

Steepness is a slippery slope

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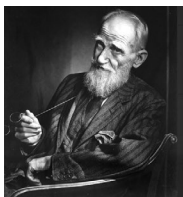
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Abstract

The Beverton–Holt and Ricker stock-recruit functions were derived in terms of two pre-recruit mortality parameters. Mace, & Doonan, (1988, A generalized bioeconomic simulation model for fish population dynamics) reparameterized the stock-recruit function in terms of steepness, which combines pre-recruit mortality with post-recruit biological parameters defining unfished spawning biomass per recruit. Their parameterization explicitly assumes a stable age distribution at unexploited conditions, but also implicitly assumes that unexploited spawning biomass per recruit is time invariant. Temporal variation could occur in either pre-recruit mortality rates or post-recruit biological parameters, but different dynamics are produced. The former results in variation in both the stock-recruit curve and the population equilibria, whereas variation in the latter only changes the points of equilibria on the curve. Thus, variation in either pre- or post-recruit parameters will result in variation in steepness, maximum sustainable yield and associated management reference points. Empirical measures of components of post-recruit productivity (maturity and mass at age, e.g.) are available for many managed fish stocks and often exhibit temporal variability. Yet use of the steepness parameterization requires an analyst to specify one set of post-recruit biological parameters to define unexploited spawning biomass per recruit for the full time series. This misspecification leads to misperception of biological reference points and has implications for meta-analyses of steepness, and interpretation of the dynamic B_0 concept. Returning to the original parameterization allows the isolation of any temporal or inter-population variation in pre- and post-recruit productivity and reduces the potential for mechanistic bias in stock-recruit parameters.

KEYWORDS

biological reference points, maximum sustainable yield, post-recruit productivity, pre-recruit mortality, stock assessment, stock-recruit



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Etymology of Ghoti

George Bernard Shaw (1856–1950), polymath, playwright, Nobel prize winner, and the most prolific letter writer in history, was an advocate of English spelling reform. He was reportedly fond of pointing out its absurdities by proving that 'fish' could be spelt 'ghoti'. That is: 'gh' as in 'rough', 'o' as in 'women' and 'ti' as in palatial.

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1 | INTRODUCTION

Stock-recruit functions describe the production of new recruits to a fish population and the dependence of that production on the spawning component of the population. These functions are useful for understanding the dynamics of populations, providing advice on sustainable yields and forecasting likely future states of the population. Although the form of that relationship may be difficult to discern, fundamentally it is accepted that you cannot have recruitment without spawners (Myers & Barrowman, 1996), and recruitment cannot increase without bounds. These two conditions necessitate that stock-recruit functions pass through the origin and exhibit some form of density dependence.

For age-structured fish population models, one of the most commonly assumed forms of a stock-recruit function is attributed to Beverton and Holt (1957). This model describes recruitment as a function of spawning biomass S that increases towards an asymptotic value with increased spawning biomass. The other most common stock-recruit relationship derived by Ricker (1954) describes recruitment as an asymmetric dome-shaped function of spawning biomass. In terms of the underlying pre-recruitment mortality mechanisms, the distinction is that density dependence pertains to coexisting pre-recruits (e.g. through competition) in the Beverton–Holt function and to spawning biomass (e.g. through cannibalism) in the Ricker.

While these two functional forms offer contrasting outcomes for recruitment as spawning biomass increases, many other forms have been derived (see review in Needle, 2001). We focus on these two relationships because of their prevalence in age-structured fish stock assessment models, and in particular because an alternative “steepness” parameterization introduced by Mace and Doonan (1988) has been broadly implemented by practitioners. However, many implementations violate an important condition pointed out in the original derivation: stable egg production at unexploited conditions (i.e. with no fishing; Beverton & Holt, 1957; Mace & Doonan, 1988). We demonstrate how steepness is ill-specified under such circumstances and illustrate the consequences with a case study. We conclude with suggestions for avoiding this misspecification in practice, and for providing management advice that characterizes the uncertainty arising from this issue.

2 | ALTERNATIVE PARAMETERIZATIONS OF THE STOCK-RECRUIT RELATIONSHIP

In the original derivations of Beverton and Holt (1957) and Ricker (1954), the units of spawning stock was eggs. For the Beverton–Holt, the numbers surviving to the age of recruitment a_r is clearly derived in Beverton and Holt (1957) as.

$$R_{t+a_r} = \frac{E_t e^{-M_I a_r}}{1 + E_t \frac{M_D}{M_I} (1 - e^{-M_I a_r})} \quad (1)$$

where E_t is the number of eggs spawned at time t , M_D and M_I are instantaneous density-dependent and density-independent mortality rates. For the Ricker, a range of density-dependent mortality mechanisms are proposed including competition, predation, and cannibalism. While Ricker (1954) describes cannibalism as an action by the mature stock on the eggs that they lay, for the sake of derivation he appears to express the mature stock in terms of the initial number of eggs laid (p. 210). Various authors have implemented some form of this assumption when rederiving a Ricker relationship (Brooks & Powers, 2007; Quinn & Deriso, 1999), and we adopt the same approach. Thus, let M_E represent density-dependent mortality where the subscript indicates that it is proportional to the initial number of eggs E_t , and recruitment is then given by

$$R_{t+a_r} = E_t e^{-(M_I + M_E E_t) a_r} \quad (2)$$

Although both functions were originally expressed in terms of eggs, it is much more common to reparameterize these functions in terms of spawning biomass because the number of eggs produced by a fish of a given age or size is usually unknown. For example,

$$E_t = \sum_{a=a_r}^{\infty} f_{at} m_{at} w_{at} N_{at} \quad (3)$$

where f_{at} , m_{at} , w_{at} and N_{at} are the relative fecundity (eggs per unit mass), proportion mature, mass and abundance at age. Typically relative fecundity is assumed to be invariant to mass or age so that

$$E_t = f \sum_{a=a_r}^{\infty} m_{at} w_{at} N_{at} = f S_t \quad (4)$$

which conveniently allows total egg production to be proportional to spawning biomass S_t and stock-recruit functions to be almost universally defined in terms of S_t . For the Beverton–Holt function, the assumption in Equation (4) results in

$$R_{t+a_r} = \frac{\alpha S_t}{1 + \beta S_t}$$

where

$$\alpha = f e^{-M_I a_r} \quad (5)$$

and

$$\beta = f \frac{M_D}{M_I} (1 - e^{-M_I a_r}) = \frac{M_D}{M_I} (f - \alpha) \quad (6)$$

The first term α is proportional to the fraction surviving the pre-recruit stage from density-independent mortality (M_I), and it is the rate of recruitment when $S_t = 0$. The second term β includes both

mortality components. One undesirable feature of this parameterization is that it can be misinterpreted that α and β are independent when in fact β is a function of α (final term in Equation (6)). The Ricker function of spawning biomass is

$$R_{t+a_r} = \alpha S_t e^{-\beta E S_t}$$

where α is defined as in Equation (5) and $\beta_E = fM_E a_r$. Unlike the Beverton–Holt model, the α and β_E terms in the Ricker model are independent (aside from them both being a function of the age at recruitment a_r and relative fecundity f).

