



An alternative stock-recruitment function for age-structured models



Ricardo T. Lemos^{a,b,*}

^a The Climate Corporation, 201 3rd St., Suite 1100, San Francisco, CA 94103, USA

^b Centre for Applications in Natural Resource Mathematics, School of Mathematics and Physics, The University of Queensland, St. Lucia 4072, Queensland, Australia

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ABSTRACT

In this work I introduce a probabilistic stock-recruitment function, of the Cushing family, that stands as an alternative to the canonical formulas provided by Beverton-Holt and Ricker, among others. I embed this function in a mathematically tractable (dynamic linear) population model, which renders inference of abundance-at-age and unknown biological parameters (natural mortality, virgin stock's egg production rate, and steepness), as well as fisheries parameters (catchability and selectivity), easier than with canonical representations. To assist management, I provide formulas for exact and approximate reference points, associated with Maximum Sustainable Yield (MSY) and Maximum Excess Recruitment (MER). I also introduce a new summary statistic, called bottleneck abundance ratio, which requires no knowledge of steepness under the proposed stock-recruitment function. With simulated data and the concept of Pretty Good Yield, I generate bounds for MSY- and MER-based reference points and show that those based on the new function have greater resilience to uncertainty about steepness. As a case study, I apply a state-space model to the US Gulf menhaden fishery, 1964–2004. Results suggest higher than previously considered natural mortality and a discernible connection between parental stock abundance and recruitment, undetected with Beverton-Holt and Ricker models.

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1. Introduction

Sustainable management of living resources relies on the ability to predict productivity, based on current parental abundance. In fisheries science, we address this issue via the stock-recruitment relationship (SRR), which consists of a parametric function that provides an estimate of recruitment, based on an index of the parental stock's capacity to produce fertilized eggs (Needle, 2002).

Although the functional form of the SRR should satisfy certain properties (Ricker, 1975; Hilborn and Walters, 2001; Haddon, 2011), several alternatives often provide equally good fits, given the available data (Dorn, 2002; Simmonds et al., 2011; Mangel et al., 2013). To help decide which to employ, Murawski et al. (2001) and Morgan et al. (2009) advocate refining spawning potential indexes, while Myers et al. (1999) and Punt et al. (2005) recommend eliciting consistent patterns from meta-analyses of large numbers of stocks. Other authors explore new SRRs, ranging from non-parametric (Rothschild and Mullen, 1985; Cadigan, 2013) to

more complex functional forms, tailored for particular groups of fish species (Maunder and Deriso, 2013).

In general, scientists do not perceive a large scatter of points around the SRR curve as a refutation of the theory that parental stock size drives recruitment (Ulltang, 1998). Nevertheless, a significant body of literature, attempting to associate recruitment variability with abiotic fluctuations, has grown concurrently to SRR theory (Gilbert, 1997; Rothschild, 2000; Vert-Pre et al., 2013). Debate still remains about the relative importance of the environment versus spawning biomass in determining recruitment (Simmonds et al., 2011; Maunder and Deriso, 2013). In any case, Needle (2002) prescribes abiotic factors as predictors of recruitment only when the former present strong and predictable signals, as well as clear causal linkages to the latter. Along the same line, Ludwig and Walters (1981) point out that only the spawning stock, not offspring itself, can change through management decisions.

Inference on SRR parameters also faces numerous difficulties, including: (i) uncertainty in recruitment and spawning stock size, due to measurement error (Walters and Ludwig, 1981; Hilborn and Walters, 2001); (ii) fluctuations in recruitment magnified at low stock sizes (Myers, 2001; Anderson et al., 2008); (iii) parameter non-stationarity, as an adaptive response to exploitation (Enberg et al., 2010); (iv) insufficient information in fisheries data, also

* Correspondence to: The Climate Corporation, 201 3rd St., Suite 1100, San Francisco, CA 94103, USA.

E-mail address: ricardo.lemos@climate.com

known as “lack of contrast” (Conn et al., 2010; Shertzer and Conn, 2012); (v) other confounding factors (Hilborn and Walters, 2001). Aware of this, Needle (2002) calls for accurate and efficient estimation of component parameters, irrespective of the process used to select the functional form of the SRR.

Concurrently with other approaches, state-space methods, applied to catch-at-age and effort data, have emerged as promising tools to estimate SRR parameters and mitigate some of the difficulties listed above (Mendelsohn, 1988; Millar and Meyer, 2000; Peterman et al., 2003; Rivot et al., 2004; Fleischman et al., 2013). These methods treat stock and recruitment as autocorrelated and cross-correlated time-series, contaminated with measurement error and process uncertainty. Under a Bayesian setting, prior information about parameters and/or the state can enter the model; output consists of posterior probability densities, instead of point estimates or densities that rely on asymptotic theory (McAllister and Kirkwood, 1998).

