive).

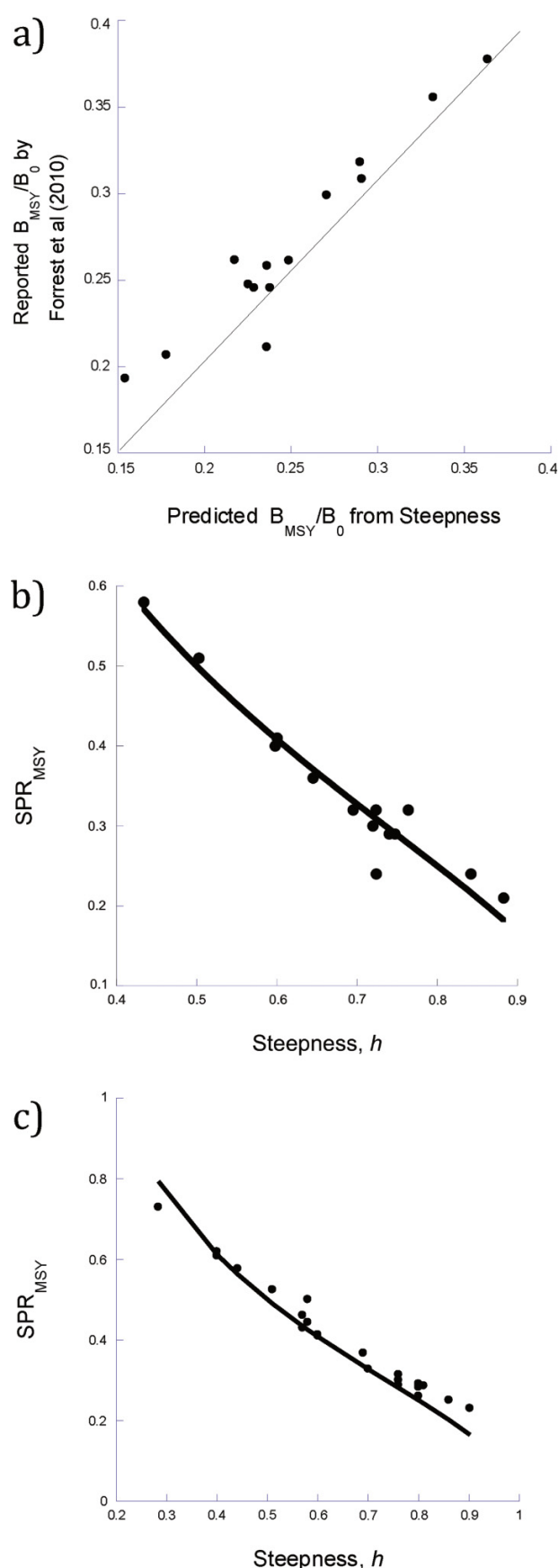
Fixing life history parameters and steepness in the BH-SRR in a stock assessment fixes RPs

We begin with additional examples of the patterns reported by Williams (2002), Punt et al. (2008), and Brooks et al. (2010). In Fig. 1a, we compare the posterior mean B_{MSY}/B_0 computed by Forrest et al. (2010) from a Bayesian hierarchical ASM and that predicted from steepness only from a PM (see below), and in Fig. 1b, the SPR_{MSY} reported by Forrest et al. (2010) as a function of steepness (points) is compared with that predicted only from steepness and the PM. In Fig. 1c, we show the same for the stock assessments listed in Table 1. These figures suggest that specifying steepness and natural mortality in a stock assessment using the BH-SRR nearly perfectly fixes the RPs, begging the question of why this is so.

Forrest et al. (2010) remarked on the tight relationship between SPR and steepness (top panel of their fig. 8 on p. 1625): "Some other observations are worth noting For the 14 populations, there was strong negative relationship between h and $\% \text{SPR}_0$ at U_{MSY} [the MSY harvest fraction] under both Beverton-Holt ($r = -0.96$) and Ricker ($r = -0.94$) recruitment (Figs. 8a, 8b)." They also noted that it was the low M rather than the high steepness that was the principle determinant of U_{MSY} and that estimates of steepness and U_{MSY} depended strongly on the assumption about M for the most data-limited stocks — showing the interdependence and confounding of these two parameters. They noted that our "... results serve as a reminder that evidence of high steepness per se is insufficient to make statements about sustainable harvest rates, as other factors, particularly natural mortality and the selectivity schedule, must be considered simultaneously" (see eq. 15 below).

Overview of the models

We begin with a PM, which has the advantage that clear, concise, and general analytical results can be obtained. We then in-



roduce a general ASM and specify the values and functions used for numerical calculation.

The production model

To directly connect to the ASM, we assume that the generation of biomass is given by a BH-SRR (see Appendix A for the R-SRR) and that the removal of biomass is due to time-independent rates of natural mortality and fishing. Thus, if $B(t)$ is the biomass at time t , its dynamics are

$$(4) \quad \frac{dB}{dt} = \frac{\alpha B}{1 + \beta B} - (M + F)B$$

where α and β are as above, and M and F are rates of natural mortality and fishing mortality, respectively. If $\beta B \ll 1$, the denominator on the right-hand side can be Taylor-expanded, leading to $\frac{dB}{dt} = \alpha B(1 - \beta B) - (M + F)B$, which is the Schaeffer model (Quinn and Deriso 1999; Walters and Martell 2004) and provides mechanistic interpretation of r and K of the logistic.

In the absence of fishing, the steady state biomass associated with eq. 4 is

$$(5) \quad B_0 = \frac{1}{\beta} \left(\frac{\alpha}{M} - 1 \right)$$

and steepness (Myers et al. 1999; Brooks and Powers 2007; Martell et al. 2008, their Appendix A; Punt et al. 2008; Brooks et al. 2010; Mangel et al. 2010)

$$(6) \quad h = \frac{\frac{\alpha}{M}}{4 + \frac{\alpha}{M}}$$

is a function of the dimensionless ratio α/M but not of β , so that steepness is independent of compensatory processes prior to recruitment.

The age-structured model

We track only the female biomass (Mangel et al. 2010), which is equivalent to the assumptions that reproduction is not limited by males and that males and females have similar patterns of growth and mortality. We let $N(a, t)$ denote the number of individuals of age a at time t . If $M(a)$ is the rate of natural mortality for fish of age a , $F(t)$ is the rate of fishing mortality in year t , and $p_s(a)$ is the selectivity of the fisheries for fish of age a to fishing mortality; then for individuals beyond the recruited class

$$(7) \quad N(a, t) = N(a - 1, t - 1) \exp[-M(a - 1) - p_s(a - 1)F(t)]$$

If $W_f(a)$ is the mass of a female of age a and $p_r(a)$ is the probability that a female of age a is reproductively mature, spawning biomass in year t is

$$(8) \quad B_s(t) = \sum_{a=1}^{a_{\max}} N(a, t) W_f(a) p_r(a)$$

Assuming a BH-SRR and that fecundity is directly proportional to mass, the number of recruits in year t is

$$(9) \quad N(0, t) = \frac{\alpha B_s(t)}{1 + \beta B_s(t)}$$

If $S(a)$ is survival to age a , determined by natural and fishing mortality as in eq. 7, then the expected spawning biomass per recruit, $SBR(0)$, in the absence of fishing mortality, is

$$(10) \quad \bar{W}_f = \sum_{a=1}^{a_{\max}} S(a) W_f(a) p_r(a)$$

and steepness is (Myers et al. 1999; Brooks and Powers 2007; Mangel et al. 2010)

$$(11) \quad h = \frac{\alpha \bar{W}_f}{4 + \alpha \bar{W}_f}$$

Mangel et al. (2010) describe the conditions on growth and mortality under which eq. 11 reduces to eq. 6.

