An explicit solution for calculating optimum spawning stock size from Ricker's stock recruitment curve

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ABSTRACT

Ricker's stock recruitment model is widely used to describe the spawner-offspring relationship for fishes. After model fitting, the spawning stock size that produces the maximum sustainable yield (S_{MSY}), and the harvest corresponding to it (U_{MSY}), are two of the most common biological reference points of interest to fisheries managers. However, to date there has been no explicit solution for either reference point because of the transcendental nature of the equation needed to solve for them. Therefore, numerical or statistical approximations have been used for more than 30 years. Here I provide explicit formulae for calculating both S_{MSY} and U_{MSY} in terms of the productivity and density-dependent parameters from Ricker's model.

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INTRODUCTION

One of the most difficult problems in the assessment of fish stocks is establishing the relationship between the spawning stock and subsequent recruitment (Hilborn and Walters 1992). Stock-recruitment models have been used for decades in fisheries management as a means of formalizing this relationship (Beverton and Holt 1957; Ricker 1954). Over time, a variety of functional forms have emerged to capture varying assumptions about depensatory and compensatory mortality (Hilborn and Walters 1992). In a classroom setting, deterministic versions of the models provide useful constructs for teaching about management reference points such as maximum sustained yield (MSY).

In particular, Ricker's stock recruitment model (Ricker 1954; Ricker 1975) is one of the most widely used models to describe the population dynamics of fishes, such that

$$R = \alpha S e^{-bS}, \quad (1)$$

R is the number of recruits produced, S is the number of spawners, α is the dimensionless number of recruits per spawner produced at very low spawner density, and b is the strength of density dependence (units: spawner^{-1}). It is common to substitute $\alpha = e^a$ into equation (1) and rewrite it as

$$R = S e^{a-bS}. \quad (2)$$

To make the model reflect a stochastic process, equation (2) is typically multiplied by a log-normal error term, so that

$$R = S e^{a-bS} e^{\varepsilon}, \quad (3)$$

and ε is a normally distributed error term with a mean of -½σ and variance σ. The non-zero mean ensures that a is interpreted as the mean recruits per spawner rather than the median

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(Hilborn 1985). Part of the model's popularity is due to the relative ease with which its parameters are estimated. After log transformation, equation (3) is typically rewritten as

$$\ln(R/S) = a - bS + \varepsilon, \tag{4}$$

and the parameters are estimated via simple linear regression. I note here that estimation of the parameters via a simple observation-error model like (4) can lead to substantial biases in a and b if the sample size is low ($n \leq 10$) due to autocorrelation in the residuals ε (Walters 1985).

Once the model has been fit to data and any necessary bias corrections made, the parameters can be used to derive various biological reference points of interest to fisheries managers. Some of these metrics are rather trivial to compute. For example, the spawning stock size leading to maximum recruit production (S_{MSR}) is simply $1/b$. Other reference points are much less straightforward to calculate, however. In particular, the spawning stock expected to produce the maximum sustainable yield (S_{MSY}) under deterministic dynamics is of common interest.

To find S_{MSY}, I express the yield (Y) as

$$Y = R - S = Se^{a-bS} - S, \tag{5}$$

and then take the derivative of Y with respect to S:

$$\frac{dY}{dS} = (1 - bS)e^{a-bS} - 1. \tag{6}$$

S_{MSY} is then determined by setting equation (6) to zero and solving for S. Upon initial inspection, however, there does not appear to be an explicit solution to this equation in terms of S, and therefore S_{MSY} is typically solved "by trial" (Ricker 1975) with some form of gradient method (e.g., Newton's as in Hilborn 1985).

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To simplify this issue for common applications, Hilborn (1985) developed a linear model relating the ratio of S_{MSY} to equilibrium spawning stock size ($S_r = a/b$) to the parameter a. Specifically, for $0 < a \leq 3$ he estimated that

$$\frac{S_{MSY}}{S_r} = \frac{S_{MSY}}{(a/b)} = 0.5 - 0.07a \text{, and} \quad (7a)$$

$$S_{MSY} = \frac{a(0.5 - 0.07a)}{b}. \quad (7b)$$

Although this approximation is very useful due to its simplicity, there is no underlying fundamental support for the statistical form of the relationship.