Mace and Doonan (1988) introduced the alternative parameterization for the Beverton–Holt function in terms of steepness h , equilibrium unexploited recruitment \bar{R}_0 or spawning biomass \bar{S}_0 , and the unexploited spawning biomass per recruit $\bar{S}_0/\bar{R}_0 = \phi_0$. We note that Mace and Doonan (1988) used the symbol Δ for steepness; however, Francis (1992) introduced h for steepness and that notation is more frequently used. Mace and Doonan (1988) defined steepness to be the proportion of equilibrium unexploited recruitment produced by 20% of unexploited spawning stock size ($0.2\bar{S}_0$). The fraction 0.2 was chosen to define an equilibrium recruitment at what would generally be viewed as a “low” spawning stock size (Pamela Mace, pers. comm.). The Beverton–Holt function is

$$R_{t+a_r} = \frac{4\bar{R}_0 h S_t}{(1-h)\bar{R}_0 \phi_0 + (5h-1)S_t} \quad (7)$$

where steepness and unexploited recruitment are

$$h = \frac{\alpha \phi_0}{4 + \alpha \phi_0} \quad (8)$$

and

$$R_0 = \frac{1}{\beta} \left(\alpha - \frac{1}{\phi_0} \right), \quad (9)$$

respectively. The Ricker function is

$$R_{t+a_r} = \frac{S_t}{\phi_0} (5h)^{\frac{5}{4}} \left(1 - \frac{S_t}{R_0 \phi_0} \right) \quad (10)$$

where steepness and unexploited recruitment are

$$h = \frac{(\alpha \phi_0)^{\frac{5}{4}}}{5} \quad (11)$$

and

$$R_0 = \frac{\log(\alpha \phi_0)}{\beta_E \phi_0}, \quad (12)$$

respectively (see Supplementary Materials for derivations). Analogous to the β term for the Beverton–Holt model, the steepness parameterization of the Beverton–Holt and Ricker models can lead to the misperception that steepness and unexploited recruitment are unrelated to other terms in the model. In both models, steepness is a function only of the product of the slope when $S = 0$ (α),

which is a function of pre-recruit density-independent mortality, and the equilibrium unexploited spawning biomass per recruit ϕ_0 . This product is defined by Myers et al. (1999) as $\hat{\alpha}$ and represents “the number of spawners produced by each spawner over its lifetime at very low spawner abundance, i.e., assuming absolutely no density dependence.” Stock-recruit functions can also be parameterized in terms of $\hat{\alpha}$; however, they suffer from the same misspecification that we detail below. Unexploited recruitment is a function of both types of pre-recruit mortality and unexploited spawning biomass per recruit. Therefore, the steepness parameterization implicitly assumes that both the pre-recruit mortality sources and the productivity of recruited individuals (through ϕ_0) are constant.

The assumption of a stable age distribution at unexploited conditions is important, because it implies a stable equilibrium at the point (S_0, R_0) . This is the point of intersection of the stock-recruit curve and the replacement line that passes through the origin and has a slope of $1/\phi_0$ (i.e. $R_0 = S_0/\phi_0$). As noted by Beverton and Holt (1957), the assumption of a steady state implies equivalence, in both egg production and yield, between a single cohort over its lifetime and the sum from each constituent cohort in the population during one year of life. This equivalence can only occur when the biological parameters are constant.

3 | MISSPECIFICATION WHEN BIOLOGICAL PARAMETERS VARY

When one or more of the post-recruit biological parameters (natural mortality, maturity, or mass at age) that compose ϕ_0 (Eq. S7) change over time, then steepness also varies. Consider a simple case where there is a time series of annual observations of length T , where pre-recruit mortality rates (and α and β) are constant, but mass at each age changes after $T/2$ by a constant proportion k . Fitting a stock-recruit curve to the full time series of points (S_t, R_{t+a_r}) in the original parameterization would yield estimates of α and β . There would be no misspecification because α and β (functions of M_j and M_D) do not depend on the biological parameters for the recruited spawning stock other than through the annual spawning biomass estimates used in fitting the stock-recruit curve. However, the steepness parameterization of the stock-recruit function requires the analyst to pick a time point to define ϕ_0 because of the change in mass at age. If $t \leq T/2$ were taken, then we would simply have ϕ_0 as in Eq. S7. On the other hand, if $t > T/2$, then the replacement line would be $1/(k\phi_0)$. The estimates of steepness in these two situations will be different even though α and β (and the stock-recruitment function) do not change over time. Calculation for unexploited spawning biomass per recruit would run the gamut from ϕ_0 to $k\phi_0$ and everything in between, depending on where one assumes that the change in mass occurs in the cohort's lifetime. If on the other hand mass at age did not change, then there would be only one way to calculate ϕ_0 and the α and β estimates using the original parameterization would be the same as those by transforming h, R_0 in the steepness parameterization.

Taking the two extreme cases for unexploited spawning biomass per recruit (ϕ_0 and $k\phi_0$), we can deduce that if $k < 1$ (mass at age has decreased), then the slope of the replacement line would be larger, causing the point of intersection to shift to the left on the stock-recruit curve with lower values of R_0 and S_0 . This is analogous to the shift in equilibrium values with fishing mortality. If $k > 1$ (mass at age has increased), then the slope would be less and the point of intersection on the stock-recruit curve would shift to the right with greater values of R_0 and S_0 . The same would be true if the scalar were applied to maturity at age. If the scalar were applied to mortality at age, then the result would be in the opposite direction.

There are two significant consequences of changes in the slope of the replacement line. The first is that the unexploited spawning biomass and recruits change and the second is that the estimate of steepness changes (it increases or decreases in the same direction as ϕ_0). These estimates change even though the estimated stock-recruit curve, α and β parameters, and observed pairs of (S_t, R_{t+a}) remain the same. The change is driven entirely by the need for the analyst to choose vectors of age-specific biological parameters and to assume that those vectors do not change over time. Similarly, when the dependence of steepness on ϕ_0 is not recognized, translating the steepness estimate to α and β using $k\phi_0$ from the latter half of the time series results in a different stock-recruit relationship compared to making the translation using ϕ_0 and could lead to a misperception that pre-recruit mortality rates have changed.

We framed this presentation of misspecification simplistically, assuming only one life history parameter to be changed at one point in a time series. In reality, each life history parameter could potentially change every year, achieving both increases and decreases. In the case study presented below, we demonstrate the effect of alternative S-R parameterizations for the Southern New England-Mid-Atlantic Bight stock of yellowtail flounder (*Limanda ferruginea*, Pleuronectidae) in the Northwest Atlantic Ocean. The demonstration illustrates the range of outcomes driven by the parameterization of the stock-recruit function, and choice of biological parameters to define the replacement line.