In this work, I follow the traditional assumption that spawning stock and recruitment relate through a simple, parametric equation. However, I depart from canonical representations (namely, Beverton-Holt and Ricker) and present an alternative, prompted by requirements that existing SRRs do not entirely fulfill: (i) the SRR should permit the construction of simple state-space models that facilitate parameter estimation from fisheries data; (ii) reference points (e.g. Maximum Sustainable Yield, Maximum Excess Recruitment) should have straightforward expressions and clear connections to individual SRR parameters; (iii) fisheries management should have some resilience against uncertainty about key SRR parameters, namely steepness. After expounding these three desiderata, I apply an age-structured model based on the new SRR to a real data set (US Gulf menhaden catch-at-age and effort), estimate parameters with Bayesian methods, and compare results with canonical models.

2. Methods

For a matter of simplicity, I use knife-edged maturation and selectivity functions, do not discriminate genders, and keep the natural mortality rate constant for all ages. Greek letters denote unknown quantities, upper case Roman letters designate functions of these unknown quantities, and lower case Roman letters represent constants and functions thereof. Namely, a_U , a_M , a_R and e stand for longevity, age at maturity, age at recruitment, and Euler’s number, respectively. Functions of constants include: mean spawning age $a_S = (1/2)(a_M + a_U)$; the number of spawning cohorts, $n_S = a_U - a_M + 1$; the number of recruited cohorts, $n_R = a_U - a_R + 1$; and the number of extant cohorts, $n_C = a_U + 1$. To conform to standard notation in fisheries modeling, a few noted exceptions occur.

2.1. Dynamics of virgin and exploited stocks

Let $N_{t,a}$ denote the abundance of individuals with age a at time instant t , and let

$$N_{0,a} = \begin{cases} e^{\rho - a\zeta}, & \text{if } 0 \leq a \leq a_U, \\ 0, & \text{otherwise,} \end{cases} \quad (1)$$

provide the deterministic equation for abundance-at-age in the virgin stock. Parameters ρ and ζ represent the virgin stock’s rate of egg

production and the natural mortality rate, respectively. Under this formulation, steady-state abundance equates to

$$\sum_{a=0}^{a_U} N_{0,a} = \frac{1 - e^{-(a_U+1)\zeta}}{1 - e^{-\zeta}} e^{\rho},$$

and the e^{ρ} eggs produced per time instant cancel with the number of individuals lost due to natural mortality:

$$e^{\rho} - \left(N_{0,a_U} + (1 - e^{-\zeta}) \sum_{a=0}^{a_U-1} N_{0,a} \right) = e^{\rho} - e^{\rho} = 0.$$

The abundance of new recruits in the virgin stock, typically symbolized by R_0 instead of N_{0,a_R} , combines parameters and constants:

$$R_0 = e^{\rho - a_R\zeta}. \quad (2)$$

Information on egg production seldom exists. For this reason, several statistics, which summarize the virgin population’s spawning stock size, can act as surrogates. Popular ones include spawning stock abundance (Lowerre-Barbieri et al., 1998; Lipcius and Stockhausen, 2002),

$$S_0 = \sum_{a \geq a_M} N_{0,a} = \frac{1 - e^{-n_S\zeta}}{1 - e^{-\zeta}} e^{\rho - a_M\zeta},$$

and spawning stock biomass (Ricker, 1954; Beverton and Holt, 1957),

$$SSB_0 = \sum_{a \geq a_M} N_{0,a} W_a,$$

where W_a stands for weight-at-age. Morgan et al. (2009) provide a critique of SSB, as well as extensions. With mathematical tractability of the SRR in mind, I propose the geometric mean number of mature individuals as an alternative,

$$\tilde{S}_0 = \sqrt[n_S]{\prod_{a \geq a_M} N_{0,a}}, \quad (3)$$

which simplifies to $\tilde{S}_0 = e^{\rho - a_S\zeta}$.

Eq. (1) captures the long-term dynamics of a virgin stock. In the short term, stochastic fluctuations typically occur, due to environmental variability. The canonical approach to account for this consists of two steps:

1. use log-normal multiplicative shocks, whereby the change in abundance from ages $a - 1$ to a (with $a > a_R$), at time t , becomes

$$N_{t,a} = N_{t-1,a-1} e^{-\zeta + \epsilon_{t,a}},$$

with $\epsilon_{t,a} \sim N[0, e^{\tau}]$;

2. define a compensatory SRR, with spawning stock abundance, S_t , or biomass, SSB_t , as the summary statistic for parental cohorts.

In this work, I also employ multiplicative log-normal errors for all ages but, instead of the canonical Beverton-Holt and Ricker SRRs, I introduce a new function. Starting from the spawning stock statistic at time t ,

$$\tilde{S}_t = \sqrt[n_S]{\prod_{a \geq a_M} N_{t,a}}, \quad (4)$$

I define a quantity called “reproductive health index”, as

$$H_t = \left(\frac{\tilde{S}_t}{\tilde{S}_0} \right)^{1-\phi}, \quad (5)$$

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