METHODS

Here I make use of the Lambert W function, $W(z)$, to demonstrate an explicit solution to equation (4) that precludes the need to estimate S_{MSY} via numerical methods or Hilborn's (1985) statistical model. This function has been used for explicit solutions to Roger's random predator equation in ecology (McCoy and Bolker 2008) and susceptible-infected-removed (SIR) models in epidemiology (Reluga 2004; Wang 2010). Specifically, $W(z)$ is defined as the function that satisfies

$$W(z)e^{W(z)} = z \quad (8)$$

for any complex number z (Lambert 1758 and Euler 1783 as cited in Corless et al. 1996). Here we are interested only in real values, however, so I replace z with x and note that $W(x)$ is only defined for $x \geq -1/e$ (Corless et al. 1996). Furthermore, this function is not injective and has two values for $-1/e \leq x \leq 0$, but as I show below, we are concerned only with the region where $x > 0$ and $W(x)$ is a singular, non-negative value.

I begin my explicit solution of S_{MSY} by setting equation (6) to zero, such that

$$(1 - bS_{MSY})e^{a - bS_{MSY}} = 1. \quad (9)$$

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After rearranging terms and multiplying both sides by e, we arrive at

$$\left(1-bS_{MSY}\right)e^{1-bS_{MSY}}=e^{1-a}. \tag{10}$$

At this point I note the relationship between equations (10) and (8), with $1 - bS_{MSY} = W(z)$ and $e^{1\text{-a}} = z$. Therefore, we can write

$$1-bS_{MSY}=W\left(e^{1-a}\right), \text{ and hence} \tag{11}$$

$$S_{MSY}=\frac{1-W\left(e^{1-a}\right)}{b}. \tag{12}$$

We now have an explicit solution for S_{MSY} that depends only on the parameters a and b from equation (2). As mentioned above, $W(x)$ is only defined for $x \geq -1/e$, which does not pose any problems here because $x = e^{1-a} > 0 \; \forall \; a \in \mathbb{R}$. For visualization purposes, I show a plot of $W(e^{1-a})$ versus a in Figure 1.

We can also derive an explicit formula for calculating the fraction of the return harvested at S_{MSY}, which I call U_{MSY}. As Ricker (1975) shows,

$$U_{MSY}=bS_{MSY}, \tag{13}$$

and therefore substituting (12) into (13) gives

$$U_{MSY}=1-W\left(e^{1-a}\right). \tag{14}$$

In practice $W(x)$ may be approximated numerically using some form of gradient method. Corless et al. (1996) recommend Halley's method, with the update equation given by

$$w_{j+1}=w_j-\frac{w_je^{w_j}-x}{e^{w_j}\left(w_j+1\right)-\frac{\left(w_j+2\right)\left(w_je^{w_j}-x\right)}{2w_j+2}}. \tag{15}$$

I use an initial guess of $w_0 = ¾ \ln(x+1)$ based on the shape of $W(x)$ over the range of a typically considered in fisheries research (i.e., $0 < a < 3$; Hilborn 1985). Although implementing equation

(15) may seem a bit daunting to individuals less familiar with numerical methods, a variety of contemporary software packages (e.g., MATLAB, R) include built-in functions to calculate $W(x)$ directly. This means that anyone using a personal computer to estimate the parameters in a Ricker model can easily estimate S_{MSY} from equation (12) as I demonstrate in Table 1. I show the results from my R implementation for a range of a and b in Figure 2.

For those preferring to use Excel, there is unfortunately no built-in function to calculate $W(x)$, but I have implemented equation (15) as the VBA function 'LAMBERTW' and include it as the Excel Add-In file 'LambertWfunc.xlam' as part of the supplementary material[1]. For those unfamiliar with installing Excel add-ins, I also provide instructions on how to do so in the supplementary material (Figure S1).

RESULTS AND DISCUSSION

In addition to its convenience, solving for S_{MSY} via $W(x)$ also offers an appreciable computational advantage. As a test, I randomly selected 1000 values of a and b over the same ranges as shown in Figure 2, and then solved for S_{MSY} using both Newton's method as suggested by Ricker (1975), and Halley's method as in equation (15). Although both methods were remarkably quick, Halley's method was always faster and less variable (Figure 3). Therefore, estimating S_{MSY} via Halley's method might save significant time in applications such as management strategy evaluations that are much more computationally intensive than a simple one-case solution.

Here I have outlined a new method to easily calculate S_{MSY} from the productivity (a) and density-dependent (b) parameters in a Ricker model using readily available functions in several software packages. This method is much more straightforward than trying to solve for S_{MSY} using

[1] Available for download at http://faculty.washingon.edu/scheuerl/LabertWfunc.xlam

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numerical methods and should be useful in many classroom settings. Although there could be some utility in actually going through the exercise of numerically deriving the answer, it is rare nowadays, for example, for anyone to code a random number generator because of their ubiquitous implementation in standard software. In addition, the explicit analytical solution is closed-form with respect to the special functions, and therefore precludes the need to estimate S_{MSY} via Hilborn's (1985) approximation. Thus, due to the speed and ease with which these new equations are calculated, I recommend that practitioners use them for S_{MSY} and U_{MSY} in lieu of those listed in Appendix III of Ricker (1975) and Table 7.2 of Hilborn and Walters (1992).