For illustrative numerical computations with eqs. 7–11, we make the assumptions

- of von Bertalanffy growth so that length at age is $L(a) = L_{\infty} \{1 - \exp[-k(a - a_0)]\}$, where the values of asymptotic size, von Bertalanffy growth rate, and theoretical age of 0 size are, respectively, $L_{\infty} = 35$ cm, $k = 0.5$ year⁻¹, and $a_0 = -0.5$ year and a maximum age of 30 years;
- that mass is proportional to length cubed;
- that annual mortality has size-independent and size-dependent components $M(a) = m_0 + \frac{m_1}{L(a)}$, where the values for the size-independent and size-dependent mortality rates are $m_0 = 0.2$ year⁻¹ and $m_1 = 3.25$ year⁻¹, respectively (picked for illustration rather than to match any particular species);
- of a logistic ogive for maturity of the form $p_r(a) = \frac{\exp\left(\frac{a - a_m}{\sigma_m}\right)}{1 + \exp\left(\frac{a - a_m}{\sigma_m}\right)}$ with base case age at 50% maturity $a_m = 6$ years and base case dispersion parameter $\sigma_m = 0.5$ years;
- that the Beverton–Holt density dependent parameter is $\beta = 0.000001$ -kg⁻¹; and
- of a logistic selectivity curve $p_s(a) = \frac{\exp\left(\frac{a - a_{50}}{\sigma_f}\right)}{1 + \exp\left(\frac{a - a_{50}}{\sigma_f}\right)}$ for the rate of fishing mortality at age a (i.e., $F(a) = p_s(a)F$, where F is fishing mortality), with a_{50} and σ_f chosen as described below.

In the steady state, the number of individuals of age a is $N(a)$ and yield is

$$(12) \quad \bar{Y}(F) = \sum_{a=1}^{30} \bar{N}(a) W_f(a) \{1 - \exp[-M(a) - p_s(a)F]\} \frac{p_s(a)F}{M(a) + p_s(a)F}$$

We determine the value of F_{MSY} by numerical search.

The expression in eq. 11 is a process-based understanding of steepness in the ASM. From it, we see that steepness is intimately connected to life history parameters characterizing growth and mortality (cf. Shertzer and Conn 2012; Brodziak and Mangel 2012). Thus, an estimate of steepness in an assessment model is sensitive to, and most likely confounded with, other assumptions about life history parameters. Two-dimensional plots of steepness versus natural mortality or steepness versus age at maturity (Shertzer and Conn 2012) show considerable scatter across different species. The reason is that steepness is a multidimensional function of many life history parameters, and to project from this high-

dimensional space into two dimensions is almost guaranteed to generate a scatter that obscures biological relationships.

Steepness and RPs in the production model

The steady state biomass in the population associated with eq. 4 is

$$(13) \quad \bar{B}(F) = \frac{1}{\beta} \left(\frac{\alpha}{M + F} - 1 \right)$$

so that the steady state yield is

$$(14) \quad \bar{Y}(F) = F\bar{B} = \frac{F}{\beta} \left(\frac{\alpha}{M + F} - 1 \right)$$

We use eq. 14 to find the fishing mortality that produces MSY. Doing this and substituting using eq. 6 shows that

$$(15) \quad \frac{F_{MSY}}{M} = \sqrt{\frac{\alpha}{M}} - 1 = \sqrt{\frac{4h}{1-h}} - 1$$

This equation explains the observation of Forrest et al. (2010) above. High steepness in itself only guarantees that the ratio F_{MSY}/M is high. The actual value of F_{MSY} may still be relatively small if M is sufficiently low. Similarly,

$$(16) \quad \frac{B_{MSY}}{B_0} = \frac{\sqrt{\frac{4h}{1-h}} - 1}{\frac{4h}{1-h} - 1}$$

and

$$(17) \quad SPR_{MSY} = \frac{SBR(F_{MSY})}{SBR(0)} = \sqrt{\frac{M}{\alpha}} = \sqrt{\frac{1-h}{4h}}$$

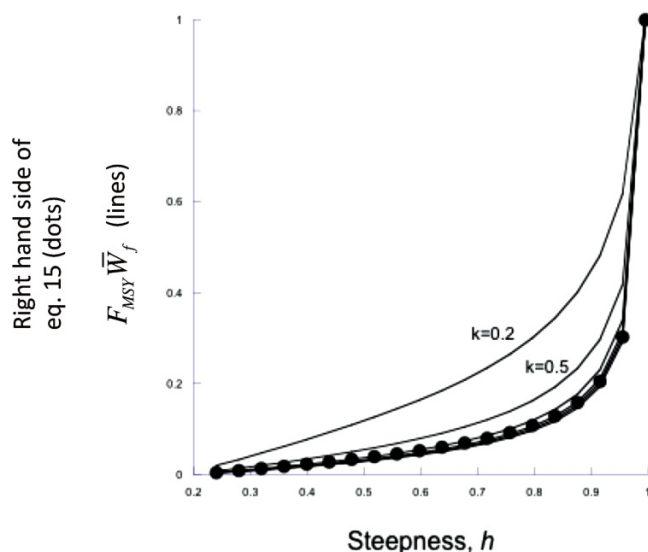
which is exactly the value of SPR_{MER} derived by Brooks et al. (2010) for an age-structured model. The reason is that the production model could equally concern numbers as well as biomass, and SPR_{MER} is focused on numbers.

These equations add to the set of analytical solutions for RPs as a function of α and M (e.g., Schnute and Kronlund 1996; Schnute and Richards 1998; Forrest et al. 2008; Martell et al. 2008). The optimal rate of fishing mortality is independent of β , which sets the size of the unfished biomass. That is, the level of fishing mortality maximizing yield is a function of productivity of the population but not its scale. The left-hand sides of eqs. 15–17 are dimensionless numbers that allow comparison across species. Thus, for example, two species with very different life histories but assigned the same value of steepness will have the same ratio of F_{MSY} to M . It is also apparent from eq. 15 that the fraction of total mortality due to fishing when the stock is fished at MSY, $F_{MSY}/(F_{MSY} + M)$, will be a function of steepness only.

The values of B_{MSY}/B_0 predicted by steepness in Fig. 1a were based on eq. 16. Thus, steepness both fully determines a key RP, and a deterministic PM nearly perfectly predicts the results of a more complex, computer-intensive stochastic ASM.

From the perspective of estimating stock assessment parameters with a PM, there are only two free parameters among the set $\{h, \alpha, M, F_{MSY}\}$. Assuming fixed values of steepness and natural mortality completely determines the value of the RP F_{MSY} . Furthermore, the single parameter steepness is doing double-duty, simultaneously determining two major RPs (eqs. 16 and 17). Suppose in a particular situation we assert that $h = 0.8$ and $M = 0.15$ (both very reasonable choices; Rose and Cowan (2003), discussion

Fig. 2. A comparison of the right-hand side of eq. 16, scaled to its value when $h = 0.99$ (dots) and $F_{MSY}\bar{W}_f$, also scaled to its maximum value, as a function of h when the von Bertalanffy growth parameter increases as $k = 0.2, 0.5, 1.0, 1.5, 2.0, 3.0$, and 4.0 .



around their fig. 3). The analysis given above implies that $B_0 = 15/\beta$, $F_{MSY} = 3M = 0.45$, $B_{MSY} = 0.2B_0$, and $MSY = 0.09B_0$. The only free parameter that can be estimated in the PM given these assumptions is B_0 (or alternatively β), and it is clear that its estimated value is strongly conditional on assumed values of M or h .

