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Effects of variable reproductive potential on reference points for fisheries management

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ABSTRACT

Analytical and simulation results with hypothetical vectors of biological parameters were employed to demonstrate the impact of variable reproductive potential on reference points based on spawning potential ratio (SPR). Implications for stock recruit function parameterizations are also noted. For the range of variability explored in this illustration, skipped spawning had a negligible impact on reference points, while factors related to spawner condition or experience and density independent survival of recruits (i.e. slope at the origin) had greater effects. When estimating yield per recruit (YPR) associated with a specified SPR, the variability in the biological parameters was greatly dampened. Estimating correlations between the observed trends in maturity and fecundity, and developing models to forecast the probabilities associated with observing a biological state in the future, would be an important contribution to understanding uncertainty in rebuilding projections and future catch advice.

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1. Introduction

Maintaining fishery resources at sustainable, profitable levels is the primary goal of most management actions. To assess stock status and to align future quotas with these goals, reference points associated with maximum sustainable yield (MSY) are estimated in the course of performing a stock assessment. MSY reference point estimates can be derived from a stock recruit function, or if that is not estimable, then proxy reference points based on spawning potential ratio (SPR) are often specified (Gabriel et al., 1989; Goodyear, 1993). A common reason that the stock recruit function is inestimable arises from a boundary solution for the parameter steepness, which measures the proportion of unexploited recruitment produced at 20% of unexploited spawning biomass. Typically, this parameter is estimated at its upper bound of 1.0, implying no reduction in recruitment regardless of the amount of spawning biomass, i.e. a steepness value of 1.0 implies that recruitment is constant and independent of spawners (Quinn and Deriso, 1999; Conn et al., 2010). This can occur when there is insufficient contrast in the observed range of spawning biomass, and also when the variability in recruitment is so large as to mask the underlying relationship. Basing management advice on a steepness estimate of 1 would be risky because it implies that the same recruitment will be produced regardless of the magnitude of fishing mortality, and that the stock can never collapse. Although estimation of a stock-recruit function may not be supported by data for a given assessment, there is no sensible debate about whether spawners are needed to produce recruits (Myers and Barrowman, 1996).

Estimating the stock recruit function is typically done internally in a stock assessment model, where the biological parameters of fecundity or weight at age, maturity at age, and natural mortality at age are treated as known and fishery selectivity is estimated based on the catch at age data. Specification of proxy SPR reference points is done outside of a stock assessment model, but still requires estimates of the same biological parameters and in addition it requires an estimate of fishery selectivity at age. In calculating an SPR reference point, one solves for a fishing mortality (F) that reduces the number of spawners produced per recruit over its lifetime to x% of the amount produced with no fishing (Goodyear, 1977, 1993; Gabriel et al., 1989). For example, let φ_0 be unexploited spawners per recruit, and let φ_F be spawners per recruit given fishing mortality, F. Then the resulting SPR is given by

$$\%\mathrm{SPR} = \frac{\varphi_F}{\varphi_0} = \frac{\sum_{\mathrm{age}=r}^{\mathrm{Max\ age}} m_{\mathrm{age}} w_{\mathrm{age}} \prod_{j=r}^{\mathrm{age}-1} e^{-M_j-F_j}}{\sum_{\mathrm{age}=r}^{\mathrm{Max\ age}} m_{\mathrm{age}} w_{\mathrm{age}} \prod_{j=r}^{\mathrm{age}-1} e^{-M_j}} \qquad (1)$$

In the above, m_{age} is maturity at age, w_{age} is fecundity at age, M_j is natural mortality at age, and $F_j = Fs_j$ *is* taken to be the product of an annual fishing rate (F) and age-specific selectivity (s_j). The measure used for fecundity can be a direct measure, such as viable eggs, or it could be a proxy measure such as weight at age.

An immediate point to be made in Eq. (1) is that the parameters of maturity, weight, and natural mortality do not have a subscript for year. Typically, one uses a fixed vector of each parameter at age

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to make the calculation, often informed by mean values observed in recent years. However, the literature is rife with observations and hypotheses about temporal changes in these life history parameters with time or by cohort (Saborido-Rey and Junquerra, 1999; Marshall et al., 2003; Lambert et al., 2003). For example, changes in fecundity (or weights) at age over time are associated with fish being smaller at age, potentially due to density-dependent growth, environmental constraints, or as a consequence of fishing removing the larger, faster growing fish within a cohort (Kjesbu et al., 1998; Sinclair et al., 2002; Stergiou, 2002; Conover and Munch, 2002; Trippel and Neil, 2004). Changes in maturity over time have been interpreted as either a consequence of environmental conditions, as a life history choice with regard to energy investment (mature earlier at the expense of growth), as a result of fishing removing the large mature fish, or due to population sampling (Morgan, 1999; Rideout et al., 2005; Jørgensen and Fiksen, 2005). Natural mortality is generally assumed to be both time and age invariant. This is an obvious simplification of reality, due to the difficulty of estimating age-specific rates and the ease of inferring a constant rate based on longevity (Hoenig, 1983; Hewitt and Hoenig, 2005). However, many mechanisms can be hypothesized that would produce different mortality rates at age and by year (Lorenzen, 1996, 2000; Chen and Watanabe, 1989; Jørgensen and Fiksen, 2005).