4 | ILLUSTRATIVE EXAMPLE

We fit assessment models for Southern New England-Mid-Atlantic Bight (SNE-MA) yellowtail flounder assuming Beverton-Holt and Ricker stock-recruitment functions. The assessment model is a state-space age-structured model similar to that used by Miller et al. (2016) and Stock and Miller (In review) for this same stock, and it is available at github.com/timjmiller/steepness. However, the full details of the configuration of the assessment model are not important because the demonstration is intended to illustrate general consequences rather than pertain to management of this particular yellowtail flounder stock. Maximum sustainable yield (MSY) and related biological reference points are calculated internally in the model using Newton-Raphson procedures and the estimated parameters

of the stock-recruit function and equilibrium spawning biomass and yield per recruit (Miller et al., 2016). We calculate annual equilibrium spawning biomass ϕ_F and yield per recruit (Eqs. S7 and S8 in Supplementary Materials) at a given fishing mortality rate using natural mortality, maturity and mass at age which are input data for the SNE-MA yellowtail flounder assessment model, and fishery selectivity at age (estimated in the model) for a given year. Unexploited spawning biomass per recruit ϕ_0 is calculated with $F = 0$. Interannual variability in ϕ_F is due entirely to the annual variation in mass at age and is driven particularly by the mass of individuals at the oldest ages (Figure 1). The annual calculated values of ϕ_0 range from 0.83 in 1973 to 2.13 in 1999, implying that the expected biomass of spawners produced per recruit in the absence of fishing has varied by more than double the initial value. Because selectivity (see Fig. S1 in Supplementary Materials) is estimated in the assessment model it could possibly vary between the fits assuming Beverton-Holt and Ricker functions, but in this case the absolute differences in any of the selectivities at age were less than 0.001.

We first fit stock-recruit functions parameterized in terms of α, β (Figure 2). From each annual calculated value of ϕ_0 , we plot where the replacement line ($R = 1/\phi_0$) would intersect the stock-recruit curve, which implies a range of unexploited conditions. There is a single curve defined by α, β on which the various equilibria lie. For this case study, unexploited spawning stock biomass (S_0) ranges from 20,249 to 64,685 mt, and unexploited recruitment (R_0) ranges from 24.431 to 30.321 million fish because they are functions of ϕ_0 (Figure 3). Both R_0 and h increase with ϕ_0 for the Beverton-Holt model, but R_0 peaks at $\phi_0 = e/\alpha$ for the Ricker model (Figure 3). Analogously, the variation in mass at age that is an input to ϕ_F and yield per recruit also result in variation in MSY-related equilibria (Tables S1 and S2).

The alternative stock-recruit estimation in terms of steepness requires a decision to choose a set of post-recruit biological inputs. If we choose to use those values from 2016 where $\phi_0 = 1.06$, then the estimates of R_0 and h are 26.516 million fish and 0.53 for the Beverton-Holt function and 28.852 million fish and 1.00 for the Ricker function. Translating these estimates of R_0 and h into α and β using the annual ϕ_0 values produces annual estimates of α and β , which defines a different curve for each value of ϕ_0 (Figure 4). The use of 2016 steepness and R_0 estimates with the annual ϕ_0 values also implies a different set of estimates for S_0 than for those using the α, β parameterization. Alternatively, if we parameterize in terms of S_0 instead of R_0 , the estimates of S_0 are 28,048 and 30,519 mt for the Beverton-Holt and Ricker functions, respectively, and there is a different set of estimates of annual R_0 values than would be obtained using the α, β parameterization. From these calculations, we can see that it is inappropriate to take the R_0 and h estimated with one value of ϕ_0 and use them with another value of ϕ_0 . Using the steepness parameterization when there is temporal variation in the post-recruit components of stock productivity (i.e. inputs to the ϕ_F and yield-per-recruit calculations), there is a danger that h and R_0 are perceived to be constant over the time period and that any variation over time is attributed to α and β which are the pre-recruit productivity components, not the post-recruit components.

