# Metamodeling for Bias Estimation of Biological

# Reference Points

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## <sub>5</sub> 1 Introduction

- 6 Data for a typical surplus-production model comes in the form of an index of abundance
- <sup>7</sup> through time which is assumed to be proportional to the reproducing biomass for the popu-
- 8 lation of interest. The index is often observed alongside a variety of other known quantities,
- 9 but at a minimum, each observed index will be observed in the presence of some known
- 10 catch for the period.

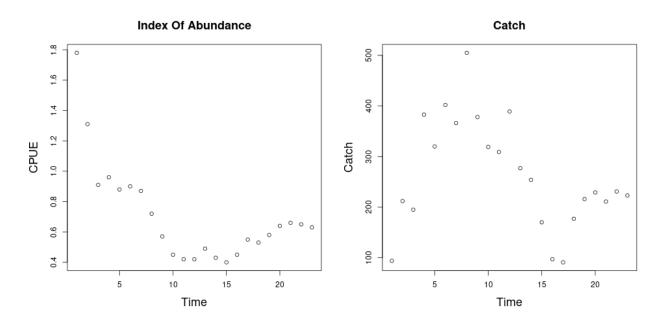


Figure 1: *left*: An observed series of index of abundance data for Namibian Hake from 1965 to 1987 (Hilborn & Mangel, 1997). *right*: The associated catch data for Namibian Hake over the same time period.

The observed indices are assumed to have multiplicative log-normal errors, and thus the following observation model arises naturally,

$$I_t = qB_t e^{\epsilon} \quad \epsilon \sim N(0, \sigma^2). \tag{1}$$

Above q is often referred to as the "catchability parameter"; it serves as the proportionality constant mapping between the observed index of abundance and biomass.  $\sigma^2$  models residual variation. Biologically speaking q and  $\sigma^2$  are often treated as nuisance parameters with the

- "biological parameters" entering the model through a process model on biomass.
- Biomass is assumed to evolve as an ODE; in this case I focus on the following form,

$$\frac{dB}{dt} = P(B(t); \boldsymbol{\theta}) - Z(t)B(t). \tag{2}$$

Here biomass is assumed to change in time by two processes, net production of biomass into the population, P(B), and various sources of biomass removal, Z, from the population.

Firstly, the population grows through a production function, P(B). Production in this setting is defined as the net biomass increase due to all reproduction and maturation processes. The production function is assumed to be a parametric (generally non-linear) function relating the current biomass of the population to an aggregate production of biomass.

Secondly, the population decreases as biomass is removed by various sources that are assumed to remove biomass linearly with biomass. Above, Z(t), is an aggregate rate of removal. When the fishing rate, F(t), is the only source of removal Z(t) = F(t), however often models will also included other linear terms in Z(t). Commonly the rate of "natural mortality", M, is also included as an additional term so that Z(t) = M + F(t).

From a management perspective a major goal of modelling is to accurately infer a quantity 27 known as maximum sustainable yield (MSY). One could maximize simple yield at a particular 28 moment in time (and only for that moment) by fishing all available biomass in that moment. 29 This strategy is penny-wise but pound-foolish (not to mention ecologically devastating) since 30 it doesn't leave biomass in the population to reproduce in the future. We seek to fish in a way 31 that allows (or even encourages) future productivity in the population. This is accomplished 32 by maximizing the equilibrium level of catch over time. Equilibrium yield is considered by 33 replacing the steady state biomass  $(\bar{B})$  in the assumed form for catch, so that  $\bar{Y} = F\bar{B}(F)$ , 34 where indicates a value at steady state. The steady state biomass is a function of F. MSY 35 is found by optimizing  $\bar{Y}(F)$  with respect to F, and  $F^*$  is the fishing rate at MSY. Going 36 forward let \* decorate any value derived under the condition of MSY. 37

Fisheries are very often managed based upon reference points (RPs) which serve as simplified heuristic measures of population behavior. The mathematical form of RPs depends upon the model assumptions through the production function. While a number of different

RPs exist which describe the population in different (but related) ways, the most common RPs revolve around the concept of MSY (or robust ways of measuring MSY (Hilborn, 2010; 42 Punt et al., 2016)). Here the focus is primarily on the RPs  $\frac{B^*}{\bar{B}(0)}$  and  $F^*$  ( $\frac{F^*}{M}$  when appropriate) 43 for their pervasive use in modern fisheries (Mangel et al., 2013; Punt & Cope, 2019).  $F^*$  is the afore mentioned fishing rate which results in MSY.  $\frac{B^*}{\overline{B}(0)}$  is the depletion of the 45 stock at MSY. That is to say  $\frac{B^*}{\bar{B}(0)}$  describes the fraction of the unfished population biomass 46 that will remain in the equilibrium at MSY. In general  $F^* \in \mathbb{R}^+$  and  $\frac{B^*}{\overline{B}(0)} \in (0,1)$ , however 47 under the under the assumption of a two parameter production function the model will be 48 structurally unable to capture the full theoretical range of RPs (Mangel et al., 2013). 49 Many of the most commonly used production functions depend only on two parameters. 50 For example, the Schaefer model (cite) depends only on the biological parameters r and K, 51 and limits RP inference so that under the Schaefer model  $\left(F^*, \frac{B^*}{\overline{B}(0)}\right) \in \left(\mathbb{R}^+, \frac{1}{2}\right)$ . Similarly 52 the Beverton-Holt (Beverton & Holt, 1957, BH) and Ricker (Ricker, 1954) curves are also 53 two parameter production functions that do not model the full theoretical space of RPs 54 (Mangel et al., 2013). 55 The bias-variance trade-off (Ramasubramanian & Singh, 2017) makes it clear that the 56 addition of a third parameter in the production function will necessarily reduce estimation 57 bias. However the utility of this bias reduction is still under debate because the particular 58 mechanisms and behavior (direction and magnitude) of these biases for key management 59 quantities are not fully understood or described. Lee et al. (2012) provides some evidence 60 that estimation of productivity parameters are dependent on biomass contrast as well as 61 model specification. Conn et al. (2010) comes to similar conclusions via calibration modeling 62 techniques. These studies indicate improtant factors that contribute to inferential failure, 63 but they do not offer mechanisms of model failure, nor do they consider how different types of model misspecification interact with the information content of a given biomass series. 65 In this study I consider the behavior of inference when index data are simulated from 66 three parameter PT and Schnute production models, but the simulated data are fit using 67 intentionally misspecified two the parameter logistic or BH production models. The work 68

begins with a derivation of RPs under the three parameter models. The parametric forms

of RPs under the three parameter models are then inverted to develop a simulation setting

for analyzing inference under the two parameter models. Finally a Gaussian Process (GP) metamodel (Gramacy, 2020) is constructed for exploration and analysis of RP biases.

A key insight of this approach is that bias is considered broadly across RP-space to uncover patterns and correlations between RPs. The GP metamodel is explicit about tradeoffs between RPs so as to inform the full utility of reducing bias, as well as to suggest mechanisms for understanding what causes bias. Further, the effect of contrast on estimation is considered together with model misspecification.

## <sub>s</sub> 2 Methods

# <sup>9</sup> 2 .1 PT/Schaffer Model

The three parameter PT family has a convenient form that includes, among others (Fox Jr., 1970; Rankin & Lemos, 2015), the logistic production function as a special case. Pella-Tomlinson production function is parameterized so that  $\boldsymbol{\theta} = [r, K, \gamma]$  and the family takes the following form,

$$P(B; [r, K, \gamma]) = \frac{rB}{\gamma - 1} \left( 1 - \left( \frac{B}{K} \right)^{(\gamma - 1)} \right). \quad (3)$$

 $\gamma$  is a parameter which breaks PT out of the restrictive symmetry of the logistic curve. In the special case of  $\gamma=2$  Eq (3) collapses back to the logistic curve, however in general  $\gamma\in(1,\infty)$ . The parameter r controls the maximum reproductive rate of the population in the absence of

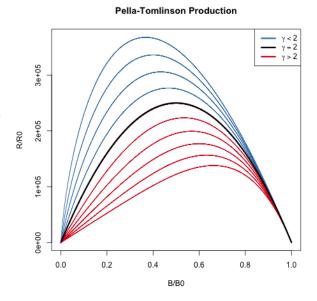


Figure 2: The PT production function plotted across a variety of parameter values. The special cases of Logistic production is shown in black, and the left-leaning and right-leaning regiems are shown in blue and red respectively.

competition for resources (i.e. the slope of production function at the origin). K is the so called "carrying capacity" of the population. In this context the carrying capacity can be formally stated as steady state biomass in the absence of fishing (i.e.  $\bar{B}(0) = K$ ). In Figure (2) PT recruitment is shown for a range of parameter values so as to demonstrate the various recruitment shapes that can be achieved by PT recruitment.

While the form of the PT curve produces some limitations (cite), importantly the introduction of a third parameter allows enough flexibility to fully describe the space of reference points used in management. To see this, the reference points are analytically derived for the PT model below.