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REFERENCES

Beverton, R. J. H., and S. J. Holt. 1957. On the Dynamics of Exploited Fish Populations. Fishery Investigations Series II Volume XIX, Ministry of Agriculture, Fisheries and Food.

Corless, R. M., G. H. Gonnet, D. E. G. Hare, D. J. Jeffrey, and D. E. Knuth. 1996. On the Lambert W function. Advances in Computational Mathematics 5(4):329-359.

Hilborn, R. 1985. Simplified calculation of optimum spawning stock size from ricker stock recruitment curve. Canadian Journal of Fisheries and Aquatic Sciences 42(11):1833-1834.

Hilborn, R., and C. J. Walters. 1992. Quantitative Fisheries Stock Assessment: Choice, Dynamics and Uncertainty. Chapman and Hall, New York.

McCoy, M. W., and B. M. Bolker. 2008. Trait-mediated interactions: influence of prey size, density and experience. Journal of Animal Ecology 77(3):478-486.

Reluga, T. 2004. A two-phase epidemic driven by diffusion. Journal of Theoretical Biology 229(2):249-261.

Ricker, W. E. 1954. Stock and recruitment. Journal of the Fisheries Research Board of Canada 11(4):559-623.

Ricker, W. E. 1975. Computation and interpretation of biological statistics of fish populations. Bulletin of the Fisheries Research Board of Canada 191:832 p.

Walters, C. J. 1985. Bias in the estimation of functional relationships from time series data. Canadian Journal of Fisheries and Aquatic Sciences 42(1):147-149.

Wang, F. 2010. Application of the Lambert W function to the SIR epidemic model. The College Mathematics Journal 41(2):156-159.

Table 1. Example code for directly calculating S_{MSY} in R, Matlab, and Excel; the values for *a* and *b* were chosen arbitrarily. Note that the R code requires the 'gsl' package to be installed, and the Excel code requires the 'LAMBERTW' function contained in the Excel Add-in file LambertWfunc.xlam.

Software	Code example

R	`> library("gsl")`
	`> a = 1`
	`> b = 5e-4`
	`> Smsy = (1 - lambert_W0(exp(1 - a))) / b`

MATLAB	`>> a = 1`
	`>> b = 5e-4`
	`>> Smsy = (1 - lambertw(exp(1 - a))) / b`

Excel	(spreadsheet below)