Clark (1991) proposed another common management strategy: to choose the fishing mortality rate that produces a steady state biomass that is a fraction x of the unfished biomass. This RP is determined by solving this equation for F_x

$$(18) \quad \frac{1}{\beta} \left(\frac{\alpha}{M + F_x} - 1 \right) = x \frac{1}{\beta} \left(\frac{\alpha}{M} - 1 \right)$$

Equation 18 can be rewritten as

$$(19) \quad \frac{\frac{\alpha}{M}}{1 + \frac{F_x}{M}} - 1 = x \left(\frac{\alpha}{M} - 1 \right)$$

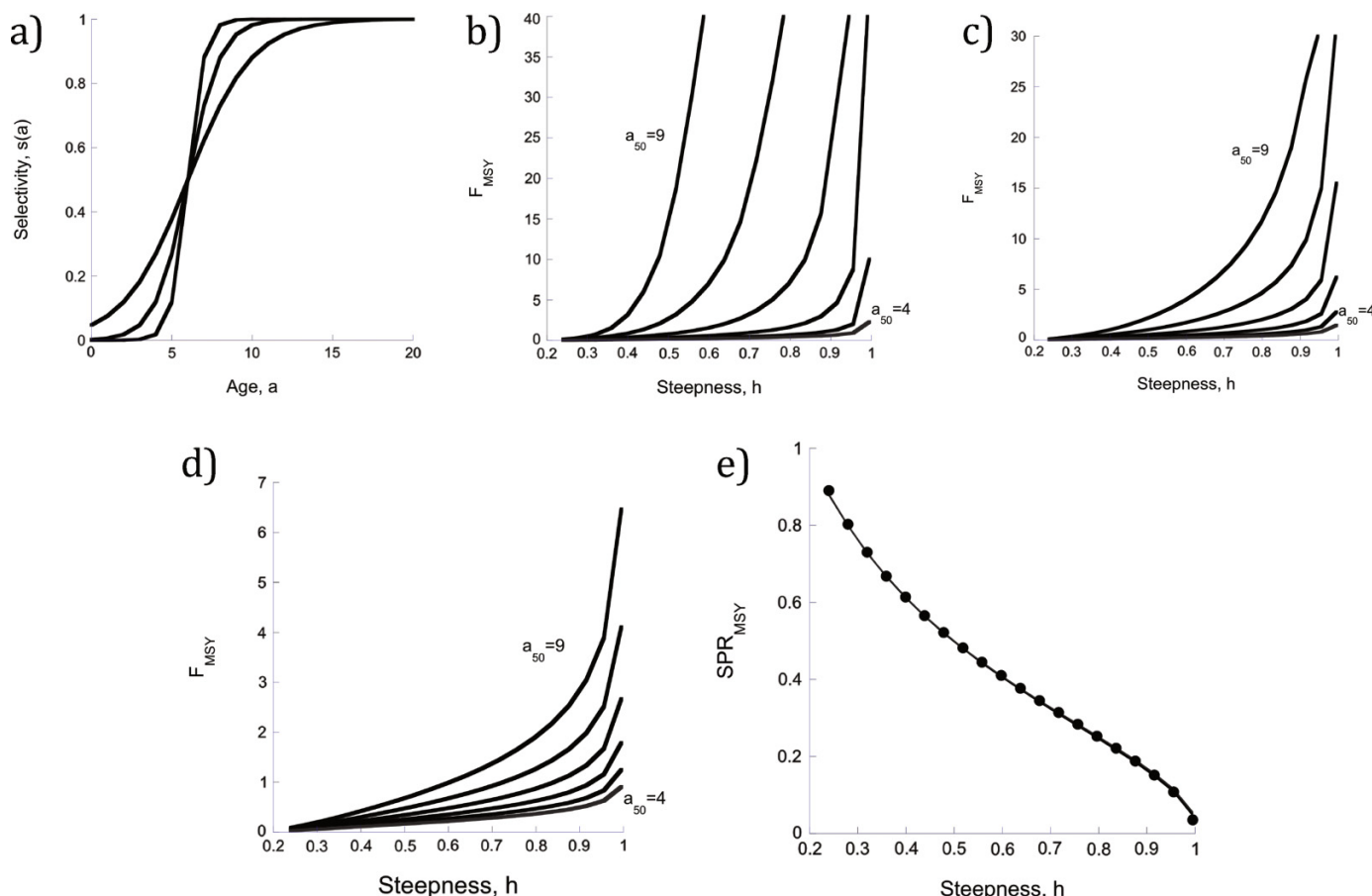
Since this equation only depends upon F_x/M , x , and α/M , we conclude that the RP F_x/M is completely determined by the value of x and steepness.

Steepness and RPs in the age-structured model

We first discuss the analogue of $\frac{F_{MSY}}{M} = \sqrt{\frac{4h}{1-h}} - 1$ and then turn to SPR results shown in Figs. 1b, 1c. Comparing eqs. 6 and 11 suggests that in the ASM $F_{MSY}\bar{W}_f$ will be a function of steepness, although it need not be the right-hand side of eq. 15. To investigate this idea, we note that as the von Bertalanffy growth rate increases, mass at age increases so that for large values of k individuals recruited to the fishery model are nearly fully grown. The consequence of this is that survival and reproduction are nearly constant, so that the ASM approximates the PM (precise conditions are given in Mangel et al. (2010)).

In Fig. 2, we show that as k increases $F_{MSY}\bar{W}_f$ clearly approaches a limiting function determined only by steepness of the PM. There is no reason to suppose that the analytical result for the PM, eq. 15, will hold for the ASM except when the limit holds. However, for

Fig. 3. (a) Three sigmoidal selectivity curves (shown here for the case in which $a_{50} = 6$ years) that differ in the value of $\sigma_f (=0.5, 1.0, \text{ and } 2.0)$. Panels (b–d) show F_{MSY} as a function of steepness for a_{50} ranging from 4 to 9 years for the case in which the probability of maturity is 50% at 6 years. (e) SPR_{MSY} for using the widest selectivity curve and the values of F_{MSY} in panels b–d. Points are the value of SPR_{MSY} from the production model, and the lines — which are visually indistinguishable — are for selectivity curves that have midpoints at ages 4, 5, 6, 7, 8, or 9.



the ASM, $F_{MSY}\bar{W}_f$ is uniquely defined by steepness, life history parameters, and the fishery selectivity pattern, as noted in Forrest et al. (2008) and Forrest and Walters (2009) for U_{MSY} , the exploitation fraction.

To investigate SPR , we held the von Bertalanffy growth rate constant at $k = 1$, we specified fixed values of steepness (ranging from 0.24 to 0.995), and determined α (eq. 11) and F_{MSY} numerically (eq. 12). We limit the results shown here to the case in which 50% of the population is mature at age 6, a_{50} varies from 4 years (so that fishing starts before maturity) to 9 years (so that fishing starts long after maturity), and three selectivity curves (Fig. 3a). Increasing steepness leads to increasing F_{MSY} regardless of the selectivity curve (Figs. 3b–3d); although F_{MSY} does not approach infinity as h approaches 1, the associated mortality rates are very large.

It should be remembered that there are six SPR_{MSY} curves in Fig. 3e, but they are visually indistinguishable. It is easily verified that the same pattern emerges with domed selectivity functions; the values of SPR_{MSY} are fixed by steepness and a BH-SRR and are virtually perfectly given by that of the production model. We thus conclude that conditioned on the other life history parameters, F_{MSY} is determined by steepness and the selectivity curves but that SPR_{MSY} is independent of the selectivity curve but strongly depends upon steepness.

Setting $h = 1$ and a prior for steepness

Setting steepness equal to 1 is equivalent to assuming that the stock is infinitely productive, since the only way to achieve $h = 1$ in eqs. 6 or 11, for finite mortality, is to have $\alpha \rightarrow \infty$; it is also equiv-

alent to the assumption that the fishing rate generating MSY is infinite, which is most easily seen in eq. 15 for the PM and hinted at in Figs. 3b–3d. Thus setting $h = 1$ is biologically unrealistic (Brodziak et al. 2002; Martell et al. 2008; Mangel et al. 2010), clearly risk-prone, and requires precautionary maintenance of an adequate minimum biomass if used as an approximation in an assessment, although it is unclear how to determine the precautionary minimum.

Alternatively, one may give a probabilistic interpretation to the assignment of a fixed value to steepness, whether the fixed value is 1 or less than 1. Setting $h = 1$ is equivalent to $\Pr\{R(0.2B_0) = R_0\} = 1$ (i.e., no variation in recruitment is allowed).