#### 96 2.2 PT Reference Points

With B(t) representing biomass at time t, under PT production, the dynamics of biomass are defined by the following ODE,

$$\frac{dB}{dt} = \frac{rB}{\gamma - 1} \left( 1 - \left( \frac{B}{K} \right)^{\gamma - 1} \right) - FB. \tag{4}$$

An expression for the equilibrium biomass is attained by setting Eq (4) equal to zero, and rearranging the resulting equation to solve for B. Thinking of the result as a function of F gives,

$$\bar{B}(F) = K \left( 1 - \frac{F(\gamma - 1)}{r} \right)^{\frac{1}{(\gamma - 1)}}.$$
 (5)

At this point it is convenient to notice that  $\bar{B}(0) = K$ . The expression for  $B^*$  is given by evaluating Eq (5) at  $F^*$ . To get an expression for  $F^*$ , the equilibrium yield is maximized with respect to F,

$$F^* = \operatorname*{argmax}_F F\bar{B}(F). \tag{6}$$

In the case of PT production this maximization can be done analytically, by differentiating the equilibrium yield with respect to F as follows,

$$\frac{d\bar{Y}}{dF} = \bar{B}(F) + F\frac{d\bar{B}}{dF} \tag{7}$$

$$\frac{d\bar{B}}{dF} = -\frac{K}{r} \left( 1 - \frac{F(\gamma - 1)}{r} \right)^{\frac{1}{\gamma - 1} - 1}.$$
 (8)

Setting Eq (7) equal to 0, substituting  $\bar{B}(F)$  and  $\frac{d\bar{B}}{dF}$  by Equations (5) and (8) respectively,

and solving for F produces the following expression for the fishing rate required to produce MSY,

$$F^* = \frac{r}{\gamma} \tag{9}$$

Plugging the above expression for  $F^*$  back into Eq (5) gives the following expression for biomass at MSY,

$$B^* = K \left(\frac{1}{\gamma}\right)^{\frac{1}{\gamma - 1}}. (10)$$

The above derived expressions for  $\bar{B}(0)$ ,  $B^*$ , and  $F^*$  can then be used to build a specific analytical form for the biological reference points in terms of only biological model parameters.

$$F^* = \frac{r}{\gamma} \qquad \frac{B^*}{\bar{B}(0)} = \left(\frac{1}{\gamma}\right)^{\frac{1}{\gamma - 1}} \tag{11}$$

# <sub>02</sub> 2 .3 Simulation

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• introduce metamodeling idea

Indices of abundance are simulated from the three parameter PT production model broadly over the space of  $F^*$  and  $\frac{B^*}{\overline{B}(0)}$  values. These PT data are then fit with a misspecified two parameter Schaefer model so as to observe the effect of productivity parameter model misspecification upon RP inference.

Generating simulated indices of abundance from the PT model requires inverting the relationship between  $\left(F^*, \frac{B^*}{\overline{B}(0)}\right)$ , and  $(r, \gamma)$ . It is not generally possible to analytically invert this relationship for many three parameter production functions (Punt & Cope, 2019; J. T. Schnute & Richards, 1998). Most three parameter production functions lead to RPs that require expensive numerical methods to invert; more over the numerical inversion procedure can often be unstable. That said, for the case of PT this relationship is analytically

invertible, and leads to the following relationship

$$r = \gamma F^* \qquad \qquad \gamma = \frac{W\left(\frac{B^*}{\overline{B}(0)}\log\left(\frac{B^*}{\overline{B}(0)}\right)\right)}{\log\left(\frac{B^*}{\overline{B}(0)}\right)}. \tag{12}$$

Above W is the Lambert product logarithm function. More details about this derivation, and the Lambert product logarithm, are given in Appendix (4).

#### 110 2 .3.1 Latin Hypercube Sampling

A Latin hypercube sample (LHS) of size n, in an m dimensional space, samples uniformly among uniform grids of size n in each dimension of the design space. By intersecting the grids of each dimension,  $n^m$  cells are produced, from which a total of n samples are taken. Crutially only one sample is taken from a given element of each grid in each dimension so as to reduce clumping of the n samples across the design space.

Letting  $\mathcal{F}$  and  $\mathcal{B}$  be equally spaced grids, of size n, on  $F_{MSY} \in (0.1, 0.7)$  and  $\frac{B_{MSY}}{B_0} \in (0.2, 0.6)$  respectively, a LHS samples 1 point in n of the  $n^2$  cells produced by  $\mathcal{F} \times \mathcal{B}$ .

Each of the sampled LHS design locations represent a unique PT model with the sampled RP values. The productivity parameters of the PT, at each design location, are obtained by applying Eq. (12). Since K does not enter the RP calculation its value is fixed arbitrarily at 10000. The value of q is fixed at a typically small value of 0.0005.  $\sigma$  is fixed at the relatively small value of 0.01 to focus specifically on the behavior of population parameters. These parameters fully specify the PT model for the purposes of generating index data for each  $(F^*, \frac{B^*}{B(0)})$  pair.

#### 125 2 .3.2 Catch

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It is known that the behavior of catch can effect inference on the productivity parameters
(Hilborn & Walters, 1992). In this setting contrast refers to changes in the long term trends
of index data. Figure (3, right) demonstrates an example of biomass that includes contrast
induced by catch. It is not well understood how contrast may factor into inferential failure
induced by model misspecification. A variety of catches are investigated.

Catch is parameterized so that F(t) can be controlled with respect to  $F^*$ . Recall that

catch is assumed to be proportional to biomass, so that C(t) = F(t)B(t). To control F(t)with respect to  $F^*$ , C(t) is specified by defining the quantity  $\frac{F(t)}{F^*}$  as the relative fishing rate. 133 B(t) is defined by the solution of the ODE, and  $F^*$  is defined by the biological parameters of 134 the model, see Eq (42). By defining  $\frac{F(t)}{F^*}$ , catch can then be written as  $C(t) = F^*\left(\frac{F(t)}{F^*}\right)B(t)$ . 135 Intuitively  $\frac{F(t)}{F^*}$  describes the fraction of  $F^*$  that F(t) is specified to for the current B(t). When  $\frac{F(t)}{F^*} = 1$ , F(t) will be held at  $F^*$ , and the solution of the ODE brings B(t) into 137 equilibrium at  $B^*$ . For constant  $\frac{F(t)}{F^*}$  biomass comes to equilibrium as an exponential decay 138 from K approaching  $B^*$ . When  $\frac{F(t)}{F^*} < 1$ , F(t) is lower than  $F^*$  and B(t) is pushed toward 139  $\bar{B} > B^*$ . Contrarily, when  $\frac{F(t)}{F^*} > 1$ , F(t) is higher than  $F^*$  and B(t) is pushed toward  $\bar{B} < B^*$ ; the precise values of  $\bar{B}$  can be calculated from Eq (15).

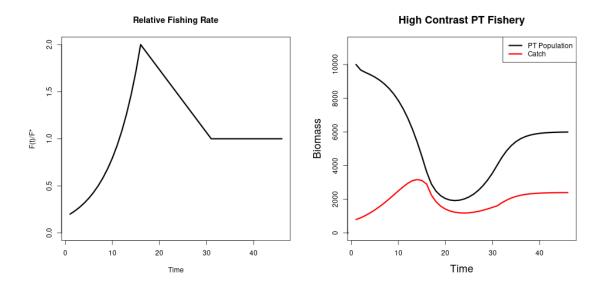


Figure 3: (left) Relative fishing specified so as to induce contrast. (right) Population biomass and catch demonstrating contrast in a PT population with  $F^* = 0.4$  and  $\frac{B^*}{B(0)} = 0.6$ .

In practice, catch is determined by a series of observed, assumed known, catches. Catch observations are typically observed on a quarterly (or yearly) basis, so that the ODE may be discretized via Euler's method with integration step sizes to match the observation frequency of the modeled data. In this case, catch is sampled as would be done in practice however, the simulation can encounter a variety of issues working with the naively discretized ODE. As a result the ODE is integrated implicitly via the Livermore Solver (Radhakrishnan, 1993, lsode), and catch is linearly interpolated between sampled epochs.

- ?quantification of degrees of information? (avg curvature?)
  - remake picture w/o PT references

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#### 2.3.3 Continuous model formulation

a preface to regularity issues: identifiability, stiffness, and continuity.

An important (and often overlooked) implementation detail is the solution to the ODE which defines the progression of biomass through time (See Eq(33)). As a statistical model it is of paramount importance that this ODE not only have a solution, but also that the solution be unique. Of primary concern, uniqueness of the ODE solution is necessary for the identifiability of the statistical model.