	A	B
1	a	1
2	b	5e-4
3	Smsy	=(1 - LAMBERTW(EXP(1 - B1))) / B2

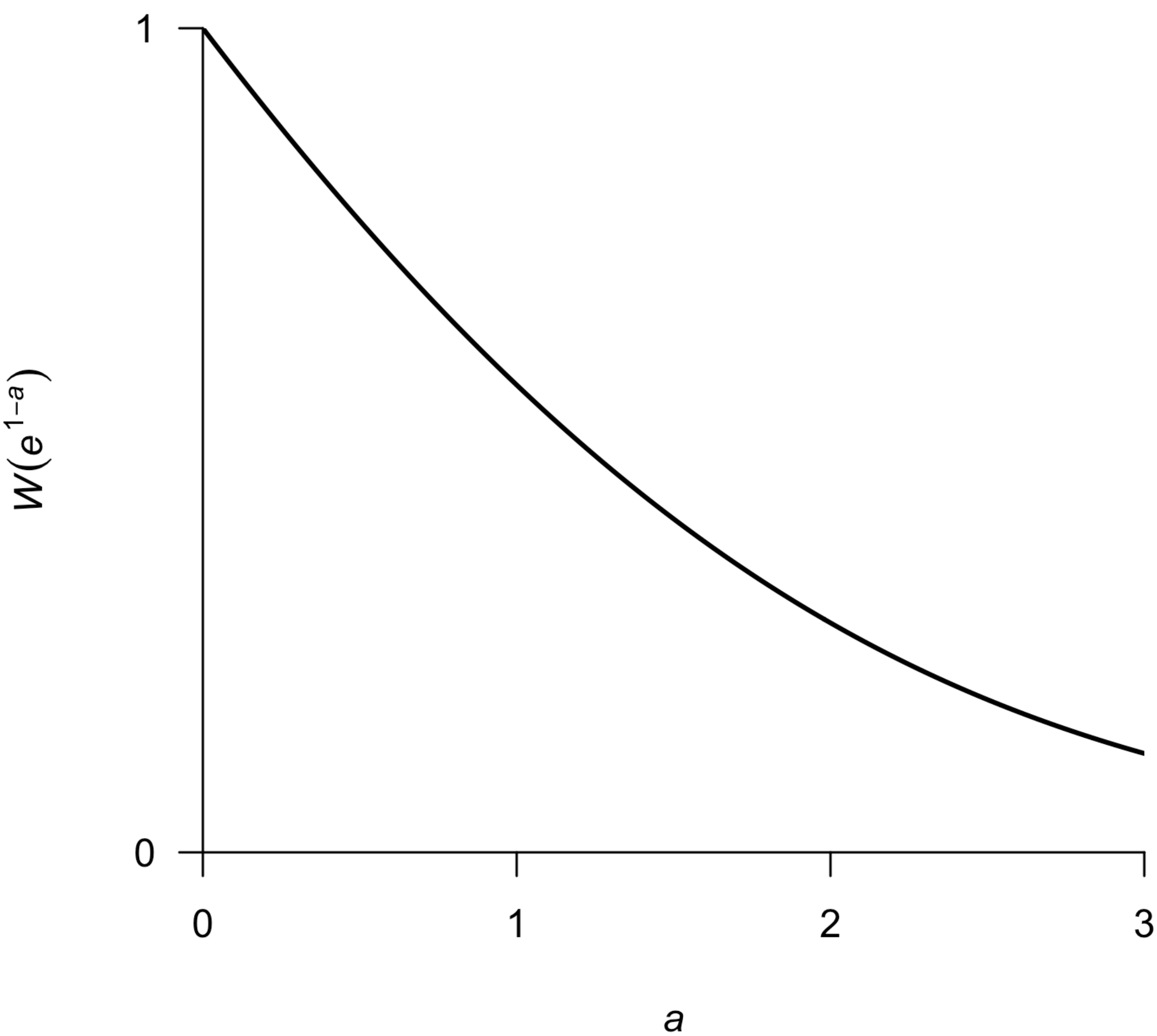

Figure 1. Plot of $W(e^{1-a})$ over a range in values of a typically encountered in fisheries.