However, maximal variation in recruitment is allowed when $R(0.2B_0)$ can take any value between $0.2R_0$ and R_0 (whether recruitment can exceed R_0 depends upon the probabilistic interpretation of the BH-SRR; Mangel et al. 2006). That is, at 20% of unfished spawning biomass, one could, in principle, obtain any level of recruitment between 20% and 100% of unfished recruitment, so steepness could take any value between 0.2 and 1.0.

Thus an appropriate prior distribution for steepness in a BH-SRR is a diffuse prior on the open interval (0.2, 1). The choice of a diffuse prior is consistent with the principle of indifference, which assigns equal probability to equally plausible hypotheses about a parameter. A diffuse beta density, constrained to be 0 at $h = 0.2$ (because the stock will not be able to persist for $h < 0.2$; He et al. 2006) and at $h = 1.0$ (since no stock can be infinitely reproductive), represents the prior knowledge about h ; also see Michielsens and McAllister (2004). Admitting broad uncertainty in

steepness, rather than fixing it at a single value, may also prove to be more robust to the problem of “errors-in-variables” bias (Hilborn and Walters 1992, chapter 7; Walters and Martell 2004, chapter 7) that arises as a result of errors in measurement of the spawning stock size.

If one has life history information, then it is possible to construct a prior for steepness using the methods of Mangel et al. (2010). More purely statistical methods would include an empirical Bayes approach using data from previous assessments or the meta-analysis results from Myers et al. (1999).

Three options for moving forward

We have shown that fixing steepness and life history parameters (natural mortality in a PM or natural mortality and growth in an ASM) fixes many important RPs. Doing so essentially limits the way that the data can inform the RP (e.g., Fig. 1). We now discuss three options for getting out of this difficult situation.

Do not fix steepness and natural mortality rate

One option is simply not to fix steepness and the natural mortality but to estimate them from the data. In this context, we advocate using constrained likelihood (e.g., Edwards 1992) or Bayesian estimation approaches that incorporate prior information on the probable distribution of h and M . However, as we discussed at the start of this paper, those parameters are often fixed because we simply cannot estimate them from the usual data in a stock assessment.

This observation prompts a challenge that can be met through thorough simulation analyses — determining what kinds of data would be necessary so that steepness and natural mortality could be estimated as part of a stock assessment. The papers of Lee et al. (2011, 2012) are a welcome step in this direction, but more work needs to be done.

Replace the BH-SRR by a SRR to avoid the difficulty

Alternatively, we may seek a SRR that avoids the difficulty of fixed RPs when steepness and life history parameters are fixed. One possibility is Shepherd SRR (S-SRR; Shepherd 1982; Quinn and Deriso 1999). For the PM this is

$$(20) \quad \frac{dB}{dt} = \frac{\alpha B}{1 + \beta B^{1/n}} - (M + F)B$$

where $n > 0$ is a parameter; $n = 1$, corresponding to a BH-SRR, separates overcompensatory geometry ($n < 1$) similar to the R-SRR and undercompensatory geometry ($n > 1$). Taylor expansion of the denominator on the right-hand side of eq. 20 leads to the Pella–Tomlinson (Pella and Tomlinson 1969) modification of the Schaefer model, much as eq. 4 leads to the Schaefer model itself. Thus, using eq. 20 also provides a mechanistic interpretation of the parameters of the Pella–Tomlinson model in terms of life history variables.

In this case, steepness is

$$(21) \quad h = \frac{0.2 \frac{\alpha}{M}}{1 + 0.2^{1/n} \left(\frac{\alpha}{M} - 1 \right)}$$

and the analogue of eq. 15 is

$$(22) \quad \frac{F_{MSY}}{M} = \frac{\frac{\alpha}{M}(1 - n) + \sqrt{\left(\frac{\alpha}{M}\right)^2(1 - n)^2 + 4\frac{\alpha n}{M}}}{2} - 1$$

Thus for the S-SRR, F_{MSY}/M involves both steepness and the compensation parameter n , providing enough flexibility for an independent parameter (e.g., a value of F_{MSY} , SPR_{MSY} , or B_{MSY}) to be estimated directly from the data (cf. Martell et al. 2008). The benefit of this approach is that the specification of the SRR is now parametrically continuous (in α , β , and n) rather than having one of the parameters fixed but hidden. As discussed above, when using the BH-SRR we are implicitly assuming that $\Pr\{n = 1\} = 1$. However, the probability that a real number takes a single precise value is almost surely 0, and as a result, the BH-SRR has a vanishingly small probability of being the actual SRR if the true recruitment dynamics were to follow a S-SRR.

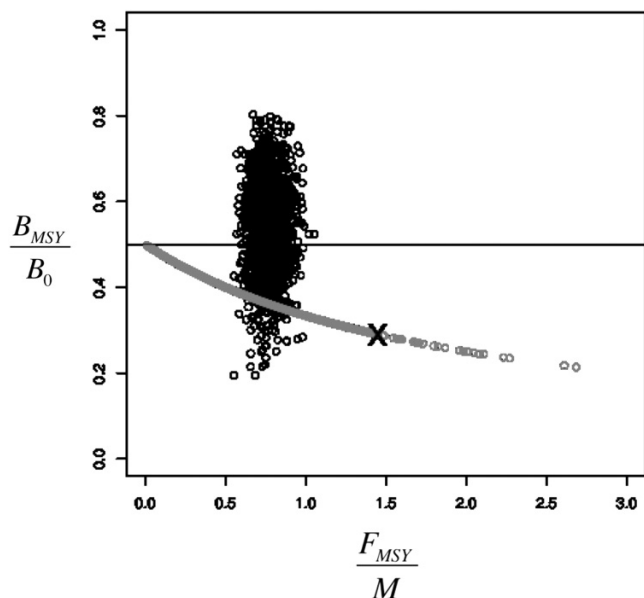
In many stock assessments, one must deal with a lack of contrast in observed spawner abundance and a lack of available historical information on age structure and size structure, and adding another shape parameter will not improve the situation. A Bayesian approach using continuous prior probability distributions for the shape and (or) other two parameters (possibly including steepness) is practical. At present, specification of prior probability distributions may necessarily be ad hoc (a common practice in Bayesian analysis), but the problem is well suited to comparative or meta-analytic approaches now that it is recognized. Previous exclusive use of conventional two-parameter forms has prevented recognition of this problem. Alternatively, one could also use a frequentist approach and set up a discrete grid of equally plausible values for the shape parameter, treat these parameter values as separate hypotheses, and model average the results, based on goodness-of-fit criteria such as AIC and the associated relative likelihood (e.g., Burnham and Anderson 2002; Ianelli 2002; Brodziak and Piner 2010). In either case, there is potential for a meta-analysis of the third parameter, which is impossible in the case of fixed assumptions for steepness and natural mortality using two-parameter SRRs.

DeYoreo et al. (2012) demonstrated the feasibility of this approach by using a three-parameter SRR (but not exactly the S-SRR) in their analysis of cowcod (*Sebastes levis*). In Fig. 4, we plot relative values B_{MSY}/B_0 versus F_{MSY}/M instead of their absolute values. These are the grey circles and show a very tight relationship. Although this relationship might be interpreted as a profound aspect of biology, it is really due to the assumptions about the BH-SRR and fixing steepness. The black X shows the particular result obtained when a value of $h = 0.6$ is asserted to be true. On the other hand, the black circles show the results when a three-parameter SRR is used. The artifactual relationship between B_{MSY}/B_0 and F_{MSY}/M disappears, giving more insight into the actual biology of the stock.