If the form of  $\frac{dB}{dt}$  is at least Lipschitz continuous, then the Cauchy-Lipschitz-Picard theo-158 rem provides local existence and uniqueness of B(t). Recall from Eq(33) that  $\frac{dB}{dt}$  is separated 159 into a term for recruitment into the population, R(B), and a term for removals via catch, C. 160 For determining Lipschitz continuity of  $\frac{dB}{dt}$ , the smallest Lipschitz constant of  $\frac{dB}{dt}$  will be the 161 sum of the constants for each of the terms R(B) and C separately. Typically any choice of 162 R(B) will be continuously differentiable, which implies Lipschitz continuity (since the set of 163 continuous differentiable functions is a subset of the set of Lipschitz continuous functions). Thus, the assumed form of R(B) does not typically introduce continuity concerns, unlike 165 some potential assumptions for C. 166

In practice C is determined by a series of observed, assumed known, catches. Catch 167 observations are typically observed on a quarterly basis, but in practice may not be complete 168 for every quarter of the modeled period. It is overwhelmingly common to discretize the 169 ODE via Euler's method with integration step sizes to match the observation frequency of 170 the modeled data. This is often convenient but can present several issues. This strategy 171 often pushes the assumption of catch continuity under the rug, but for identifiability of 172 the statistical model an implicit assumption of continuity of the catches is required. While 173 mechanistically at the finest scale fishers must only catch discrete packets of biomass (i.e. individual fish), it is sensible to consider catches at the quarterly (or yearly) scale as accruing 175 in a continuous way. Furthermore any assumption of continuity will be required to be at 176 least Lipschitz continuous for the required regularity of the model. 177

Here I assume catches accrue linearly between observed catches. This assumption defines
the catch function as a piecewise linear function of time, with the smallest Lipschitz constant
for the catch term defined by the steepest segment of the catch function. This assumption
represents one of the simplest ways of handling catch, while retaining Lipschitz continuity
overall. Furthermore linearly interpolated catch is adequately parsimonious for the typical
handling of catches.

#### 2.3.4 Integration and Stiffness

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As previously mentioned, the overwhelming majority of implementations of population dynamics models discretize the ODE using Euler's method with the integration step sized fixed
so as to match the observation frequency. In this setting we explore model parameterizations
that explore the full extent of biologically relevant reference points. This exercise produces
some combinations of parameters that result in numerically stiff ODEs.

The concept of stiffness in ODEs is hard to precisely characterize (cite). Hairer and Wanner [5, p. 2] describe stiffness in the following pragmatic sense, "Stiff equations are problems for which explicit methods don't work". It is hard to make this definition more mathematically precise, but this is without a doubt a consistent issue for models parameterized so that  $\zeta$  is greater than about  $\frac{1}{2}$ . Euler's method, as often implemented, is particularly poorly suited for these stiff regions of parameter space. In these stiff regions it is necessary to integrate the ODE with an implicate integration method.

Several of the most common implicate methods were tried including the Livermore Solver for ODEs (Isode), and the Variable Coefficient ODE Solver (vode) as implemented in the deSolve package of R (cite). The difference between implicate solvers is negligible, while most explicit methods result in wildly varying solutions to the ODE, and in still regions of parameter space explicate methods completely fail to represent the model as stated in the stiff regions of parameter space. Results shown here are computed using the Isode integration method since it runs relatively quickly and has a relatively smaller footprint in system memory.

#### Schnute/BH Model 2.4

The Schnute production function is a three parameter generalization of many of the most common two parameter production functions (Deriso, 1980; J. Schnute, 1985). It can be written in the following form, with parameters  $\alpha$ ,  $\beta$ , and  $\gamma$ ,

$$P_s(B; [\alpha, \beta, \gamma]) = \alpha B (1 - \beta \gamma B)^{\frac{1}{\gamma}}.$$
 (13)

The BH and Logistic production functions arise when  $\gamma$  is fixed to -1 or 1 re- Figure 4: case as  $\gamma \to 0$ .

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210 under a wide variety of data is of particular respectively. 211

Schnute production models can represent a quantifiably wide varienty of possible productivity 213 behaviours, they present an ideal simulation environment for inquiry of the relability of 214

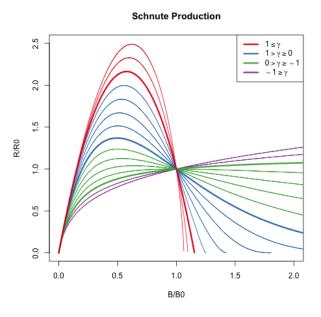
inference under the BH assumption. 215

Under Schnute production, biomass dynamics evolve accourding to the following ODE,

$$\frac{dB}{dt} = P_s(B;\theta) - (M+F)B. \tag{14}$$

This equation largely takes the same form as previously described, except that  $P_s$  is the 216 Schnute production function and natural mortality, M, is modeled explicatly here. Natural 217 mortality models the instantaneous rate of mortality from all causes outside of fishing. Ex-218 plicatly modeling natural mortality in this way is not only a typical assumption of fisheries 219 models, but is also key to the making RPs well defined over the relavant domain of  $\gamma$ . 220

The derivation of RPs under Eq. (14) follows a similar logic as under the PT model.



The Schnute production function spectively, and the Ricker model is a limiting plotted across a variety of parameter values. The special cases of BH, Ricker, and Logistic Inference of BH productivity parameters production are shown in green, blue, and red interest due to the overwhelming popularity of the BH assumption in fisheries models. Since

An expression for equilibrium biomass is attained by setting  $\frac{dB}{dt} = 0$  and rearranging the resulting expression to solve for B

$$\bar{B}(F) = \frac{1}{\gamma \beta} \left( 1 - \left( \frac{M+F}{\alpha} \right)^{\gamma} \right). \tag{15}$$

The above expression quickly yields  $B_0$ ,  $B_{MSY}$  by evaluation at F = 0 and  $F = F_{MSY}$  respectively,

$$B_0 = \frac{1}{\gamma \beta} \left( 1 - \left( \frac{M}{\alpha} \right)^{\gamma} \right) \tag{16}$$

$$\frac{B_{MSY}}{B_0} = \frac{1 - \left(\frac{M + F_{MSY}}{\alpha}\right)^{\gamma}}{1 - \left(\frac{M}{\alpha}\right)^{\gamma}}.$$
 (17)

Attaining an expression for  $F_{MSY}$  requires maximization of equilibrium yeild,  $\bar{Y} = F\bar{B}(F)$ , with respect to F. Analytically maximizing proceeds by differentiating  $\bar{Y}$  to produce

$$\frac{d\bar{Y}}{dF} = \bar{B}(F) + F\frac{d\bar{B}}{dF} \tag{18}$$

$$\frac{d\bar{B}}{dF} = -\frac{1}{\beta} \left( \frac{\left( \frac{M+F}{\alpha} \right)^{\gamma}}{F+M} \right). \tag{19}$$

Setting  $\frac{d\bar{Y}}{dF} = 0$ , filling in the expressions for  $\bar{B}(F)$  and  $\frac{d\bar{B}}{dF}$ , then rearranging to solve for  $F_{MSY}$  is less yielding here than it was in the case of the PT model. This proceedure falls short of providing an analytical solution for  $F_{MSY}$  directly in terms of  $\theta$ , but rather shows that  $F_{MSY}$  must respect the following expression,

$$0 = \frac{1}{\gamma} - \left(\frac{1}{\gamma} + \frac{F_{MSY}}{F_{MSY} + M}\right) \left(\frac{F_{MSY} + M}{\alpha}\right)^{\gamma}.$$
 (20)

The lack of an analytical solution here is understood. J. T. Schnute and Richards (1998, pg. 519) specifically points out that  $F_{MSY}$  cannot be expressed analytically in terms of productivity parameters, but rather gives a partial analytical expression for the inverse relationship. Although parameterized slightly differently, J. T. Schnute and Richards (1998) derives expressions for  $\alpha$  and  $\beta$  as a function of RPs and  $\gamma$ .

Since RPs are left without a closed form expression, computing RPs from productivity

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parameters amounts to numerically solving the system formed by collecting the expressions (20), (16), and (17).

#### 229 **2** .4.1 Simulation

For the purposed of simulation, it is not neccessary to completely know the precise relationships mapping RPs  $\mapsto \theta$  or  $\theta \mapsto$  RPs. Simulation only requires enough knowledge of these mappings to gather a list of  $(\alpha, \beta, \gamma)$  tuples, for data generation under the Schnute model, and the corresponding RPs in some reasonable spacefilling design over RP space.

Similarly to J. T. Schnute and Richards (1998), expressions (20) and (16) are solved for  $\alpha$  and  $\beta$  respectively, to produce the partial mapping  $(F_{MSY}, B_0) \mapsto (\alpha(\cdot, \gamma), \beta(\cdot, \cdot, \gamma))$  in terms of RPs and  $\gamma$ . By further working with Eq. (17), to identify  $\gamma$ , the following system is obtained,

$$\alpha = (M + F_{MSY}) \left( 1 + \frac{\gamma F_{MSY}}{M + F_{MSY}} \right)^{1/\gamma}$$

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

$$\frac{B_{MSY}}{B_0} = \frac{1 - \left( \frac{M + F_{MSY}}{\alpha} \right)^{\gamma}}{1 - \left( \frac{M}{\alpha} \right)^{\gamma}}.$$
(21)

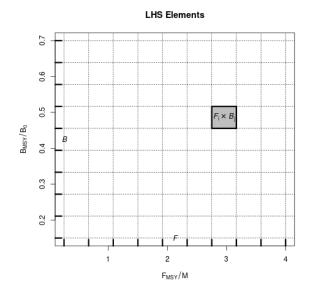
For a population experienceing natural mortality M, by fixing  $F_{MSY}$ ,  $B_0$ , and  $\frac{B_{MSY}}{B_0}$  the 234 above system can fully specify  $\alpha$  and  $\beta$  for a given  $\gamma$ . Notice for a given  $\gamma$  a cascade of 235 closed form solutions for  $\alpha$  and  $\beta$  can be obtained. First  $\alpha(\gamma)$  can be computed, and then 236  $\beta(\alpha(\gamma), \gamma)$  can be computed. If  $\alpha(\gamma)$  is filled back into the expression for  $\frac{B_{MSY}}{B_0}$ , the system 237 collapses into a single onerous expression for  $\frac{B_{MSY}}{B_0}(\alpha(\gamma), \gamma)$ . For bevity, define the function  $\zeta(\gamma) = \frac{B_{MSY}}{B_0} (\alpha(\gamma), \gamma, F_{MSY}, M)$  based on Eq. (17). Inverting  $\zeta(\gamma)$  for  $\gamma$ , and computing the cascade of  $\alpha(\gamma)$ , and then  $\beta(\alpha(\gamma), \gamma)$ , fully defines 240 the Schnute model for a given  $(\frac{F_{MSY}}{M}, \frac{B_{MSY}}{B_0})$ . However inverting  $\zeta$  accuratly is extremely 241 difficult. Inverting  $\zeta$  analytically is not feasible, and typical methods of numerically inverting 242  $\zeta$  are unstable and expensive. Rather than numerically invert precise values of  $\zeta(\gamma)$ ,  $\gamma$  is 243 sampled so that the overall simulation design is space filling.