It is also important to note that weight at age is often used as a surrogate for fecundity (egg production) in Eq. (1). Provided the two are proportional, then use of weight will not bias the calculations (Marshall et al., 2003). However, a number of authors have suggested that not all spawning biomass is created equally. Experience (age of the spawner) can be an important determinant of recruitment success as it could improve fertilization or lead to more optimal choices about where and when to spawn (Wigley, 1999; Murawski et al., 2001; O'Brien et al., 2003; Green, 2008, and references therein). Also, an individual's condition (as modified by environment), can affect both the quality and quantity of reproductive output (Kjesbu et al., 1998; Blanchard et al., 2003; Marshall et al., 2004). Additionally, growth for some stocks may be cohort dependent, so the approach of using a single vector of recent observations for mean weight at age would slice through multiple cohorts and potentially not match the growth trajectory for any of the cohorts.

Thus, while the mechanics of calculating SPR are straightforward, the decisions about what weights, maturities, and mortalities to use may not be so simple and may have consequences for reference points or estimated stock recruit curves (Murawski et al., 2001; Morgan et al., 2009). In what follows, I first review a direct analytic method to examine the influence of variability in these rates on the reference points. Next, I demonstrate with a hypothetical example the impact of incorporating that variability into the reference points. This leads to a recommendation to parameterize the stock recruit function in terms of maximum lifetime reproductive rate (Myers et al., 1999) rather than steepness to reduce misspecification. Finally, I conclude by discussing the implications of reproductive variability on stock status determination and projections for future catch limits.

2. Analytic methods

Given a stock recruit curve, and the replacement line which has slope $1/\varphi_0$, it is straightforward to solve for the point on the stock recruit curve where excess recruitment (i.e. recruitment beyond what is needed for replacement) is maximized. This point of maximum excess recruitment (MER) was described in Goodyear (1980), although similar derivations are provided in Ricker (1975). It defines the reference point where yield in numbers is maximized. Compared to maximizing yield in biomass (MSY), MER reference points generally result in slightly higher estimates of sustainable F, and consequently lower %SPR, although Brooks et al. (2010) demonstrated that the difference depends on the particular suite of biological parameters and selectivity, and that the disparity was much less at lower steepness values. Brooks et al. (2010) also demonstrated that an analytical solution exists to define SPR_{MER} in terms of the parameter $\hat{\alpha}$, which is the maximum lifetime reproductive rate as defined by Myers et al. (1999). The parameter $\hat{\alpha}$ is calculated as follows:

$$\hat{\alpha} = a\varphi_0 \tag{2}$$

where a is the slope at the origin, which reflects density-independent survival of recruits. As spawning abundance increases, the survival of recruits decreases due to density effects. Therefore, multiplying φ_0 by a gives an upper bound on the number of recruits that could be produced over an individual's lifetime, hence it is the "maximum lifetime reproductive rate." Steepness, h, is related to maximum lifetime reproductive rate as $h = \hat{\alpha}/(\hat{\alpha} + 4)$ (derived in Myers et al., 1999, for both the Beverton-Holt and Ricker). Maximum lifetime reproductive rate is simply a rescaling of h; whereas h is defined on [0.2, 1.0], $\hat{\alpha}$ is defined on $[1.0, \infty]$.

Working in the context of MER reference points, Brooks et al. (2010) demonstrated that SPR_{MER} had a simple, analytic solution for the two most common stock recruit functions (Beverton-Holt and Ricker). For example, for the Beverton-Holt function, SPR_{MER} is:

$$\text{SPR}_{\text{MER}} = 1/\sqrt{\hat{\alpha}} = \sqrt{1-h}/2\sqrt{h} \tag{3}$$

This result provides a convenient framework from which to study the impacts of reproductive variability on SPR_{MER} reference points. As discussed in Section 1, the parameters in the calculation of spawners per recruit (φ_0 and φ_F) may not be time invariant. Furthermore, the slope at the origin (a) represents density-independent survival of recruits, which could be influenced by both environmental and maternal effects (Steer et al., 2004; Green, 2008, and references therein). Eq. (3) can be modified to reflect the temporal nature of the parameters comprising $\hat{\alpha}$:

$$\begin{aligned}\text{SPR}_{\text{MER}}(t) &= \frac{1}{\sqrt{\hat{\alpha}(t)}} = \frac{1}{\sqrt{(a(t)\varphi_0(t))}}\\ &= \frac{1}{\sqrt{a(t)\sum_{\text{age}=r}^{\text{Max age}} m_{\text{age}}(t) w_{\text{age}}(t) \prod_{j=r}^{\text{age}-1} e^{-M_j(t)}}}\end{aligned} \tag{4}$$

From Eq. (4), it can be seen directly how variability in parameters that define reproductive potential, and the magnitude of that variability, translates into variability in reference points.

3. Numerical example: time varying parameters

The lifetime maximum production of recruits, $\hat{\alpha}$, will now be treated as a time varying parameter, $\hat{\alpha}(t)$, and the two parameters that comprise $\hat{\alpha}$ will be examined with respect to biological mechanisms which could cause them to vary. Broadly speaking, the mechanisms can be categorized as either maternal effects or environmental effects. This dichotomy is not absolute, as some mechanisms can be thought of as influencing both. Nevertheless, the two terms whose product is $\hat{\alpha}(t)$, namely slope at the origin ($a(t)$) and unexploited spawners per recruit ($\varphi_0(t)$), will be examined in terms of the direction of change with regard to maternal and environmental effects. For this example, natural mortality will be held constant (at 0.2) so that variability in the reference points due to reproductive potential can be isolated.