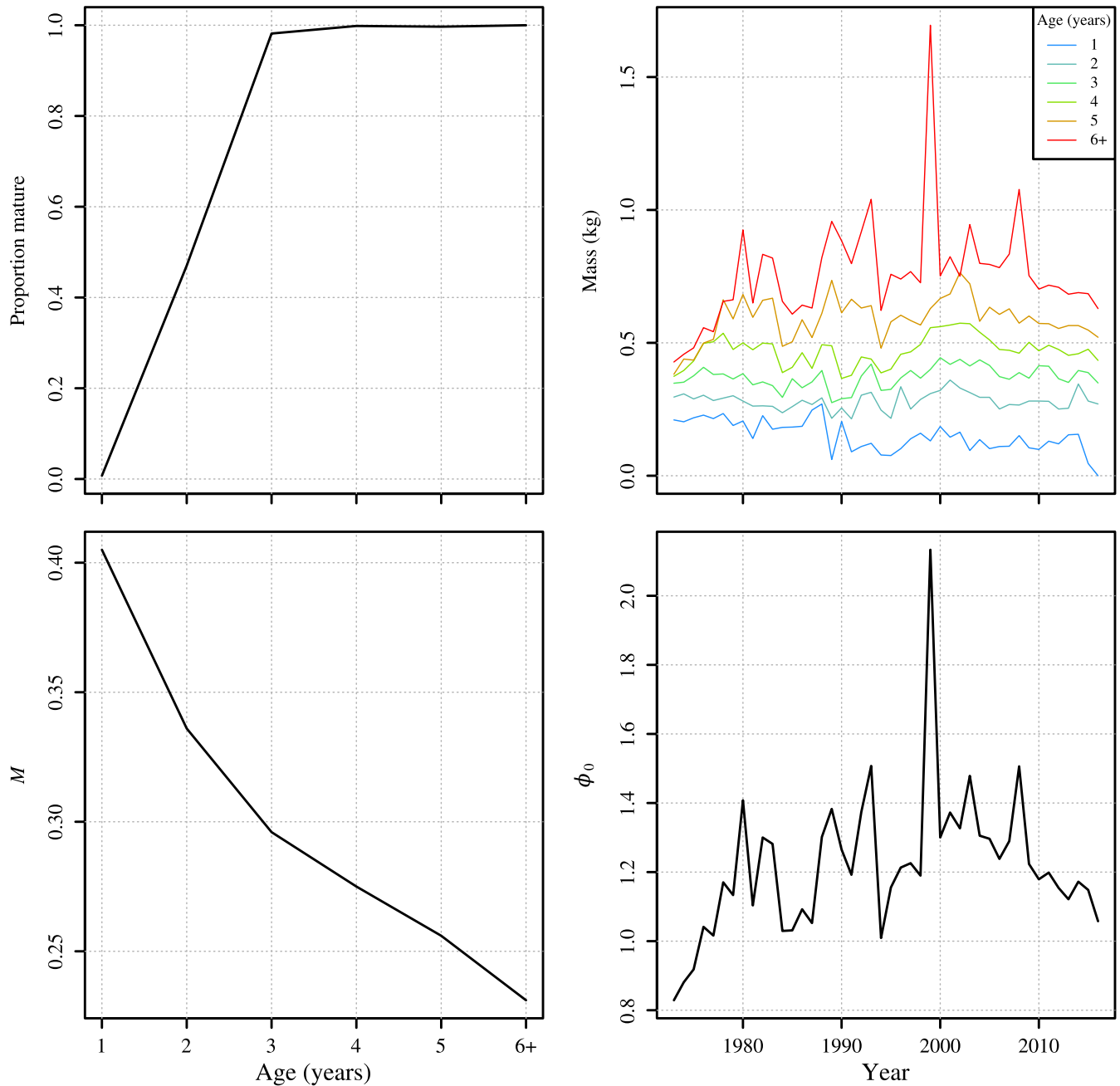


FIGURE 1 Proportion mature, natural mortality rate (M) and mass at age and annual unexploited spawning biomass per recruit for Southern New England-Mid-Atlantic Bight yellowtail flounder. (figure appears in colour in the online version only) [Colour figure can be viewed at wileyonlinelibrary.com]

Applying steepness values to stock-recruit functions with other values of ϕ_0 is also what would typically be done with results of a meta-analysis of steepness. A primary utility of such a meta-analysis would be to inform a prior on steepness for a “comparable” species where the data are not informative enough to estimate steepness on their own (Punt et al., 2011). In such a situation, the steepness “estimated” in the assessment would not be too different from the mode/mean of the prior, but uncertainty in steepness would be propagated. The difference between the calculations in Figure 4 is that R_0 (or S_0) is still freely estimated.

To demonstrate the consequences of using a meta-analysis, assume the annual ϕ_0 values we have for SNE-MA yellowtail flounder are instead for different stocks or species. We assume the steepness corresponding to the greatest = $\phi_0 2.13$ from 1999 is the posterior estimate from a meta-analysis (0.695 and 28.6 for the Beverton–Holt and Ricker functions, respectively). The “new” species with uninformative stock-recruit information has post-recruit productivity components defined by those age-specific values in 1973 where ϕ_0 is 0.83 (the lowest value in the time series). Under the constant α, β parameterization, F_{MSY} for this “new”

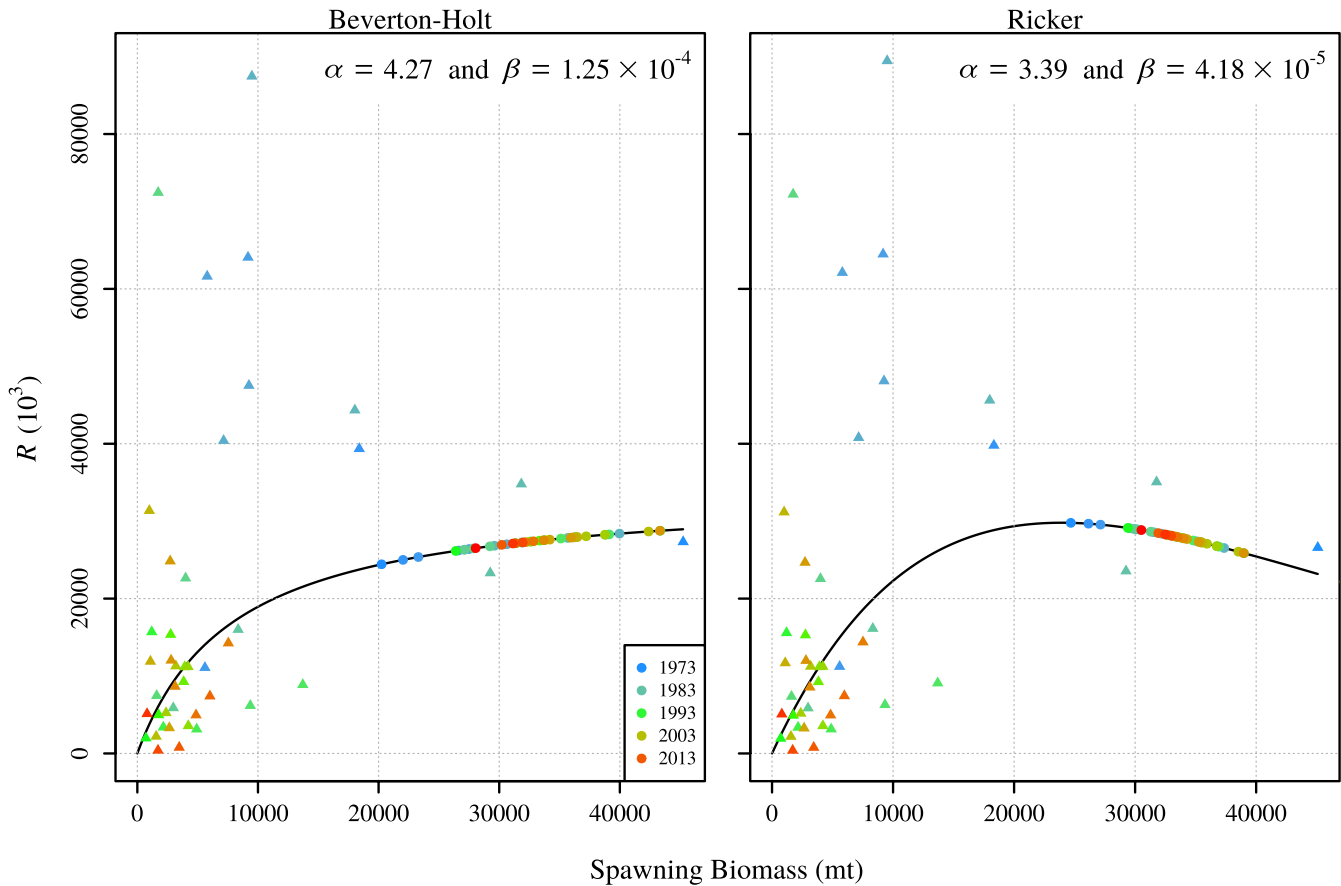


FIGURE 2 Beverton–Holt (left) and Ricker (right) stock-recruitment curves estimated from SNE-MA yellowtail flounder data using α and β parameterization with annual unexploited recruitment and spawning biomass points (filled circles) derived from corresponding values of ϕ_0 . Annual estimates of recruitment and spawning biomass are shown in filled triangles. (figure appears in colour in the online version only) [Colour figure can be viewed at wileyonlinelibrary.com]

species is 0.27 (Beverton–Holt) or 0.25 (Ricker), S_{MSY} is 7,049 mt (Beverton–Holt) or 10,648 mt (Ricker), and MSY is 1,340 mt (Beverton–Holt) or 1,841 mt (Ricker). To simulate the application of the meta-analytic posterior, we use the steepness posterior estimates as fixed inputs and refit the assessment model with R_0 estimated using the ϕ_0 for the “new” data-poor species. We also fix all of the other parameters in the assessment model so that only stock-recruit function parameters and MSY -related values are affected by the steepness prior. This type of constraint is necessary here because the data are actually informative to estimating stock-recruit function parameters and constraining steepness causes spawning biomass and recruitment estimates to deviate dramatically from what they would be without a stock-recruit relationship. Applying the meta-analytic steepness results in stock-recruit curves with lesser R_0 estimates for both the Beverton–Holt and Ricker functions (Table 1 and Figure 5). The estimate of S_{MSY} is also less using the steepness prior and less than half of the original value under the Beverton–Holt assumption. Values for F_{MSY} are more than double for either the Beverton–Holt or Ricker models whereas MSY values are similar for the Beverton–Holt models but more than double for the Ricker models.