#### 45 2 .4.2 Latin Hypercube Sampling

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#### • a quick lit review of space filling designs

A Latin hypercube sample (LHS) of size n, in an m dimensional space, samples uniformly 247 among uniform grids of size n in each dimension of the design space. By intersecting the grids of each dimension,  $n^m$  cells are produced, from which a total of n samples are taken. 249 Crutially only one sample is taken from a given element of each grid in each dimension so 250 as to reduce clumping of the n samples across the design space. 251 Letting  $\mathcal{F}$  and  $\mathcal{B}$  be equally spaced grids, of size n, on  $\frac{F_{MSY}}{M} \in (0.25, 4)$  and  $\frac{B_{MSY}}{B_0} \in (0.15, 0.7)$ 252 respectively, a LHS samples 1 point in n of the  $n^2$  cells produced by  $\mathcal{F} \times \mathcal{B}$ . Given the struc-253 tured relationship between the RPs and productivity parameters  $\alpha$ ,  $\beta$ , and  $\gamma$ , obtaining a 254 uniform LHS sample among  $\mathcal{F} \times \mathcal{B}$  requires a tactful navigation of the system of equations 255 seen in Eq. (21). The LHS grid setup and rough sampling strategy can be seen in Figure 256 (5).257



Given  $B_0$ , M, and  $F_{MSY}$ :

- 1) Draw  $\gamma^* \sim \gamma | F_{MSY}, M$ .
- 2) Compute  $\frac{B_{MSY}}{B_0} = \zeta(\gamma^*)$
- 3) Compute  $\alpha^* = \alpha(\gamma^*, F_{MSY}, M)$
- 4) Compute  $\beta^* = \beta(\alpha^*, \gamma^*, M, B_0)$

Figure 5: (left) LHS grids. Intersecting  $\mathcal{F}$  and  $\mathcal{B}$  produces  $n^2$  cells; a particular cell  $\mathcal{F}_i \times \mathcal{B}_j$  is shown in grey. (right) An outline of the sampling proceedure for  $\gamma$  (and associated quantities) given  $B_0$ , M, and  $F_{MSY}$ .

Since it is not practicle to invert  $\zeta(\gamma)$ , a uniform sample in  $\frac{B_{MSY}}{B_0}$  can be obtained by modeling  $\gamma$  as a random variable, with realization  $\gamma^*$ , and thinking of  $\zeta(\gamma)$  as its cumulatice distribution function (CDF). The aim is to model  $\gamma$  as an easily sampled random variable with a CDF that closely approximates  $\zeta$ , so that  $\zeta(\gamma^*) \dot{\sim} U(\zeta_{min}, 1)$  as closely as possible. There may be many good models for the distribution of  $\gamma$ , but in this setting the following distribution is very effective,

$$\gamma \sim \zeta_{min}\delta(\gamma_{min}) + t(\mu, \sigma, \nu)\mathbf{1}_{\gamma > \gamma_{min}}.$$
 (22)

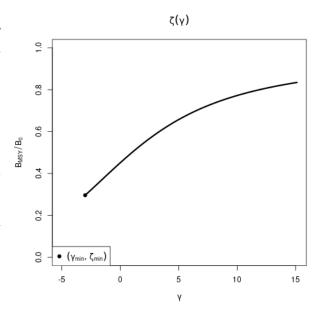


Figure 6:  $\zeta(\gamma)$  Plotted for  $F_{MSY} = 0.1$  and M = 0.2. The point  $(\gamma_{min}, \zeta_{min})$  shows the lowest biologically meaningful value of  $\gamma$ ; below which productivity is negative.

Above, t is the density of the three parameter location-scale family Student's t distribution with location  $\mu$ , scale  $\sigma$ , and degrees of freedom  $\nu$ .  $\mathbf{1}_{\gamma>\gamma_{min}}$  is an indicator function that serves to truncate Student's t distribution at the lower bound  $\gamma_{min}$ .  $\delta(\gamma_{min})$  is the dirac delta function evaluated at  $\gamma_{min}$ , which is scaled by the known value  $\zeta_{min}$ ; this places probability mass  $\zeta_{min}$  at the point  $\gamma_{min}$ . Since sampling from Student's t distribution is readily doable, sampling from a truncated Student's t mixture only requires slight modification.

Let T be the CDF of the modeled distribution of  $\gamma$ . Since the point  $(\gamma_{min}, \zeta_{min})$  is known from the dynamics of the Schnute model at a given RP, full specification of Eq. (22) only requires determining the values for  $\mu$ ,  $\sigma$ , and  $\nu$  which make T best approximate  $\zeta(\gamma)$ . Thus, the values of  $\mu$ ,  $\sigma$ , and  $\nu$  are chosen by minimizing the  $L^2$  distance between  $T(\gamma)$  and  $\zeta(\gamma)$ .

$$[\hat{\mu}, \hat{\sigma}, \hat{\nu}] = \underset{[\mu, \sigma, \nu]}{\arg\min} \int_{\Gamma} \left( T(\gamma; \mu, \sigma, \nu) - \zeta(\gamma) \right)^2 d\gamma \tag{23}$$

```
Fitting the distribution T(\gamma|\hat{\mu}, \hat{\sigma}, \hat{\nu}) for
                                                                         Algorithm 1 LHS of size n on rectangle R.
268
                                                                           1: procedure LHS_n(R)
      use generating \gamma^* values at a specific F_{MSY}
269
                                                                                   Define n-grids \mathcal{F}, \mathcal{B} \in R
                                                                           2:
      and M releases the need to invert \zeta.
270
                                                                                   for each grid element i do
                                                                           3:
     T(\gamma|\hat{\mu},\hat{\sigma},\hat{\nu}), together with the structure in
271
                                                                                         Draw \frac{F_{MSY}}{M} \sim Unif(\mathcal{F}_i)
     Eq. (21), allows for the collection of an
                                                                           4:
                                                                                         Compute [\hat{\mu}, \hat{\sigma}, \hat{\nu}] given F_{MSY} \& M
                                                                           5:
     approximate LHS sample via the algorithm
273
                                                                                         while \mathcal{B}_j not sampled do
                                                                           6:
     seen in Algorithm (1).
274
                                                                                             Draw \gamma^* \sim T(\gamma | \hat{\mu}, \hat{\sigma}, \hat{\nu})
           \frac{F_{MSY}}{M} is drawn uniformly from \mathcal{F}_i. Con-
                                                                           7:
275
                                                                                             Compute \zeta^* = \zeta(\gamma^*)
     ditioning on the sample of F_{MSY}, and M,
                                                                          8:
276
                                                                                              Compute j such that \zeta^* \in \mathcal{B}_i
     T(\gamma|\hat{\mu},\hat{\sigma},\hat{\nu}) is fit and \gamma^* is sampled. \zeta^* is
                                                                          9:
277
                                                                                         end while
     then computed and placed into the appropri-
                                                                         10:
278
                                                                                         Compute \alpha^* = \alpha(\gamma^*, F_{MSY}, M)
     ate grid element \mathcal{B}_{j}. Given \gamma^{*}, the cascade
                                                                         11:
279
                                                                                         Compute \beta^* = \beta(\alpha^*, \gamma^*, M, B_0)
     \alpha(\gamma^*), and \beta(\alpha(\gamma^*), \gamma^*), can be computed.
                                                                         12:
280
                                                                                        Save (\frac{F_{MSY}}{M}, \zeta^*) \Leftrightarrow (\alpha^*, \beta^*, \gamma^*) in \mathcal{F}_i \times \mathcal{B}_j
                                                                         13:
      The algorithm continues until all of the de-
281
                                                                                   end for
     sign elements, \left(\frac{F_{MSY}}{M}, \zeta^*\right) \Leftrightarrow (\alpha^*, \beta^*, \gamma^*),
                                                                         14:
282
                                                                         15: end procedure
     have been computed for all i \in [1, ..., n].
283
```

#### 284 2 .4.3 Design Refinement

Since the behavior of RP inference, under misspecified models, will vary in yet-unkown ways, the exact sampling design density may be hard to know a'priori. Several factors, including the particular level of observation uncertainty, high variance (i.e. hard to resolve) features of the response surface, or simply "gappy" instanciations of the initial LHS design may necessitate adaptive design refinement, to accuratly describe RP biases. Given the tempermental relationship between RPs and productivity parameters in the Schnute model, a recursive refinement algorithm, that makes use of the previously described LHS routine, is developed.