Be fully honest about the limitations of the data and the stock assessment

An alternative interpretation of our findings is that management policy with biomass targets or rebuilding plans on a fixed timetable with specified probability is often overstepping what can realistically be expected from a defensible assessment of an individual stock. That is, the community of stock assessment scientists needs to agree on workable protocols for several classes of life history parameters, ecosystem types, and fishery histories that are reasonably robust in achieving management objectives in the face of scientific uncertainty. Stock assessment scientists cannot become so conservative that fisheries become unviable, and the agreed-upon protocols should be applied to individual stocks as a process matter, not making believe they represent best science for each assessment. In this case, it will also be important to formulate an adaptive approach for managing fisheries that explicitly accounts for uncertainties and risks. There are certainly some situations where the data have enough information content that estimating more parameters is practicable, and other situations where proxies and agreed protocols are the best we can do. Developing good proxies and protocols is a scientific matter. It

Fig. 4. DeYoreo et al. (2012) used both a BH-SRR and three-parameter SRR, similar to the S-SRR in a stock assessment of cowcod (*Sebastes levis*). We show samples from posterior distributions arising from different values of steepness. Unlike most stock assessments, we plot B_{MSY}/B_0 versus F_{MSY}/M . The grey circles show the results for the BH-SRR. This curve is another way of representing the constraint placed on a stock assessment by using a BH-SRR and specifying steepness — results must lie along this curve. The black circles represent the outcome of the three-parameter SRR. The black X represents the result when steepness is asserted to be 0.6.



should be based on meta-analyses and management strategy evaluation.

One reason that fisheries management has evolved to greater and greater specificity, thus demanding more from stock assessments (e.g., 10-year and longer projections of stock size, biomass targets that are sometimes extrapolations) and less flexibility, is that flexibility was abused leading to widespread overfishing. However, the first responsibility of scientists is to the integrity of science, and it is critical to be explicit about what is known and not known.

Discussion

Our results show that if one assumes fixed values for steepness and natural mortality and also assumes a two-parameter SRR (e.g., BH-SRR or R-SRR), then key RPs are determined a priori so that subjective decisions masquerade as objective analysis. This is a very undesirable situation because incorrect assumptions will lead to inaccurate estimates of target biomass and the overfishing rate, which are critical RPs.

Thus, the point estimates or posterior samples of a fitted stock assessment model can provide a false sense of precision and information because an important source of uncertainty is hidden by constraints associated with the decision to use a particular two-parameter SRR with fixed M and h . In these situations, unfished biomass (or β of the BH- or R-SRR) is the only estimable parameter. An ASM using a two-parameter SRR with estimated recruitment deviations has many ways of explaining observed catch time series, survey indices, and fishery CPUE information. What will be viewed as “noise” in the estimation process may actually be forcing RPs to be even less reliable, as results are constrained by the limits to SPR imposed by the fixed value of steepness.

B_0 , F_{MSY} , and B_{MSY} are standard RPs that are expected to be estimated by standard data-rich stock assessments. However, assessments have often had a difficult time finding them, especially for resources that have been chronically overexploited (e.g., Brodziak et al. 2008). It may be that the data contain insufficient information to estimate RPs with much precision, particularly since they are likely to change with environmental conditions (Mangel et al. 2002). We have identified another potential source of the problem of being unable to estimate RPs in a stock assessment.

Current practice for US west coast groundfish stocks is to determine a value for steepness (estimated, if possible, but usually fixed at a single value) and independently assert a target proxy value for SPR_{MSY} , but as Figs. 1 and 3 show these are not independent quantities. For purposes of rebuilding overfished stocks, an additional target proxy for B_{MSY} is adopted, but that is also fixed, relative to unfished biomass, by steepness. Differences between RPs based on alternative targets have been acknowledged in recent assessments (e.g., PFM 2012, p. 21).

In the PM, we treated α as an independent parameter, which together with M specified the value of h . However, in an ASM, the value of α is typically a derived parameter, which depends on estimates of B_0 , R_0 , and h and the fishery data, and this can be used to provide information on the likely consistency of values of h and M . As a simple illustration, suppose a fishery has experienced a prolonged stable period of overfishing so that a low biomass has been maintained for some length of time and the catch (C) has an observed mean age of T years. At this low biomass, the ratio of recruits to spawners is close to the value of α implied by estimates of B_0 , R_0 , and h . The spawning population (in numbers, S) is given by estimated $S = C/F$, and the recruitment is estimated by virtual population projection of that abundance back to the age of recruitment, or $R = (C/F)\exp(TM)$. An approximate estimate of α is thus given by $R/S = \exp(TM)$, where T is an observed value. Accordingly, we can rewrite eq. 6 as $\frac{\exp(TM)}{M} \approx \frac{4h}{1-h}$, which further demonstrates the lack of independence between M and h in standard stock assessment practice. This relationship can also be used as a cross-check for suggested values of M and h given T . It is also interesting to note that if the mean age of the catch is approximately $T \approx 1/M$, the value of α is approximately $\exp(1)$ or about 2.7, which is remarkably near the geometric mean (2.6) of the range of 1–7 obtained for a lognormally distributed α estimated by Myers et al. (1999) in their meta-analysis of 700 spawner–recruitment data sets.

Assessments are being attempted on stocks with progressively more limited data. In these data-limited cases, more assumptions combined with fewer data tend to reduce the chances for reliable science. The choice of a SRR tends to be driven by local conventions. As described above, for groundfish the BH-SRR is entrenched on the US west coast, though for the same species (e.g., bocaccio) the R-SRR was used by the Canadians for an adjacent stock. These SRRs are adopted with surprisingly strong levels of belief, though analyses have consistently shown no statistical ability to distinguish among them (e.g., Dorn 2002; Brodziak 2002). Furthermore, many of the SRRs assume density-dependent mortality in early life history stages. Clearly, there is a wide range of conditions under which this general mechanism operates, but whether per capita mortality rate of eggs and larvae can be adequately approximated by a linear function of cohort population size, which is assumed under the BH-SRR, remains to be determined. It is difficult to envision that this is the case when larvae are distributed on spatial scales of 1000 km of coastline. Furthermore, multiple mechanisms are nearly always present, ranging from effects on parental fecundity and maturity to survival and growth of propagules (e.g., Ralston and O'Farrell 2008).

Some recent efforts to explore ASMs using Markov chain Monte Carlo (MCMC) simulations for Bayesian methods have encoun-

tered severe difficulty if all parameters (including M and h) are estimated either freely or with informative priors. In a rather simple five-parameter stock assessment model of cowcod, Dick et al. (2007) encountered convergence problems requiring extreme chain thinning to 1 in 10 000 iterations. Similarly, Stewart et al. (2012) conducted a MCMC exploration of sablefish (*Anoplopoma* spp.) requiring thinning of 1 in 50 000 runs. Although high correlations may exist among other parameters in the model, such as those describing selectivity curves (Hamel and Stewart 2009), we suspect that a fundamental problem lies in the confounding of M and α or equivalently in the strong relationship between M and h . In particular, the strong linkage between M and h shows that model approximation errors in fishery selectivity, SRR, and life history parameters will propagate into the implied value of F_{MSY} . Using inconsistent values of M and h will also cause model approximation errors, which will affect convergence of MCMC simulations to the target posterior distribution.

Martell et al. (2008) used an ASM to estimate F_{MSY} directly and treated steepness as a derived quantity rather than an input. They noted that the derived posterior distribution has the property that “the modes of all three distributions are considerably less than the value of $h = 0.75$ in Helser and Martell (2007)” (p. 1594). They further noted that “...steepness is derived from estimates of F^* [F_{MSY}], life history parameters, and the vulnerability schedule” (p. 1594). In light of our results, given F^* the life history parameters, and the vulnerability schedule, steepness is fixed. If those input quantities have a distribution, then so will steepness. Indeed Martell et al. (2008) noted some “artifacts” of the way that selectivity and mortality interact to shape steepness and then showed (their Appendix A) that these are indeed fixed. Martell et al. (2008), Forrest et al. (2008), and Forrest and Walters (2009) provide further details quantifying the interaction among life history parameters, selectivity, steepness (via the Goodyear compensation ratio), and optimal harvest.