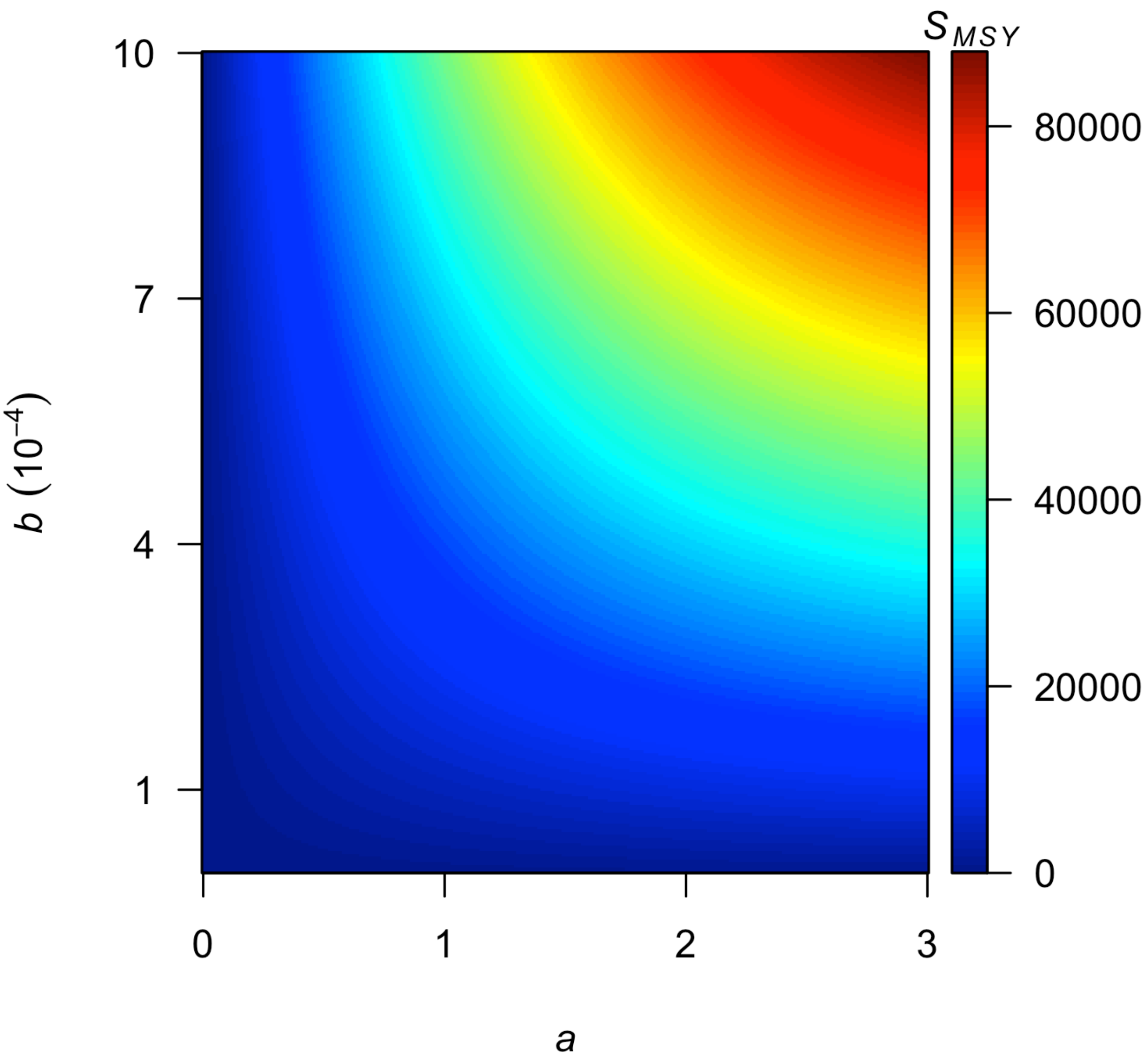

Figure 2. Contour plot showing values of S_{MSY} for combinations of the *a* and *b* parameters in Equation (2).

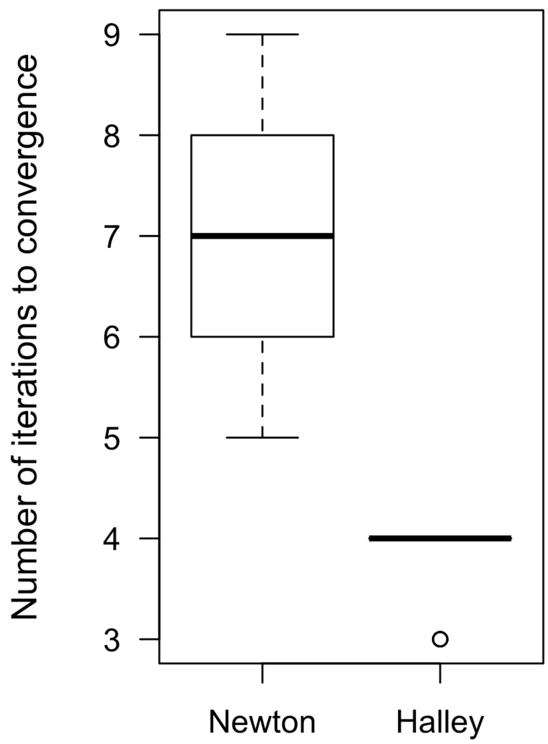

Figure 3. Box-and-whisker plots showing the distribution of the number of iterations that each of the two numerical methods takes to converge to S_{MSY} using a threshold of 10^{-6}.

1) Download **LambertWfunc.xlam** and save it anywhere on your hard drive.
2) Start Excel.
3) Depending on your version of Excel, do either (a) or (b) below
   a) Microsoft Excel for Mac 2011:
      i) Click **Tools**, and then select **Add-ins...**
      ii) From the dialog box, click **Select…**
      iii) Browse to wherever you saved the file in Step (1) and select **LambertWfunc.xlam**.
      iv) Click **Open**, which returns you to the **Add-Ins** dialogue box.
      v) Verify the box is checked next to **LambertWfunc.xlam**.
      vi) Click **OK**.
   b) Microsoft Excel for Windows (versions 2007, 2010, 2013)
      i) Click the **Office Button** (v2007) or the **File** tab (v2010/2013).
      ii) Click on **Options** near the bottom of the list.
      iii) From the pop-up window, choose the **Add-Ins** category.
      iv) In the **Manage** box at the bottom, click **Excel Add-ins**, and then click **Go**.
      v) In the **Add-Ins** dialog box that appears, click **Browse**.
      vi) Browse to wherever you saved the file in Step (1) and select **LambertWfunc.xlam**.
      vii) Click **OK**.
      viii) Click **OK** to close the **Add-Ins** dialog box.

Figure S1. Instructions for installing the LAMBERTW function in Excel.

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