Holes in the existing design are identified based on maximin design principles. That is to say, new design points are collected based on areas of the RP design space which maximizes

the minimum distance between all pairs of points in the current design.

$$d(\boldsymbol{x}, \boldsymbol{x'}) = \sqrt{(\boldsymbol{x} - \boldsymbol{x'})^T \boldsymbol{D}^{-1} (\boldsymbol{x} - \boldsymbol{x'})}$$

$$\boldsymbol{D} = \operatorname{diag} \left[ \left( \max(\mathcal{F}) - \min(\mathcal{F}) \right)^2, \left( \max(\mathcal{B}) - \min(\mathcal{B}) \right)^2 \right]$$
(24)

Above, d is a scaled distance function that defines the distance between points in the differing scales of  $\frac{B_{MSY}}{B_0}$  and  $\frac{F_{MSY}}{M}$ .  $\boldsymbol{D}$  is a diagonal matrix that measures the squared size of the domain in each axis of so as to normalizing distances to a common scale.

If  $X_n$  is the initial design, computed on  $R_{full}$ , let  $x_a$  be the augmenting point which maximizes the minimum distance between all of the existing design points,

$$\boldsymbol{x_a} = \underset{\boldsymbol{x'}}{\operatorname{argmax}} \min\{d(\boldsymbol{x_i}, \boldsymbol{x'}) : i = 1, ..., n\}.$$
 (25)

The point  $x_a$  is used as an anchor for augmenting  $X_n$ . An additional  $LHS_{n'}$  (via Algorithm (1)) is collected, adding n' design points, centered around  $x_a$ , to the overall design. The augmenting region,  $R_{(x_a,d_a)}$ , for collecting  $LHS_{n'}$  is defined based on the square centered at  $x_a$  with side length  $2d_a$ , where  $d_a = \min\{d(x_i, x_a) : i = 1, ..., n\}$ , in the space defined by the metric d.

Due to the tendency of maximin sampling to cluster augmenting points on the edges of the design space,  $R_{(x_a,d_a)}$  is truncated by the outer most limits of  $R_{full}$  so as to focus design augmentation within the specified domain of the simulation. Furthermore, since the design space has a nonlinear constraint, the calculation of  $x_a$  is further truncated based on a convex hull defined by the existing samples in the overall design.

In summary, an initial  $X_n = LHS_n(R_{full})$  design is computed based on an overall simulated region of RPs  $R_{full}$ . The maximin augmenting point,  $x_a$ , is computed at a maximin distance of  $d_a$  from the existing samples. An augmenting design  $X_{n'} = LHS_{n'}(R_{(x_a,d_a)})$  is collected and added to  $X_n$ . Design refinement carries on recursively collecting augmenting designs in this way until the desired maximin distance falls below the desired level.

#### 2.5 Gaussian Process Metamodel

• add metamodeling context

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A GP is a stochastic process generalizing the multivariate normal distribution to an infi-313 nite dimensional analog. GPs are often specified primarily through the choice of a covariance 314 (or correlation) function which defines the relationship between locations in an index set. 315 Typically the index set is spatial for GPs, with points closely related in the index set result-316 ing in correlated effects in the model. In this setting the model is over the space of reference 317 points. A GP model implies an n dimensional multivariate normal distribution on the ob-318 servations of the model with a correlated error structure defined by the modeled covariance 319 function. 320

Each design location of the simulation produces an estimate of two productivity parameters under the restricted production model. Each of the fitted productivity parameter estimates are then modeled using independent instances of the following model in Eq (26).

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Let  $\mathbf{y}$  be a vector collecting the fitted log productivity parameter MLEs under the restricted two parameter production models. Furthermore, let  $\boldsymbol{\omega}$  be a vector of the MLE standard error estimates, on the variance scale (via the inverted Fisher information of the production model log likelihood).  $\boldsymbol{X}$  is the  $n \ge 2$  LHS design matrix of RPs derived above for each respective three parameter data generating model.

$$\mathbf{y} = \beta_0 + \mathbf{X}\boldsymbol{\beta} + \mathbf{v} + \boldsymbol{\epsilon}$$

$$\mathbf{v} \sim N_n(\mathbf{0}, \tau^2 \mathbf{R}_{\ell})$$

$$\boldsymbol{\epsilon} \sim N_n(\mathbf{0}, \boldsymbol{\omega}' \mathbf{I})$$
(26)

 $\epsilon$  models independent normally distributed error, which provides an ideal mechanism for propagating uncertainty from inference in the simulation step into the metamodel. By matching each  $y_i$  with an observed  $\omega_i$  variance term,  $\epsilon$  serves to down weight the influence of each  $y_i$  in proportion to the inferred production model sampling distribution uncertainty. This has the effect of smoothing the GP model in a way similar to the nugget effect (Gramacy & Lee, 2012), although the application here models this effect heterogeniously.

The term, v, contains spatially correlated GP effects. The correlation matrix,  $R_{\ell}$  describes how RPs closer in the simulation design are more correlated. This spatial effect is

modeled with a squared exponential correlation function,

$$R(\boldsymbol{x}, \tilde{\boldsymbol{x}}) = \exp\left(\sum_{i=1}^{2} \frac{-(x_i - \tilde{x}_i)^2}{2\ell_j^2}\right).$$
 (27)

R has an anisotropic separable form which allows for differing length scales,  $\ell_1$  and  $\ell_2$ , in the different RP axes. The flexibility to model correlations separately in the different RP axes is key due to the differences in the extent of the RP domains marginally. The metamodel parameters  $\beta_0$ ,  $\beta$ ,  $\tau^2$ ,  $\ell_1$  and  $\ell_2$  are fit via MLE against the observations  $\mathbf{y}$ ,  $\mathbf{X}$ , and  $\boldsymbol{\omega}$  from simulation fits.

Predictive estimates are obtained via kriging (cite).

$$\hat{y}(\mathbf{x}) = \beta_0 + \mathbf{x}\boldsymbol{\beta} + \mathbf{r}(\mathbf{x})'\boldsymbol{R}_{\ell}^{-1}(\mathbf{y} - (\beta_0 + \boldsymbol{X}\boldsymbol{\beta}))$$
(28)

 $\hat{y}(\mathbf{x})$  is a predicted value of the metamodel at the RP location  $\mathbf{x}$ .  $\mathbf{r}(\mathbf{x})$  is defined as the vector of correlation function evaluations for the predictive location  $\mathbf{x}$  against all observations in  $\mathbf{X}$  (i.e.  $\mathbf{r}(\mathbf{x}) = \mathbf{R}(\mathbf{x}, \mathbf{x}_i) \ \forall \ \mathbf{x}_i \in \mathbf{X}$ ).

Maybe a bit of hinting at uses.

# 340 Results

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While metamodeling occurs on the inferred productivity parameters of the restricted production model, the metamodel can also be used to build metamodeled estimates of major biological RPs. The relavant transformations are given Eqs. (11, 17, 20) with  $\gamma$  fixed to the restricting case.

Applying the metamodel predictive surfaces to the RP estimate allows for the quantification of RP bias induced by model misspecification of two parameter production functions. Below RP bias is quantified by the following relative measure of bias, similar to a percent error calculation.

Relative Bias = 
$$\frac{\hat{RP} - RP}{RP}$$
 (29)

Above RP is a stand in for the true value of any of the biological reference points under

the three parameter data generating production model, and  $\hat{RP}$  refers to the metamodel estimate of each RP quantity under the two parameter restricted cases.

# $_{348}$ 3.1 PT/Schaffer

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region of chaotic fits due to model misspecification

• RP break out plots with mechanism of failure

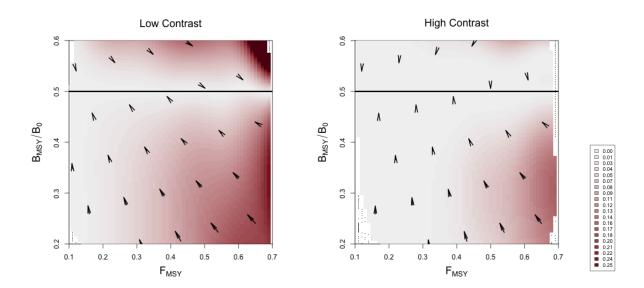


Figure 7: Joint bias direction for  $(F_{MSY}, \frac{B_{MSY}}{B_0})$  estimates under the misspecified Schaefer Model. The intesity of color represents the excess bias relative to the shortest possible mapping.

- Mechanism plot on SRR LHS Grid plot
- some detail views in  $B_{MSY}$ ,  $B_0$ ,  $F_{MSY}$ ,  $?F_{SPR}$ , MSY

Figure (8) shows four of the most misspecified example production function fits as compared to the true data generating PT production functions. In the rug plots below each set of curves the observed biomasses demonstrate the exponential decay from K to  $B^*$  in each case. In particular, notice how only biomasses greater than the PT  $B^*$  are observed.