Martell (2009) provided an alternative stock assessment for Pacific hake (*Merluccius productus*) in Canadian and US waters that was based on management-oriented methodologies developed at the Pacific Biological Station (Schnute and Kronlund 1996; Schnute and Richards 1998) and The University of British Columbia (Martell et al. 2008). In this approach, both M and F_{MSY} are given probability distributions, and steepness is obtained by analytical transformation. As noted in Martell (2009), “a prior probability for F^* [F_{MSY}] is nearly equivalent to a prior probability for steepness h ” (p. 8). Our results have shown in the simplest way possible (for the PM) that this is a mathematical certainty. The same is true for the ASM, although uncertainty in the selectivity and maturity ogives means that we are dealing with an unknown function of steepness. In an earlier stock assessment for Pacific hake (Helser and Martell 2007), steepness was fixed at 0.75, natural mortality was set at $M = 0.23 \text{ year}^{-1}$, and a BH-SRR relationship was used. In such a case, there is little left to estimate, other than the scale of the population size, conditioned on the fixed parameters.

In conclusion, there is much work to be done to resolve the difficulties caused by the linkage among steepness, life history parameters, and RPs. The fate of fish stocks virtually rests on this work, and there is not a moment to be lost in resolving the problems.

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References

- Beverton, R.J.H., and Holt, S.J. 1957. On the dynamics of exploited fish populations. HMSO, London. Republished by Chapman and Hall 1993.
- Brodziak, J. 2002. In search of optimal harvest rates for west coast groundfish. *N. Am. J. Fish. Manage.* 22: 258–271. doi:10.1577/1548-8675(2002)022<0258:ISOHR>2.0.CO;2.
- Brodziak, J.K.T., and Mangel, M. 2012. Estimating probable values of stock-recruitment steepness based on life history parameters: a case study for the Western and Central North Pacific Striped Marlin stock. *Bull. Mar. Sci.* [In review.]
- Brodziak, J., and Piner, K. 2010. Model averaging and probable status of North Pacific striped marlin, *Tetrapturus audax* Can. J. Fish. Aquat. Sci. 67(5): 793–805. doi:10.1139/F10-029.
- Brodziak, J.K.T., Overholtz, W.J., and Rago, P.J. 2002. Reply: Does spawning stock affect recruitment of New England groundfish? Interpreting spawning stock and recruitment data in New England. *Can. J. Fish. Aquat. Sci.* 59(1): 193–195. doi:10.1139/f01-208.
- Brodziak, J.K.T., Cadrin, S.X., Legault, C.M., and Murawski, S.A. 2008. Goals and strategies for rebuilding New England groundfish stocks. *Fish. Res.* 94: 355–366. doi:10.1016/j.fishres.2008.03.008.
- Brodziak, J., Ianelli, J., Lorenzen, K., and Methot, R.D., Jr. (Editors). 2011. Estimating natural mortality in stock assessment applications. US Dep. Commer. NOAA Tech. Memo. NMFS-F/SPO-119.
- Brooks, E.N., and Powers, J.E. 2007. Generalized compensation in stock-recruit functions: properties and implications for management. *ICES J. Mar. Sci.* 64: 413–424. doi:10.1093/icesjms/fsl046.
- Brooks, E.N., Powers, J.E., and Cortes, E. 2010. Analytical reference points for age-structured models: application to data-poor fisheries. *ICES J. Mar. Sci.* 67: 165–175. doi:10.1093/icesjms/fsp225.
- Burnham, K.P., and Anderson, D.R. 2002. Model selection and multimodel inference. 2nd ed. Springer Verlag, New York.
- Clark, W.G. 1991. Groundfish exploitation rates based on life history parameters. *Can. J. Fish. Aquat. Sci.* 48(5): 734–750. doi:10.1139/f91-088.
- Cope, J.M., and Key, M. 2009. Status of Cabezon (*Scorpaenichthys marmoratus*) in California and Oregon Waters as Assessed in 2009. Status of the Pacific Coast Groundfish Fishery through 2009, Stock Assessment and Fishery Evaluation: Stock Assessments, STAR Panel Reports, and Rebuilding Analyses. Pacific Fishery Management Council, Portland, Oregon.
- DeYoreo, M., Dick, E.J., and MacCall, A.D. 2012. Incorporating abundance data into Depletion-Based Stock Reduction Analysis (DBSA). [In preparation.]
- Dick, E.J., Ralston, S., and Pearson, D. 2007. Status of cowcod, *Sebastes levis*, in the Southern California Bight [online]. Pacific Fishery Management Council, Portland, Oregon. Available from http://www.pcouncil.org/wp-content/uploads/certified_cowcod_Dec_2007.pdf.
- Dick, E.J., Ralston, S., Pearson, D., and Wiedenmann, J.R. 2009. Updated status of cowcod, *Sebastes levis*, in the Southern California Bight. Status of the Pacific Coast Groundfish Fishery through 2009, Stock Assessment and Fishery Evaluation: Stock Assessments, STAR Panel Reports, and Rebuilding Analyses. Pacific Fishery Management Council, Portland, Oregon.
- Dick, E.J., Pearson, D., and Ralston, S. 2011. Status of greenspotted rockfish, *Sebastes chlorostictus*, in U.S. waters off California [online]. Pacific Fishery Management Council, Portland, Oregon. Available from http://www.pcouncil.org/wp-content/uploads/Greenspotted_Rockfish_2011_Assessment.pdf.
- Dorn, M.W. 2002. Advice on west coast rockfish harvest rates from Bayesian meta-analysis of stock-recruit relationships. *N. Am. J. Fish. Manage.* 22: 280–300. doi:10.1577/1548-8675(2002)022<0280:AOWCRH>2.0.CO;2.
- Edwards, A.W.F. 1992. Likelihood. The Johns Hopkins University Press, Baltimore, Maryland.
- Field, J.C. 2008. Status of the chilipepper rockfish, *Sebastes goodei*, in 2007. Status of the Pacific Coast Groundfish Fishery through 2008, Stock Assessment and Fishery Evaluation: Stock Assessments, STAR Panel Reports, and Rebuilding Analyses. Pacific Fishery Management Council, Portland, Oregon.
- Field, J.C., and Pearson, D. 2011. Status of the blackgill rockfish, *Sebastes melanostomus*, in the Conception and Monterey INPFC areas for 2011 [online]. Pacific Fishery Management Council, Portland, Oregon. Available from http://www.pcouncil.org/wp-content/uploads/G4a_ATT13_STATUS_BLACKGILL_SEPT2011BB.pdf.
- Field, J.C., Dick, E.J., and MacCall, A.D. 2007. Stock assessment model for the shortbelly rockfish, *Sebastes jordani*, in the California Current. NOAA Tech. Memo. NMFS, NOAA-TM-NMFS-SWFSC-405.
- Field, J.C., Dick, E.J., Pearson, D., and MacCall, A.D. 2009. Status of bocaccio, *Sebastes paucispinis*, in the Conception, Monterey and Eureka INPFC areas for 2009 [online]. Pacific Fishery Management Council, Portland, Oregon. Available from http://www.pcouncil.org/wp-content/uploads/Bocaccio_Final_Jan15_2010.pdf.
- Forrest, R.E., and Walters, C.J. 2009. Estimating thresholds to optimal harvest rate for long-lived, low-fecundity sharks accounting for selectivity and density dependence in recruitment. *Can. J. Fish. Aquat. Sci.* 66(12): 2062–2080. doi:10.1139/F09-137.