5 | DISCUSSION

We have demonstrated that the steepness parameterization (and likewise $\hat{\alpha}$ parameterization) is problematic when post-recruit productivity components are variable (i.e. more than one ϕ_0 can be calculated) because steepness and R_0 combine both pre- and post-recruit productivity components and requires that analysts specify a single value of ϕ_0 for stationarity. The post-recruit productivity components also affect the more critical biological reference points based on MSY because these inputs are also used in the ϕ_F and yield-per-recruit calculations to find MSY and S_{MSY} . Variation in the pre- and post-recruit components have very different implications. Variation in the pre-recruit mortality rates implies variation in the stock-recruit curve, whereas variation in ϕ_F for $F = 0$ or otherwise only implies variation in the replacement line and equilibrium point of recruitment and spawning biomass on the stock-recruit curve (e.g. S_0 and R_0 or S_{MSY} and R_{MSY}). Interestingly, when Beverton and Holt (1957, pg. 54) derived their stock-recruit curve, they described these same concepts: how changes in spawning biomass (egg production) per recruit result in different equilibrium recruitment and spawning biomass on the same curve and changes in larval mortality rates result in different equilibria on different stock-recruit curves.

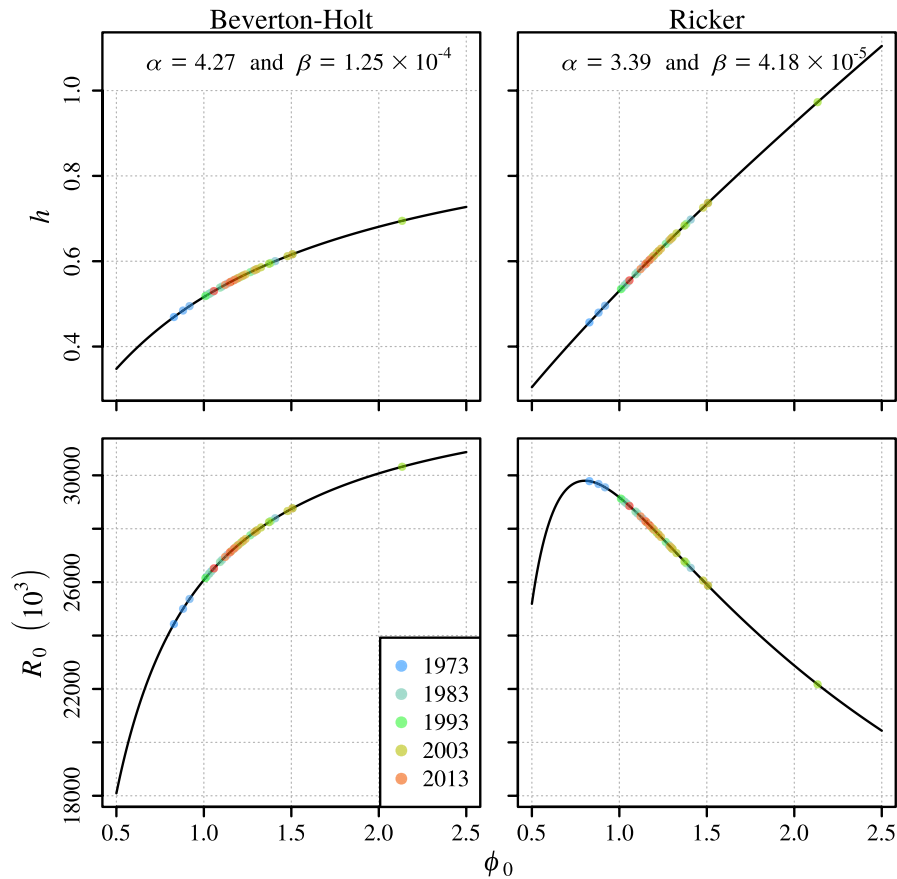


FIGURE 3 Relationships of steepness (h) and unexploited recruitment (R_0) to ϕ_0 (black lines) with annual values (filled circles) estimated by transforming the stock-recruitment α and β estimated from SNE-MA yellowtail flounder data. (figure appears in colour in the online version only) [Colour figure can be viewed at wileyonlinelibrary.com]

We recognize that there may be temporal variability in either or both the pre-recruit mortality and post-recruit productivity components of equilibrium points and MSY-based reference points. To avoid the confounding of variability in pre- and post-recruit processes, we recommend retaining the traditional parameterization of the stock-recruit functions in terms of α and β rather than in terms of steepness. The α, β parameterization is a function only of pre-recruit mortality rates and therefore not affected by interannual variation in post-recruit productivity components. Variability in pre-recruit mortality sources is implicitly subsumed in σ_R^2 the variance of recruitment deviations from the stock-recruit relationship. We suspect that treating α, β as constant when they are variable would lead to higher estimates of σ_R and that estimated α, β parameters should be similar to the average values over the time series, but further research on the statistical behaviour of these estimates is recommended. Variability in pre-recruit mortality can also be modelled explicitly as a function of hypothesized covariates (Miller et al., 2016), or unexplained sources of variation where α and/or β (or M_I and/or M_D, M_E) are considered as autoregressive processes, or both. It is straightforward to calculate steepness, if necessary, as a function of α and ϕ_0 , and it forces the practitioner to determine which post-recruit productivity components to use and to ensure that components are consistent between ϕ_0 and ϕ_F when calculating reference points. For example, one might use an average of recent post-recruit components for both ϕ_0 and $\phi_{F_{MSY}}$.