F<sub>MSY</sub>=0.12 
B<sub>MSY</sub>/B<sub>0</sub>=0.573

□ B<sub>MSY</sub>/B<sub>0</sub>=0.22

F<sub>MSY</sub>=0.096

200

PT Truth

4000

000

Production 600 800

Production

F<sub>MSY</sub>=0.674 
B<sub>MSY</sub>/B<sub>0</sub>=0.599

6000 B

F<sub>MSY</sub>=0.699

PT Truth

Due to the leaning of the true PT curves, 357 and the symmetry of the logistic parabola, 358 the logistic curve only observes information 359 about its slope at the origin from data ob-360 served on the right portion of the PT curves. 361 Above the Schaefer line PT is steeper on the right of  $B^*$  than it is on the left, and so the 363 the logistic curve over-estimates r, and thus 364  $F^*$ , for data generated above the Schaefer 365 line. Below the Schaefer line the vice versa 366 phenomena occurs. Below the Schaefer line 367 PT is shallower to the right of  $B^*$  than it is 368 on the left and so the logistic parabola esti-369 mate tends to under estimate  $F^*$ . 370

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Figure (8) indicates that the individual biases of  $B^*$  and K may behave quite differently.  $B^*$  appears to be estimated fairly accurately while K does not.

Figure (17) also gives some examples of the relative behavior of  $B^*$  and K. In Figure

1377 (16) it is clear that the bias behavior of  $\frac{B^*}{\overline{B}(0)}$  is locked in a fixed pattern under the Schaefer model. Figure (17) indicates that the individual biases of  $B^*$  and K may behave quite differently.  $B^*$  appears to be estimated fairly accurately while K does not.

# Figure 8: A comparison of the true PT production function (in black) and the estimated logistic curve (in red) with 95% CI shown. The examples shown represent the four corners of maximum model misspecification in the simulated RP-space. Observed biomasses are plotof ted in the rug plots below the curves.



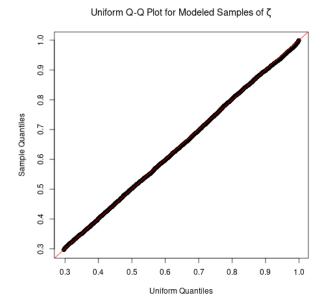


Figure 9: Uniform Q-Q plot for sampled  $\zeta$  against theoretical uniform quantiles.

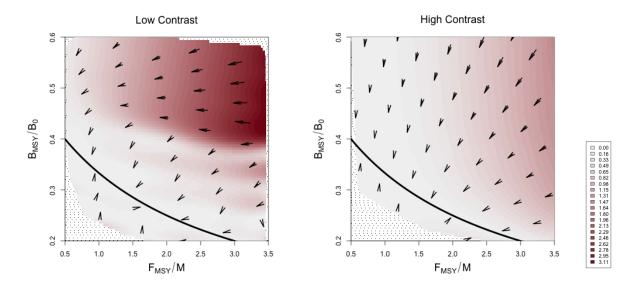


Figure 10: Joint bias direction for  $\left(\frac{F_{MSY}}{M}, \frac{B_{MSY}}{B_0}\right)$  estimates under the misspecified BH Model. The intesity of color represents the excess bias relative to the shortest possible mapping.

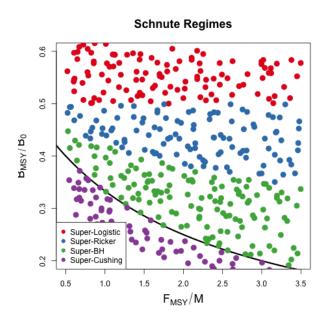


Figure 11: grid plot of production functions.)

# Appendix: Inverting $\frac{B^*}{\bar{B}(0)}$ and $\gamma$ for the PT Model

For bevity let  $\zeta = \frac{B^*}{\bar{B}(0)}$ .

$$\zeta = \left(\frac{1}{\gamma}\right)^{\frac{1}{\gamma - 1}}$$

$$\zeta = \gamma \zeta^{\gamma}$$

$$\zeta = \gamma e^{\gamma \log(\zeta)}$$

$$\zeta \log(\zeta) = \gamma \log(\zeta) e^{\gamma \log(\zeta)}$$

The Lambert product logarithm, W, is defined as the inverse function of  $z = xe^x$  such that x = W(z). Applying this definition allows for the isolation of  $\gamma$ .

$$\gamma \log(\zeta) = W(\zeta \log(\zeta))$$

$$\gamma = \frac{W(\zeta \log(\zeta))}{\log(\zeta)}$$
(30)

The Lambert product logarithm is a mulivalued function with a branch point at  $-\frac{1}{e}$ . The principal branch,  $W_0(z)$ , is defined on  $z \in \left(-\frac{1}{e}, \infty\right)$ , and the lower branch,  $W_{-1}(z)$ , is 383 defined on  $z \in \left(-\frac{1}{e}, 0\right)$ . Taken individually, each respective branch is analytic, but cannot 384 be expressed in terms of elementary functions. 385 When  $\zeta \in (0, \frac{1}{e})$  the solution of interest in Eq. (12) comes from  $W_0$ . When  $\zeta \to \frac{1}{e}$ , the 386 Fox Model emerges as  $\gamma \to 1$ . When  $\zeta \in \left(\frac{1}{e}, 1\right)$  the solution of interest comes from  $W_{-1}$ . For 387 the use case presented here, Eq. (12) is to be interpreted as, 388

$$\gamma = \begin{cases}
\frac{W_0(\zeta \log(\zeta))}{\log(\zeta)} & \zeta \in (0, \frac{1}{e}) \\
\frac{W_{-1}(\zeta \log(\zeta))}{\log(\zeta)} & \zeta \in (\frac{1}{e}, 1)
\end{cases}$$
(31)

Prager 2002, Figure(2). 389

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https://math.stackexchange.com/questions/3004835/is-the-lambert-w-function-analytic-390 if-not-everywhere-then-on-what-set-is-it-ana https://researchportal.bath.ac.uk/en/publications/algebraic-391 properties-of-the-lambert-w-function-from-a-result-of-r 392

https://cs.uwaterloo.ca/research/tr/1993/03/W.pdf

## 5 Introduction

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The most fundamental model in modern fisheries management is the surplus-production 395 model. These models focus on modeling population growth via nonlinear parametric ordi-396 nary differential equations (ODE). Key management quantities called reference points (RP) 397 are commonly derived from the ODE equilibrium equations and depend upon the parameter-398 ization of biomass production. Two-parameter parameterizations of the production function 390 have been shown to limit the theoretical domain of RPs (Mangel et al., 2013). The limited 400 RP-space of two parameter models are a major source of model misspecification for RPs 401 and thus induce bias in RP estimation. The behavior of RP estimation bias is not well 402 understood and as a result often underappreciated. A metamodeling approach is developed 403 here to describe RP biases and explore mechanisms of model failure in the Schaefer model. 404 Data for a typical surplus-production model comes in the form of an index of abundance 405 through time which is assumed to be proportional to the reproducing biomass for the popu-406 lation of interest. The index is often observed alongside a variety of other known quantities, but at a minimum, each observed index will be observed in the presence of some known 408 catch for the period. 409

The observed indices are assumed to have multiplicative log-normal errors, and thus the following observation model arises naturally,

$$I_t = qB_t e^{\epsilon} \quad \epsilon \sim N(0, \sigma^2). \tag{32}$$

Above q is often referred to as the "catchability parameter"; it serves as the proportionality constant mapping between the observed index of abundance and biomass.  $\sigma^2$  models residual variation. Biologically speaking q and  $\sigma^2$  are often treated as nuisance parameters with the "biological parameters" entering the model through a process model on biomass.

Biomass is assumed to evolve as an ODE; in this case I focus on the following form,

$$\frac{dB}{dt} = P(B(t); \boldsymbol{\theta}) - C(t). \tag{33}$$

Here biomass is assumed to change in time by two processes, net production of biomass into

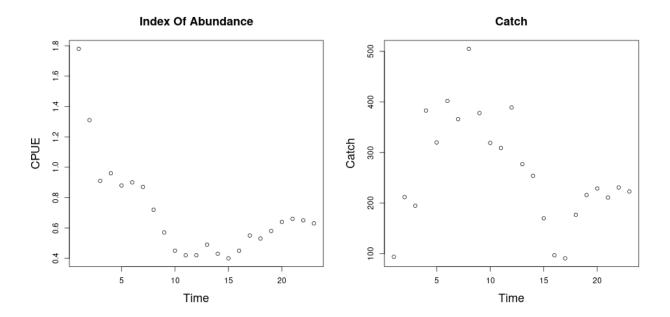


Figure 12: *left*: An observed series of index of abundance data for Namibian Hake from 1965 to 1987 (Hilborn & Mangel, 1997). *right*: The associated catch data for Namibian Hake over the same time period.

the population, and catches removing biomass from the population.

Firstly, the population grows through a production function, P(B). Production in this setting is defined as the net biomass increase due to all reproduction and maturation processes accounting for all naturally occurring sources of mortality other than the recorded fishing from humans. The production function is assumed to be a parametric function that relates the current biomass of the population to an aggregate production of biomass.