- Forrest, R.E., Martell, S.J.D., Melnychuk, M.C., and Walters, C.J. 2008. An age-structured model with leading management parameters incorporating age-specific selectivity and maturity. *Can. J. Fish. Aquat. Sci.* **65**(2): 286–296. doi:10.1139/f07-156.
- Forrest, R.E., McAllister, M.K., Dorn, M.W., Martell, S.J.D., and Stanley, R.D. 2010. Hierarchical Bayesian estimation of recruitment parameters and reference points for Pacific rockfishes (*Sebastes* spp.) under alternative assumptions about the stock-recruit function. *Can. J. Fish. Aquat. Sci.* **67**(10): 1611–1634. doi:10.1139/F10-077.
- Francis, R.I.C.C. 2012. The reliability of estimates of natural mortality from stock assessment models. *Fish. Res.* **119–120**: 133–134. doi:10.1016/j.fishres.2011.12.005.
- Gertseva, V.V., and Schirripa, M.J. 2008. Status of the longnose skate (*Raja rhina*) off the continental US Pacific Coast in 2007. Pacific Fishery Management Council, Portland, Oregon.
- Gertseva, V., and Taylor, I.G. 2011. Status of the spiny dogfish shark resource off the continental U.S. Pacific Coast in 2011 [online]. Pacific Fishery Management Council, Portland, Oregon. Available from http://www.pcouncil.org/wp-content/uploads/Spiny_Dogfish_2011_Assessment.pdf.
- Gertseva, V.V., Cope, J.M., and Pearson, D.E. 2009. Status of the U.S. splitnose rockfish (*Sebastes diploproa*) resource in 2009. Status of the Pacific Coast Groundfish Fishery through 2009, Stock Assessment and Fishery Evaluation: Stock Assessments, STAR Panel Reports, and Rebuilding Analyses. Pacific Fishery Management Council, Portland, Oregon.
- 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*. Edited by W. Van Winkle. Pergamon Press, New York. pp. 186–195.
- Goodyear, C.P. 1980. Compensation in fish populations. In *Biological monitoring of fish*. Edited by C. Hocutt and C.J. Stauffer. D.C. Heath Co., Lexington, Mass. pp. 252–280.
- Hamel, O., and Stewart, I.J. 2009. Stock assessment of Pacific hake, *Merluccius productus*, (a.k.a. whiting) in U.S. and Canadian waters in 2009. Pacific Fishery Management Council, Portland, Oregon. Available from http://www.pcouncil.org/bb/2009/0309/G1a_ATT1_0309.pdf.
- Hamel, O.S., Sethi, S.A., and Wadsworth, T.F. 2009. Status and future prospects for lingcod in waters off Washington, Oregon, and California as assessed in 2009. Status of the Pacific Coast Groundfish Fishery through 2009, Stock Assessment and Fishery Evaluation: Stock Assessments, STAR Panel Reports, and Rebuilding Analyses. Pacific Fishery Management Council, Portland, Oregon.
- He, X., Mangel, M., and MacCall, A. 2006. A prior for steepness in stock-recruitment relationships, based on an evolutionary persistence principle. *Fish. Bull.* **104**: 428–433.
- Helser, T.E., and Martell, S. 2007. Stock Assessment of Pacific Hake (Whiting) in U.S. and Canadian Waters in 2007. Report of the U.S.–Canada Pacific hake Joint Technical Committee (JTC).
- Hicks, A.C., Haltuch, M.A., and Wetzel, C. 2009. Status of greenstriped rockfish (*Sebastes elongatus*) along the outer coast of California, Oregon, and Washington. Status of the Pacific Coast Groundfish Fishery through 2009, Stock Assessment and Fishery Evaluation: Stock Assessments, STAR Panel Reports, and Rebuilding Analyses. Pacific Fishery Management Council, Portland, Oregon.
- Hilborn, R., and Walters, C.J. 1992. Quantitative fisheries stock assessment: choice, dynamics and uncertainty. Routledge, Chapman, and Hall, New York.
- Hoening, J.M. 1983. Empirical use of longevity data to estimate mortality rates. *Fish. Bull.* **81**: 898–903.
- Ianelli, J.N. 2002. Simulation analyses testing the robustness of productivity determinations from west coast Pacific ocean perch stock assessment data. *N. Am. J. Fish. Manage.* **22**: 301–310. doi:10.1577/1548-8675(2002)022<0301:SATTRO>2.0.CO;2.
- Jensen, O.P., Branch, T.A., and Hilborn, R. 2012. Marine fisheries as ecological experiments. *Theor. Ecol.* **5**: 3–22. doi:10.1007/s12080-011-0146-9.
- Kaplan, I.C., and Helser, T.E. 2007. Stock assessment of the arrowtooth flounder (*Atheresthes stomias*) population off the west coast of the United States in 2007. Status of the Pacific Coast Groundfish Fishery through 2008, Stock Assessment and Fishery Evaluation: Stock Assessments, STAR Panel Reports, and Rebuilding Analyses. Pacific Fishery Management Council, Portland, Oregon.
- Key, M., MacCall, A.D., Field, J., Aseltine-Neilson, D., and Lynn, K. 2008. The 2007 assessment of blue rockfish (*Sebastes mynustinus*) in California. Status of the Pacific Coast Groundfish Fishery through 2008, Stock Assessment and Fishery Evaluation: Stock Assessments, STAR Panel Reports, and Rebuilding Analyses. Pacific Fishery Management Council, Portland, Oregon.
- Kimura, D.K. 1988. Stock-recruitment curves as used in the stock-reduction analysis model. *J. Cons. Int. Explor. Mer.* **44**(3): 253–258. doi:10.1093/icesjms/44.3.253.
- Lee, H.-H., Maunder, M.N., Piner, K.R., and Methot, R.D. 2011. Estimating natural mortality within a fisheries stock assessment model: an evaluation using simulation analysis based on twelve stock assessments. *Fish. Res.* **109**: 89–94. doi:10.1016/j.fishres.2011.01.021.
- Lee, H.-H., Maunder, M.N., Piner, K.R., and Methot, R.D. 2012. Can steepness of the stock-recruitment relationship be estimated in fishery stock assessment models? *Fish. Res.* **125–126**: 254–261. doi:10.1016/j.fishres.2012.03.001.
- Mace, P.M., and Doonan, I.J. 1988. A generalized bioeconomic simulation model for fish population dynamics. *N. Z. Fish. Assess. Res. Doc.* **88**/4.
- Mangel, M. 2006. The theoretical biologist's toolbox. Quantitative methods for ecology and evolutionary biology. Cambridge University Press, Cambridge, UK.
- Mangel, M., Marinovic, B., Pomeroy, C., and Croll, D. 2002. Requiem for Ricker: unpacking MSY. *Bull. Mar. Sci.* **70**: 763–781.
- Mangel, M., Levin, P., and Patil, A. 2006. Using life history and persistence criteria to prioritize habitats for management and conservation. *Ecol. Appl.* **16**: 797–806. doi:10.1890/1051-0761(2006)016[0797:ULHAPC]2.0.CO;2. PMID: 16711063.
- Mangel, M., Brodziak, J., and DiNardo, G. 2010. Reproductive ecology and scientific inference of steepness: a fundamental metric of population dynamics and strategic fisheries management. *Fish. Fish.* **11**: 89–104. doi:10.1111/j.1467-2979.2009.00345.x.
- Martell, S.J.D. 2009. Assessment and management advice for Pacific hake in U.S. and Canadian waters in 2009. DFO Can. Sci. Adv. Sec. Res. Doc. 2009/021.
- Martell, S.J.D., Pine, W.E., and Walters, C.J. 2008. Parameterizing age-structured models from a fisheries management perspective. *Can. J. Fish. Aquat. Sci.* **65**(8): 1586–1600. doi:10.1139/F08-055.
- Maunder, M. 2003. Is it time to discard the Schaefer model from the stock assessment scientist's toolbox? *Fish. Res.* **61**: 145–149. doi:10.1016/S0165-7836(02)00273-4.
- Michielsens, C.G.J., and McAllister, M.K. 2004. A Bayesian hierarchical analysis of stock-recruit data: quantifying structural and parameter uncertainties. *Can. J. Fish. Aquat. Sci.* **61**(6): 1032–1047. doi:10.1139/F04-048.
- Monk, M.H. 2013. Fishery stock assessment values of natural mortality and steepness. doi:10.6084/m9.figshare.104717.
- Myers, R.A., Bowen, K.G., and Barrowman, N.J. 1999. Maximum reproductive rate of fish at low population sizes. *Can. J. Fish. Aquat. Sci.* **56**(12): 2404–2419. doi:10.1139/f99-201.
- Pella, J.J., and Tomlinson, P.K. 1969. A generalized stock production model. *Bull. Inter-Am. Trop. Tuna Comm.* **13**: 419–496.
- PFMC. 2012. Terms of reference for the groundfish stock assessment and review process for 2011–2012 [online]. Pacific Fishery Management Council. Available from <http://www.pcouncil.org/groundfish/stock-assessments/terms-of-reference/>.
- Prager, M. 2003. Reply to the letter to the editor by Maunder. *Fish. Res.* **61**: 151–154. doi:10.1016/S0165-7836(02)00274-6.
- Punt, A.E., Smith, A.D.C., and Koopman, M.T. 2005. Using information for 'data-rich' species to inform assessments of 'data-poor' species through Bayesian stock assessment methods. Final report to Fisheries Research and Development Corporation Project No. 2002/094. Primary Industries Research Victoria, Queensland.
- Punt, A.E., Dorn, M.W., and Haltuch, M.A. 2008. Evaluation of threshold management strategies for groundfish off the U.S. West Coast. *Fish. Res.* **94**: 251–266. doi:10.1016/j.fishres.2007.12.008.
- Quinn, T.J., and Deriso, R. 1999. Quantitative fish dynamics. Oxford University Press, New York.
- Ralston, S., and O'Farrell, M.R. 2008. Spatial variation in fishing intensity and its effect on yield. *Can. J. Fish. Aquat. Sci.* **65**(4): 588–599. doi:10.1139/f07-174.
- Ricker, W.E. 1954. Stock and recruitment. *J. Fish. Res. Board Can.* **11**(5): 559–623. doi:10.1139/f54-039.
- Rose, K.A., and Cowan, J.H. 2003. Data, models, and decisions in U.S. marine fisheries management: lessons for ecologists. *Annu. Rev. Ecol. Syst.* **34**: 127–151. doi:10.1146/annurev.ecolsys.34.011802.132423.
- Sampson, D.B. 2007. The status of black rockfish off Oregon and California in 2007. Status of the Pacific Coast Groundfish Fishery through 2008, Stock Assessment and Fishery Evaluation: Stock Assessments, STAR Panel Reports, and Rebuilding Analyses. Pacific Fishery Management Council, Portland, Oregon.
- Schnute, J.T., and Kronlund, A.R. 1996. A management oriented approach to stock recruitment analysis. *Can. J. Fish. Aquat. Sci.* **53**(6): 1281–1293. doi:10.1139/f96-069.
- Schnute, J.T., and Richards, L.J. 1998. Analytical models for fishery reference points. *Can. J. Fish. Aquat. Sci.* **55**(2): 515–528. doi:10.1139/f97-212.
- Shepherd, J.G. 1982. A versatile new stock-recruitment relationship for fisheries, and the construction of sustainable yield curves. *J. Cons. Int. Explor. Mer.* **40**(1): 67–75. doi:10.1093/icesjms/40.1.67.
- Shertzer, K.W., and Conn, P.B. 2012. Spawner-recruit relationships of demersal marine fishes: prior distribution of steepness. *Bull. Mar. Sci.* **88**: 39–50. doi:10.5343/bms.2011.1019.
- Sissenwine, M.P., and Shepherd, J.G. 1987. An alternative perspective on recruitment overfishing and biological reference points. *Can. J. Fish. Aquat. Sci.* **44**(4): 913–918. doi:10.1139/f87-110.
- Stanley, R.D., McAllister, M., Starr, P., and Olsen, N. 2009. Stock assessment for bocaccio (*Sebastes paucispinis*) in British Columbia waters. *Can. Sci. Adv. Sec. Res. Doc.* 2009/055.
- Stephens, A., Hamel, O., Taylor, I., and Wetzel, C. 2011. Status and future prospects for the darkblotched rockfish resource in waters off Washington, Oregon, and California in 2011 [online]. Pacific Fishery Management Council, Portland, Oregon. Available from http://www.pcouncil.org/wp-content/uploads/Darkblotched_2011_Assessment.pdf.