Variability in post-recruit productivity should also be considered when developing management reference points and forecasting

stock dynamics. Unlike pre-recruit mortality, there are often annual empirical observations of one or more of the post-recruit productivity components. Post-recruit productivity is a component of both MSY and proxy reference points based on spawning potential ratio (SPR), which is a measure of the proportion of ϕ_0 that can be achieved for a given fishing mortality. Therefore, both types of reference points require a decision regarding the calculation of ϕ_F whether $F = 0$ or not. The typical approach for calculating SPR reference points is to use a recent 3–5 year average of the biological parameters (thought to characterize “prevailing environmental conditions”) and fishery selectivity. Brooks (2013) evaluated analytical expressions to characterize the change in steepness, $\hat{\alpha}$, and reference points, as well as SPR proxies, resulting from factors that modify biological rates, and emphasized the need to carry the uncertainty associated with variability in biological rates into forecasts and reference point distributions. Legault and Palmer (2016) work through two case studies where natural mortality is hypothesized to have changed towards the end of the stock assessment time series, highlighting the consequences for reference points, and specifically the trade-off between risk of overfishing and forgone yield, associated with which mortality value to use in ϕ_0 calculations. Miller et al. (2018) examined effects of covariates and unexplained temporal variation in growth and demonstrated the effects on SPR-based reference points for Georges Bank Atlantic cod (*Gadus morhua*, Gadidae).

Aside from the choice of parameterization of the stock-recruit relationship, estimability of this relationship within or external to an

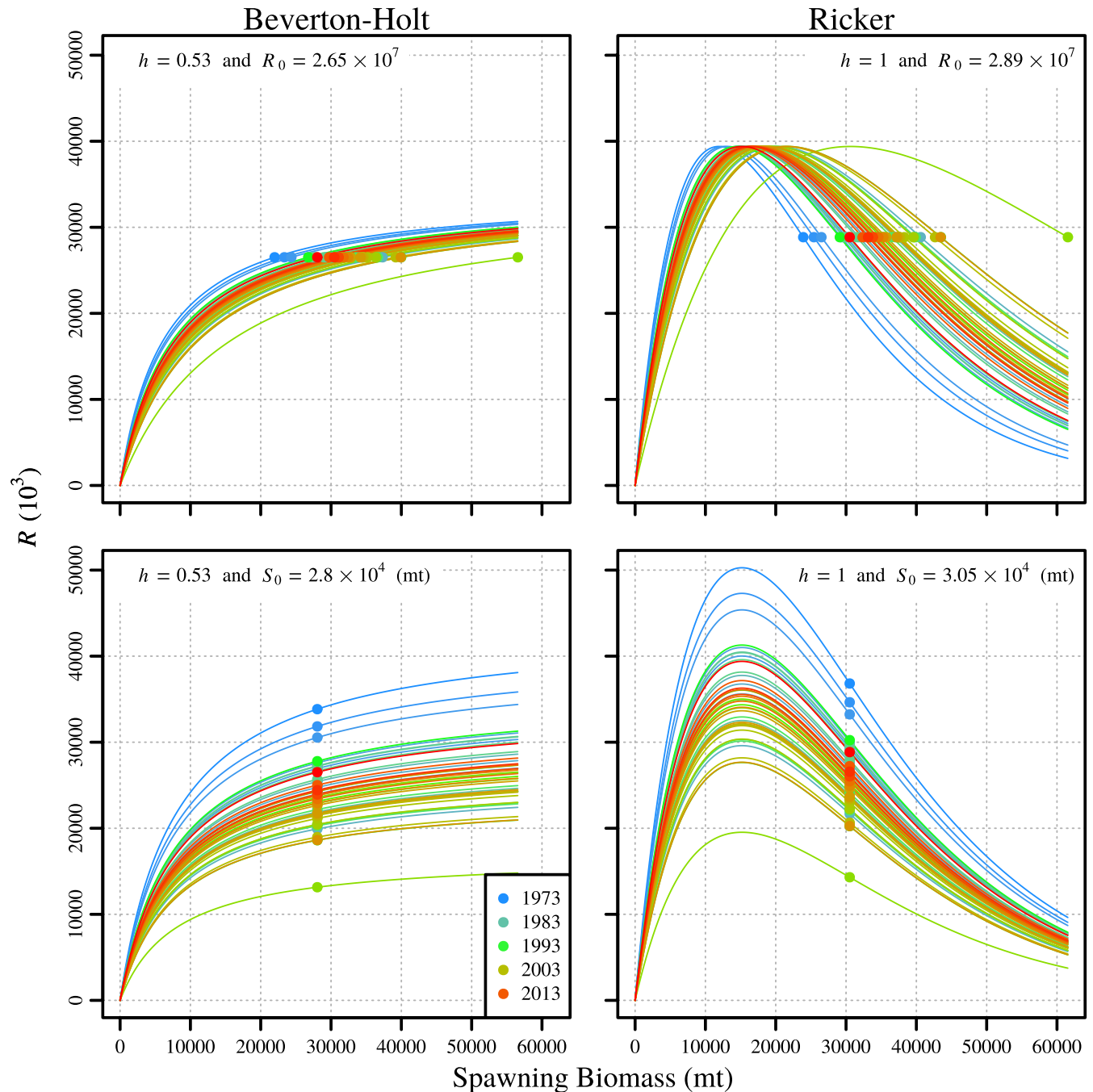


FIGURE 4 Annual Beverton-Holt (left) and Ricker (right) stock-recruitment curves produced by annual α and β and ϕ_0 values that result from steepness and unexploited recruitment (top) or unexploited spawning biomass (bottom) estimated assuming terminal year ϕ_0 (figure appears in colour in the online version only) [Colour figure can be viewed at wileyonlinelibrary.com]

age-structured assessment model continues to be a common issue for particular stock assessments (Lee et al., 2012). Contrast in stock size over time is a minimum requirement, but sufficient frequency of age composition samples both intra- and inter-annually is also important. Moreover, even with sufficient data there are various statistical approaches for estimating the stock-recruit parameters that result in different degrees of estimation bias. It is common to estimate stock-recruit functions internally in age-structured models by maximizing a penalized-likelihood (e.g. Methot & Wetzel, 2013). However, state-space approaches like that used here integrate over

these penalties and allow variance of recruitment deviations to be estimated rather than assumed. It is also common to fit stock-recruit functions externally using estimates of spawning biomass and recruitment from assessment models, but the disadvantages of such approaches are well-known (Brooks & Deroba, 2015). Even when using appropriate state-space models, the ability to distinguish appropriate stock-recruit model structure may be lacking (de Valpine & Hastings, 2002).

The parameterization of stock-recruit functions of just two types of mortality on recruitment over the entire recruitment window is

TABLE 1 Beverton–Holt and Ricker stock-recruit parameters and resulting MSY-related values under different parameterizations using the value of ϕ_0 in 1973 (0.83) for Southern New England-Mid-Atlantic Bight yellowtail flounder. In the second and fourth rows the steepness is fixed at values associated with $\phi_0 = 2.13$ in 1999.