Secondly, the population decreases as biomass is removed due to catch, C(t). While catches (aka yields) are observable quantities (Pearson & Erwin, 1997), the model assumes that catch is proportional to biomass with the proportionality constant representing the fishing rate, F(t), so that C(t) = F(t)B(t). From a management perspective a major goal of the model is to accurately infer a quantity known as maximum sustainable yield (MSY). One could maximize simple yield at a particular moment in time (and only for that moment) by fishing all available biomass in that moment. This strategy is penny-wise but pound-foolish (not to mention ecologically devastating) since it doesn't leave biomass in the population to reproduce for future time periods. We seek to fish in a way that allows (or even encourages)

future productivity in the population. This is accomplished by maximizing the equilibrium level of catch over time. Equilibrium yield is considered by replacing the steady state biomass  $(\bar{B})$  in the assumed form for catch, so that  $\bar{C} = F\bar{B}(F)$ , where  $\bar{B}$  indicates a value at steady state. Naturally the steady state biomass is a function of  $\bar{B}$ ; we will see a specific example of this in Section (6.2). MSY is found by optimizing  $\bar{C}(F)$  with respect to  $\bar{B}$ , and  $\bar{B}$  is the fishing rate at MSY. Going forward let \* decorate any value derived under the condition of MSY.

The canonical production model in fisheries is the Schaefer model. The Schaefer model is formed by choosing P to be logistic growth (Mangel, 2006) parameterized by  $\theta = [r, K]$  so that the family of production functions takes the following form,

$$P(B; [r, K]) = rB\left(1 - \frac{B}{K}\right). \tag{34}$$

r is a parameter controlling the maximum reproductive rate of the population in the absence of competition for resources (i.e. the slope of production function at the origin). K is the so called "carrying capacity" of the population. In this context the carrying capacity can be formally stated as steady state biomass in the absence of fishing (i.e.  $\bar{B}(0) = K$ ).

The logistic production function produces idealized parabolic recruitment with equilibrium quantities taking very simple forms that can be easily understood from the graphical construction seen in Figure (13). Positive recruitment is observed when  $B \in (0, K)$ . Due to the parabolic shape of the logistic production function it is straightforward to see that yield is maximized by fishing the stock down to  $B^*$ , where the stock attains its peak productivity. By symmetry it is clear that this peak occurs at  $B^* = \frac{K}{2}$ . The fishing rate required to hold the stock at MSY is  $F^* = \frac{r}{2}$ , which is half of the stock's maximum reproductive rate. MSY is then the product of  $F^*$  and  $B^*$  so that  $MSY = \frac{rK}{4}$ .

Fisheries are very often managed based upon reference points which serve as simplified heuristic measures of population behavior. The mathematical form of RPs depends upon the model assumptions through the production function. While a number of different RPs exist which describe the population in different (but related) ways, the most common RPs revolve around the concept of MSY (or robust ways of measuring MSY (Hilborn, 2010; Punt

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#### **Logistic SRR and Related Quantities**

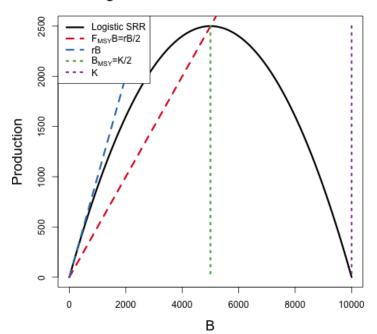


Figure 13:

The logistic production function in black plotted next to depictions of the key biological parameters and reference points. The slope at the origin (and thus r) is shown in blue, catch resulting in MSY in red, biomass at MSY in green, and K in purple at the right x-intercept. MSY is seen at the peak of the parabola, and is attained with a fishing rate of  $\frac{r}{2}$  and biomass equilibrating to  $\frac{K}{2}$ .

et al., 2016)). Here the focus is primarily on the RPs  $F^*$  and  $\frac{B^*}{\overline{B}(0)}$  for their pervasive use in modern fisheries (Mangel et al., 2013; Punt & Cope, 2019).

 $F^*$  is the afore mentioned fishing rate which results in MSY.  $\frac{B^*}{\overline{B}(0)}$  is the depletion of the stock at MSY. That is to say  $\frac{B^*}{\overline{B}(0)}$  describes the fraction of the unfished population biomass that will remain in the equilibrium at MSY. In general  $F^* \in \mathbb{R}^+$  and  $\frac{B^*}{\overline{B}(0)} \in (0,1)$ , however under the under the assumption of logistic production these quantities take the following form,

$$F^* = \frac{r}{2} \qquad \frac{B^*}{\bar{B}(0)} = \frac{1}{2} \tag{35}$$

so that  $\left(F^*, \frac{B^*}{\overline{B}(0)}\right) \in \left(\mathbb{R}^+, \frac{1}{2}\right)$ .

In current practice, production functions are typically chosen to depend only on two parameters. The Schaefer model as presented depends only on the biological parameters r and K, but other common two parameter choices of the production function are the Beverton-Holt (Beverton & Holt, 1957, BH) and Ricker (Ricker, 1954) curves. All of these two parameter production functions struggle similarly to model the full theoretical space of

 $_{3}$  RPs (Mangel et al., 2013).

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The basis of the Schaefer model is ripe with debate (Kingsland, 1982), and the debate continues within modern fisheries modeling (Prager, 2002). On the one hand, Maunder (2003) argues that the Schaefer model is insufficient in large part due to the restriction it places on  $\frac{B^*}{B(0)}$ , at  $\frac{1}{2}$ , and further argues that the three parameter Pella-Tomlinson (PT) model (Pella & Tomlinson, 1969) should replace the Schaefer model to avoid biased parameter estimates. On the other hand, while Prager (2003) appreciates the limitations of the Schaefer model, he argues its usefulness as a well understood and simple model that has the ability to reasonably approximate dynamics in many data poor stocks.

The bias-variance trade-off (Ramasubramanian & Singh, 2017) makes it clear that the 472 addition of a third parameter in the production function will necessarily reduce estimation 473 bias. However the utility of this bias reduction is still under debate because the particular 474 mechanisms and behavior (direction and magnitude) of these biases for key management 475 quantities are not fully understood or described. Lee et al. (2012) provides some evidence 476 that estimation of productivity parameters, and thus RPs via (Mangel et al., 2013), are 477 dependent on biomass contrast as well as model specification. Conn et al. (2010) comes 478 to similar conclusions via calibration modeling techniques. Despite this understanding of 479 productivity estimation, the implications have not been extended to a joint description of 480 biases on the scale of management RPs. 481

Together the general behavior of the PT model and the simplicity of the Schaefer model make the PT/Schaefer pair an ideal setting for beginning to understand the consequences of model misspecification on the production function. In this study I consider the behavior of inference when data are simulated from the three parameter PT production model but fit with the two parameter Schaefer model.

The work begins with a derivation of RPs under the three parameter PT model. The parametric forms of RPs under the PT model are then inverted to develop a simulation setting for analyzing inference under the two parameter Schaefer model. Finally a Gaussian Process (GP) metamodel (Gramacy, 2020) is constructed for exploration and analysis of RP biases.

A key insight of this approach is that bias is considered broadly across RP-space to

uncover patterns and correlations between RPs. The GP metamodel is explicit about tradeoffs between RPs so as to inform the full utility of reducing bias, as well as to suggest mechanisms for understanding what causes bias. Further, the effect of contrast on estimation is considered together with model misspecification.

## 497 6 Methods

#### $_{ ext{\tiny 498}}$ 6 .1 $\,$ PT $\,$ Model

The three parameter PT family has a convenient form that includes, among others (Fox Jr., 1970; Rankin & Lemos, 2015), the logistic production function as a special case to form the Schaefer model. The Pella-Tomlinson production function is parameterized so that  $\theta = [r, K, \gamma]$  and the family takes the following form,

$$P(B; [r, K, \gamma]) = \frac{rB}{\gamma - 1} \left( 1 - \frac{B}{K} \right)^{\gamma - 1}.$$
 (36)

 $\gamma$  is a parameter which breaks PT out of the restrictive symmetry of the logistic curve. In the special case of  $\gamma=2$  Eq (36) collapses back to the logistic curve, however in general  $\gamma \in (1,\infty)$ . The parameters r and K maintain the same interpretation as they do in the logistic production function. In Figure (14) PT recruitment is shown for a range of parameter values so as to demonstrate the various recruitment shapes that can be achieved by PT recruitment.

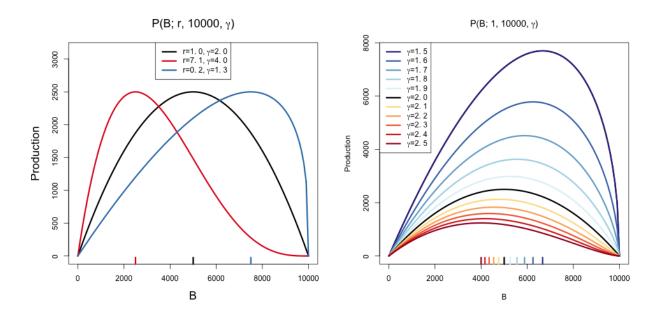


Figure 14: (left) PT production functions with parameters chosen so that MSY is consistent, but  $\frac{B^*}{\overline{B}(0)}$  is less than  $\frac{1}{2}$  (in red), greater than  $\frac{1}{2}$  (in blue), or equal to  $\frac{1}{2}$  (in black; logistic production function). (right) PT production functions over a range of  $\gamma$  values with the values of r and K fixed at 1 and 10,000 respectively.