- Stewart, I.J. 2009. Status of the U.S. canary rockfish resource in 2009 (update of 2007 assessment model). Status of the Pacific Coast Groundfish Fishery through 2009, Stock Assessment and Fishery Evaluation: Stock Assessments, STAR Panel Reports, and Rebuilding Analyses. Pacific Fishery Management Council, Portland, Oregon.
- Stewart, I.J., Hicks, A.C., Taylor, I.G., Thorson, J.T., Wetzell, C., and Kupschus, S. 2012. A comparison of stock assessment uncertainty estimates using maximum likelihood and Bayesian methods implemented with the same model framework. *Fish. Res.* **142**: 37–46. doi:10.1016/j.fishres.2012.07.003.
- Wallace, F.R., Cheng, Y.W., and Tsou, T. 2007. Status of the black rockfish resource North of Cape Falcon, Oregon to the U.S.–Canadian border in 2006. Status of the Pacific Coast Groundfish Fishery through 2008, Stock Assessment and Fishery Evaluation: Stock Assessments, STAR Panel Reports, and Rebuilding Analyses. Pacific Fishery Management Council, Portland, Oregon.
- Walters, C.J., and Martell, S.J.D. 2004. Fisheries ecology and management. Princeton University Press, Princeton, New Jersey.
- Williams, E.H. 2002. The effects of unaccounted discards and misspecified natural mortality on harvest policies based on estimates of spawners per recruit. *N. Am. J. Fish. Manage.* **22**: 311–325. doi:10.1577/1548-8675(2002)022<0311:TEOUDA>2.0.CO;2.

Appendix A. Fixing steepness and natural mortality with a Ricker SRR also fixes reference points

In this appendix, we show that the R-SRR has the same limitations as the BH-SRR. This is a bit harder to see because none of the associated equations have simple analytical solutions. The starting point is

$$(A.1) \quad \frac{dB}{dt} = \alpha B \exp(-\beta B) - MB$$

for which steepness is (Mangel et al. 2010)

$$(A.2) \quad h = 0.2 \left(\frac{\alpha}{M} \right)^{0.8}$$

In light of eq. A.2 any time results can be represented involving the ratio α/M , they will involve steepness.

For example, the steady state of the unfished system is

$$(A.3) \quad B_0 = \frac{1}{\beta} \log \left(\frac{\alpha}{M} \right)$$

and the biomass giving MSY satisfies

$$(A.4) \quad \frac{\alpha}{M} (1 - \beta B_{MSY}) = \exp(\beta B_{MSY})$$

This equation does not have an analytical solution. However, note that βB_0 and βB_{MSY} will only involve the ratio α/M . Thus $[(\beta B_{MSY})/(\beta B_0)] = (B_{MSY}/B_0)$ is fixed if steepness is fixed; this result is the equivalent of eq. 16 in the text.

Similarly, the biomass dynamics in the case of fishing are

$$(A.5) \quad \frac{dB}{dt} = \alpha B \exp(-\beta B) - (M + F)B$$

with steady state

$$(A.6) \quad \bar{B}(F) = \frac{1}{\beta} \log \left(\frac{\alpha}{M + F} \right)$$

We multiply the right-hand side of this equation by fishing mortality, differentiate with respect to fishing mortality, and set the derivative to zero to find F_{MSY} . An analytical solution is not possible, but we find

$$(A.7) \quad \frac{\frac{F_{MSY}}{M}}{1 + \frac{F_{MSY}}{M}} = \log \left(\frac{\frac{\alpha}{M}}{1 + \frac{F_{MSY}}{M}} \right)$$

so that once we specify steepness we have specified F_{MSY}/M ; this is the analogue of eq. 15 in the text.