	F_{MSY}	S_{MSY} (mt)	MSY (mt)	Φ_0	R_0 (10^3)	h	α	β
Beverton–Holt (α, β)	0.27	7,049	1,340	0.83	24,431	0.47	4.27	1.25×10^{-4}
Beverton–Holt (h from 1999 with Φ_0 from 1973)	0.55	3,233	1,404	0.83	15,621	0.69	10.98	6.26×10^{-4}
Ricker (α, β)	0.25	10,648	1,841	0.83	29,782	0.67	3.39	4.18×10^{-5}
Ricker (h from 1999 with $\alpha\Phi_0$ from 1973)	0.68	7,852	4,283	0.83	26,117	28.63	8.72	9.13×10^{-5}

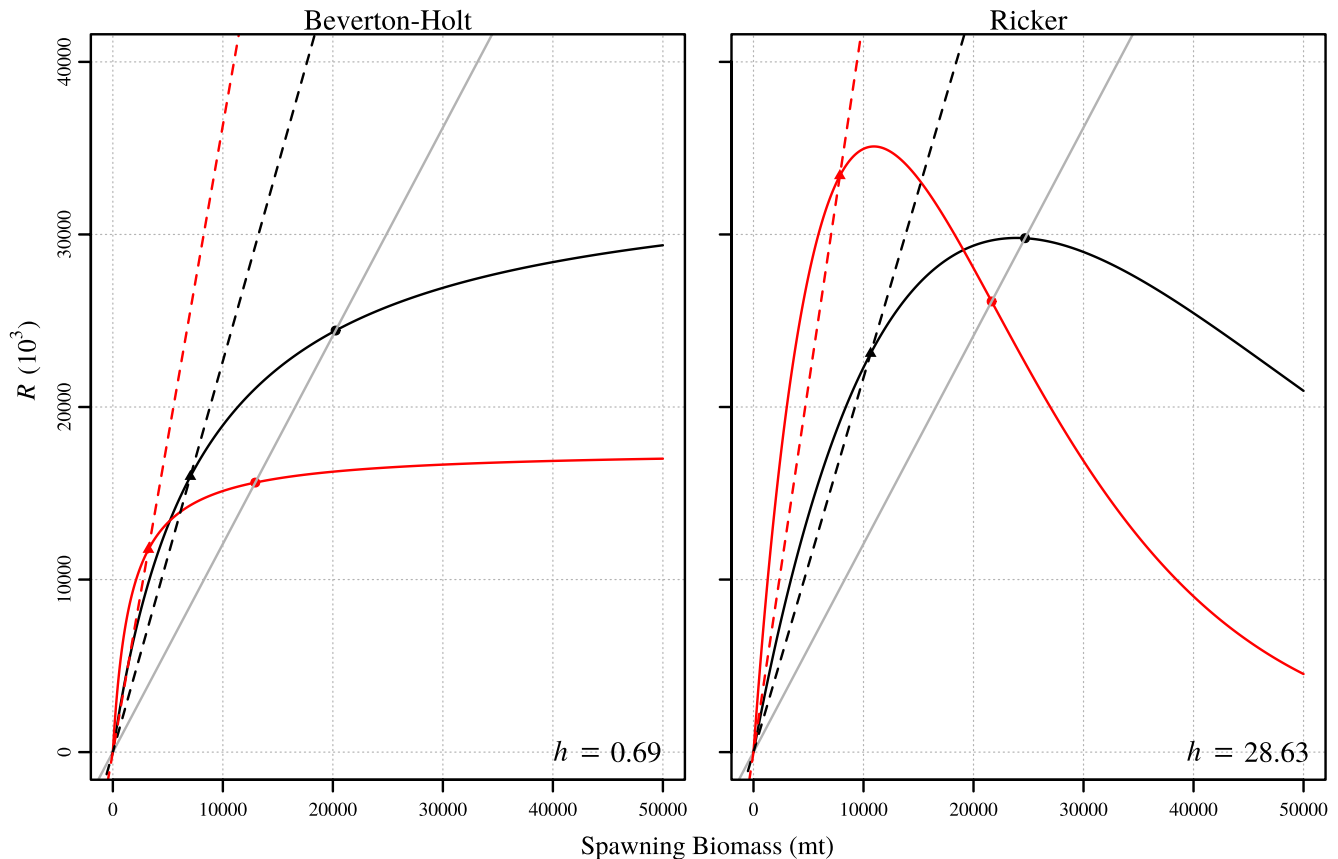


FIGURE 5 Comparison of Beverton–Holt and Ricker stock-recruit relationships that result when steepness is estimated using one ϕ_0 and then applied to estimate R_0 with another value of ϕ_0 . Black stock-recruit curves result from estimating stock-recruit functions in terms of α and β (Figure 2). Slope of grey line is $1/\phi_0$ for 1999 that provides steepness estimates of 0.69 and 28.63 for the Beverton–Holt and Ricker functions, respectively. Red stock-recruit curves result from estimating R_0 assuming the 1999 steepness, but with ϕ_0 from 1973. Dashed lines represent MSY replacement lines using biological information from 1973 in ϕ_F and yield-per-recruit calculations. (figure appears in colour in the online version only) [Colour figure can be viewed at wileyonlinelibrary.com]

likely too simplistic. Paulik (1973) theorized the existence of multiple stages with different sources of mortality within the recruitment phase. Brooks and Powers (2007) derived generalized stock-recruit functions with multiple stages and determined that density-dependent mortality early in the recruitment window dominates the range of dynamics observed in the remainder of the recruitment interval. This was confirmed in Brooks et al. (2019), where simulations demonstrated the flattening of the recruitment curve (due to reduction in observed contrast) and suggesting that such effects add

to the difficulty for model selection to identify the correct underlying function. Beyond considering more complex dynamics in the recruitment window, it is also likely that density-dependent mortality occurs within the recruited population (Powers, 2014). Using the steepness, parameterization inhibits research considering these realities because pre- and post-recruit processes are combined.

The “dynamic B_0 ” concept (MacCall et al., 1985) is another approach to dealing with temporal variation in stock productivity that is not to be confused with the temporal variation in equilibrium

unexploited spawning biomass due to changes in ϕ_0 (Figure 2). The analyst first fits an assessment model that assumes a stock-recruit relationship with a single equilibrium unexploited spawning stock biomass, ϕ_0 , and steepness. Then, a forecast of the population with no fishing ($F = 0$) is made from the estimated numbers at age in the stock starting early in the time series, using the previously estimated stock-recruit function. The deviations between the stock-recruit function and estimated recruitments are used to forecast recruitment from the same stock-recruit function at the spawning biomass values that are realized sequentially at each time step. The forecasted annual spawning biomass is the dynamic B_0 (note B here is equivalent in interpretation to S), and, by analogy, the forecasted recruitments would be a dynamic R_0 . This algorithm is problematic because there is an implicit inconsistency between the assumption of constant (stable) B_0 and R_0 required for the steepness-parameterized stock-recruit function and the temporally varying B_0 resulting from the forecasts using the same stock-recruit function.

A common application of dynamic B_0 assumes post-recruit productivity components are constant over time and recruitment is the only temporally varying component (Berger, 2019). Using the steepness-parameterized stock-recruit function, dynamic B_0 approaches the equilibrium values defined by where the SR curve and the replacement lines at $F = 0$ ($1/\phi_0$) intersect, as the variance of the recruitment deviations approaches zero (Figure S2). Therefore, dynamic B_0 with all post-recruit productivity components constant implies all variation is attributable to pre-recruit mortality sources (time-varying α and β). Otherwise, the values of spawning biomass used to estimate the stock-recruit curve would be incorrectly defined. When there is temporal variability in post-recruit productivity components, this contributes to the variability in dynamic B_0 (Figure S5), but it is inconsistent with the ϕ_0 assumed for the steepness-parameterized stock-recruit relationship.

Coincidentally, dynamic B_0 was first introduced over 30 years ago to understand temporal variation in stock productivity around the same time as the steepness parameterization of the stock-recruit function. Today there are methods to model the variability of the different components that generate the variability in dynamic B_0 . We can consider effects of covariates mechanistically on either pre- or post-recruit productivity components (Miller et al., 2016, 2018; Xu et al., 2018). We can also account for temporal variation due to unconsidered covariates by modelling those components as autoregressive processes (Miller et al., 2018). We then have a better mechanistic understanding of the variability in “dynamic” unexploited spawning biomass (i.e. product of ϕ_F and \tilde{R}_F for $F = 0$) by modelling the inputs as dynamic. Furthermore, it is not straightforward how dynamic MSY-based reference points would be calculated in a way that is consistent with the algorithm for dynamic B_0 , but it is using the equilibrium equations (although see A’mar et al., 2009 and O’Leary et al., 2020 for approaches with SPR-based reference points). Again, modelling the variability in the components makes it clear which are contributing to the variation in the reference points.

There is a large body of research in fisheries about performing meta-analyses on various aspects of the dynamics of fish

populations (e.g. Liermann & Hilborn, 1997; Myers, 2001; Myers et al., 1999; Szuwalski et al., 2015; Thorson et al., 2015). Applications range from a suite of closely-related stocks inhabiting similar environmental conditions (Dorn, 2002; Forrest et al., 2010), global meta-analysis to draw inference about a single species throughout its range (Mantzouni et al., 2010; Michielsens & McAllister, 2004), and the “Robin Hood” approach of developing priors from data-rich stocks to inform data-poor stocks (Punt et al., 2011). Unfortunately, meta-analyses for steepness suffer from the same issue of implicitly combining variability in pre- and post-recruit productivity except the variability is among stocks rather than through time for a given stock. The posterior distributions for steepness therefore include variability in post-recruit productivity across stocks. Furthermore, our illustrative example where we used steepness derived from one ϕ_0 and applied it to another shows how MSY-based reference points for the “data-poor” stock can be misperceived. Pulkkinen and Mantyniemi (2013) raise a similar concern about the use of steepness in meta-analyses due to its dependence on life history parameters. They recommend fitting stock-recruit functions with number of eggs rather than biomass as the independent variable so that the meta-analysis is focused on inference about egg survival ($\alpha = e^{-M_0}$, where f is not needed when the units are eggs) instead of steepness. The availability of estimates of total egg production may limit the generality of their recommendation.

It appears that the pre-recruit natural mortality rates (M_I and M_D or M_E) are the stock-recruit function parameters best suited to meta-analyses across stocks. The α and β parameters are problematic due to differences in relative fecundity f and we recommend more research to obtain this information. Even when we have f for species of interest, we should ensure comparability among those stocks that are included in a meta-analysis in such aspects as egg size and pre-recruit growth which are important predictors of pre-recruit mortality rates. There is strong evidence to suggest that relative fecundity changes with size and therefore age (Barneche et al., 2018), and there are many publications indicating other variation in maternal effects with age on egg production which would suggest relaxing the assumption that fecundity is invariant to spawner age (e.g. Green, 2008; Hixon et al., 2014; Marshall et al., 2008; Trippel et al., 1997). We recommend further investigation of incorporating relative fecundity into the equilibrium per-recruit calculations analogous to Eq. S7 so that we would be back to the original egg-recruit functions as suggested by Pulkkinen and Mantyniemi (2013). Because the variation in the age at recruitment can also cause variation in α and β , it should also be specified consistently across stocks. The age at recruitment should also be greater than zero, otherwise there is no period for the pre-recruit mortality rates to act.

We found it was necessary to constrain all the non-stock-recruit parameters of the assessment model we were using with the SNE-MA yellowtail flounder example when we used steepness from one year with the ϕ_0 of another year. Freely estimating the other parameters led to large changes in the scale of the population size. Punt et al. (2011) also found that parameters of data-poor stocks were affected by the parameters that were assumed to be distributed

similarly to data-rich stocks, but the meta-analysis was focused on exploitation rates and selectivity so the effects of the prior on the assessment model parameters were intended. In the case of meta-analyses for stock-recruit parameters, there is no clear reason that application of priors on those parameters should affect estimates of exploitation rates and stock size of the “data-poor” stocks (though it would obviously affect the reference points and status determination). When using meta-analytic results to specify stock-recruit parameters in an assessment model of another stock, we recommend comparing parameter estimates and derived output from the model with and without the stock-recruit relationships to evaluate the effect of the priors. A model without a stock-recruitment function estimates recruitment freely without making any assumptions on the nature of the stock-recruitment relationship. If attributes such as spawning biomass, recruitment, selectivity or fishing mortality rates differ, then the assumed variance of the recruitment deviations should be increased until the difference becomes negligible.

We recognize the intuitive appeal of a stock-recruit parameterization in terms of steepness, which is unitless, has an interpretable scale (greater resilience with larger values of steepness) and appears to be comparable among stocks. However, closer inspection of the dependence of steepness on the post-recruit biological parameters of productivity (those which define ϕ_0) reveals great potential for misspecification once an analyst starts down this path. Variability in biological rates leads to variable unexploited equilibria and reference points. Fitting the stock-recruit function requires a choice of a constant set of post-recruit biological parameters that implicitly defines unexploited conditions and has a cascade of implications for meta-analysis, reference points and management advice. We therefore recommend returning to the α, β parameterization for fitting stock-recruit functions because that parameterization does not depend on ϕ_0 (which will vary depending on the presence of interannual changes in maturity, mass, and natural mortality at age). It is simple enough to calculate the range of steepness after the fact, using alternative estimates of ϕ_0 . The utility in that case could be related to a harvest control rule if risk were somehow codified to a stock's resilience. Similarly, reference points can be estimated as a secondary calculation, and the dynamic range resulting from varying biological parameters can be summarized without impacting the stock-recruit fit. In summary, the α, β parameterization provides surer footing in the face of varying post-recruit biological parameters, avoiding the slippery slope of misspecification that can result from the steepness parameterization.

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DATA AVAILABILITY STATEMENT

The data and R code that support the findings of this study are openly available at github.com/timjmiller/steepness.

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