While the particular form of how  $\gamma$  appears in PT still produces some limitations to the form of the production function, importantly the introduction of a third parameter allows enough flexibility to fully describe the space of reference points used in management. To see this, the reference points are analytically derived for the PT model below.

#### 6.2 PT Reference Points

With B(t) representing biomass at time t, under PT production, the dynamics of biomass are defined by the following ODE,

$$\frac{dB}{dt} = \frac{rB}{\gamma - 1} \left( 1 - \frac{B}{K} \right)^{\gamma - 1} - FB. \tag{37}$$

An expression for the equilibrium biomass is attained by setting Eq (37) equal to zero, and rearranging the resulting equation to solve for B. Thinking of the result as a function of F gives,

$$\bar{B}(F) = K \left( 1 - \left( \frac{F(\gamma - 1)}{r} \right)^{\frac{1}{(\gamma - 1)}} \right). \tag{38}$$

At this point it is convenient to notice that  $\bar{B}(0) = K$ . The expression for  $B^*$  is given by evaluating Eq (38) at  $F^*$ .

To get an expression for  $F^*$ , the equilibrium yield is maximized with respect to F,

$$F^* = \operatorname*{argmax}_F F\bar{B}(F). \tag{39}$$

In the case of PT production this maximization can be done analytically (however many three parameter production functions do not result in tractable analytical solutions). In this case maximization can proceed by differentiating the equilibrium yield with respect to F as follows,

$$\frac{d\bar{Y}}{dF} = \bar{B}(F) + F\frac{d\bar{B}}{dF} \tag{40}$$

$$\frac{d\bar{B}}{dF} = -\frac{K}{F(\gamma - 1)} \left(\frac{F(\gamma - 1)}{r}\right)^{\frac{1}{\gamma - 1}}.$$
(41)

Setting Eq (40) equal to 0, substituting  $\bar{B}(F)$  and  $\frac{d\bar{B}}{dF}$  by Equations (38) and (41) respectively, and then solving for F produces the following expression for the fishing rate required to produce MSY,

$$F^* = \frac{r}{\gamma - 1} \left(\frac{\gamma - 1}{\gamma}\right)^{\gamma - 1}.\tag{42}$$

Plugging the above expression for  $F^*$  back into Eq (38) gives the following expression for biomass at MSY,

$$B^* = \frac{K}{\gamma}. (43)$$

The above derived expressions for  $\bar{B}(0)$ ,  $B^*$ , and  $F^*$  can then be used to build a specific analytical form for the biological reference points in terms of only biological model parameters.

$$F^* = \frac{r}{(\gamma - 1)} \left(\frac{\gamma - 1}{\gamma}\right)^{\gamma - 1} \qquad \frac{B^*}{\bar{B}(0)} = \frac{1}{\gamma} \tag{44}$$

# 6.3 Simulation Study

Indices of abundance are simulated from the three parameter PT production model over a grid of  $F^*$  and  $\frac{B^*}{B(0)}$  values. These PT data are then fit with a two parameter Schaefer model.

Generating simulated indices of abundance from the PT model requires inverting the relationship between  $\left(F^*, \frac{B^*}{B(0)}\right)$ , and  $(r, \gamma)$ . It is not generally possible to analytically invert this relationship for many three parameter production functions (Punt & Cope, 2019;

J. T. Schnute & Richards, 1998). Most three parameter production functions lead to RPs that require expensive numerical methods to invert; more over the numerical inversion pro-

cedure can often be unstable. That said, for the case of PT this relationship is analytically invertible, and leads to the following relationship

$$r = F^* \left( \frac{1 - \frac{B^*}{\bar{B}(0)}}{\frac{B^*}{\bar{B}(0)}} \right) \left( 1 - \frac{B^*}{\bar{B}(0)} \right)^{\left( \frac{B^*}{\bar{B}(0)} - 1 \right)} \qquad \gamma = \frac{1}{\frac{B^*}{\bar{B}(0)}}. \tag{45}$$

Indices are generated under the following conditions. Data are simulated at each point 529 on the grid  $\mathcal{F} \times \mathcal{B}$ , with  $F^* \in \mathcal{F}$  and  $\frac{B^*}{\overline{B}(0)} \in \mathcal{B}$ , where  $\mathcal{F} = \{0.1, 0.2, ..., 0.7\}$  and  $\mathcal{B} = \{0.1, 0.2, ..., 0.7\}$ 530  $\{0.2, 0.3, ..., 0.6\}$  as seen in Figure (15). These ranges of values for  $F^*$  and  $\frac{B^*}{\bar{B}(0)}$  are selected to 531 include a wide range of values thought to reflect many commonly assessed fisheries. The red 532 X's in Figure (15) show four simulation locations where the Schaefer model is misspecified to 533 a large degree and will be considered in more detail in Section(7.1). For each  $\left(F^*, \frac{B^*}{\overline{B}(0)}\right)$ , the 534 associated pair  $(r, \gamma)$  are computed from Eq (45). Since K does not enter the RP calculation 535 its value is fixed arbitrarily at 10000. The value of q is fixed at a typically small value of 536 0.0005.  $\sigma$  is fixed at the relatively small value of 0.01 to focus specifically on the behavior of population parameters. These parameters fully specify the PT model for the purposes of 538 generating index data for each  $\left(F^*, \frac{B^*}{\bar{B}(0)}\right)$  pair. 539

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Fmsy

Figure 15: circles Open show the location of the simulation grid  $\mathcal{F} \times \mathcal{B}$ . The horizontal line shows the constrained space of RPs for the Schaefer model. The red X's indicated 4 simulation locations where modelSchaefer particularly misspecified.

#### 542 6 .4 Catch

It is known that the behavior of catch can effect inference on the biological parameters (Hilborn & Walters, 1992). In particular it is thought that catch can induce "contrast" in 544 index data so as to better inform r. In this setting contrast refers to changes in the long term 545 trends of index data. Figure (19, right) demonstrates an example of biomass that includes 546 contrast induced by catch. It is not well understood how contrast may factor into biases 547 induced by model misspecification. To investigate this a variety of catches are investigated. 548 Catch is parameterized so that F(t) can be controlled with respect to  $F^*$ . Recall that 549 catch is assumed to be proportional to biomass with the proportionality constant amounting 550 to the fishing rate, so that C(t) = F(t)B(t). To control F(t) with respect to  $F^*$ , C(t) is 551 specified by defining the quantity  $\frac{F(t)}{F^*}$  as the relative fishing rate. B(t) is defined by the 552 solution of the ODE, and  $F^*$  is defined by the biological parameters of the model, see Eq. 553 (42). Thus by defining  $\frac{F(t)}{F^*}$ , catch can then be written as  $C(t) = F^*\left(\frac{F(t)}{F^*}\right)B(t)$ . 554 Intuitively  $\frac{F(t)}{F^*}$  describes the fraction of  $F^*$  that F(t) is specified to for the current 555 B(t). When  $\frac{F(t)}{F^*} = 1$ , F(t) will be held at  $F^*$ , and the solution of the ODE brings B(t)556 into equilibrium at  $B^*$ . For constant  $\frac{F(t)}{F^*}$  the Schaefer model comes to equilibrium as an 557 exponential decay from K approaching  $B^*$ . The relative fishing rate is defined on  $[0,\infty)$ ; 558 when  $\frac{F(t)}{F^*} < 1$ , F(t) is lower than  $F^*$  and B(t) is pushed toward  $\bar{B} > B^*$ . Contrarily, when 559  $\frac{F(t)}{F^*} > 1$ , F(t) is higher than  $F^*$  and B(t) is pushed toward  $\bar{B} < B^*$ ; the precise values of  $\bar{B}$ 560 can be calculated from Eq (38). 561 In practice, catch is determined by a series of observed, assumed known, catches. Catch observations are typically observed on a quarterly (or yearly) basis, so that the ODE may be 563 discretized via Euler's method with integration step sizes to match the observation frequency 564 of the modeled data. In this case, catch is sampled as would be done in practice however, 565 the simulation can encounter a variate of issues working with the naively discretized ODE. 566 As a result the ODE is integrated implicitly via the Livermore Solver (Radhakrishnan, 1993, lsode), and catch is linearly interpolated between sampled epochs.

## 6.5 Model Fitting

The goal of model fitting is to assess how the biological parameters of the two parameter Schaefer model behave under MLE inference when fit to PT data. Thus, let  $I_t$  be an observation of PT index data at time  $t \in \{1, 2, 3, ..., T\}$ . The observation model is log-normal such that,

$$I_t|q,\sigma^2, \boldsymbol{\theta} \sim LN(qB_t(\boldsymbol{\theta}),\sigma^2).$$
 (46)

For the Schaefer model  $\boldsymbol{\theta} = [r, K]$ , and  $B_t(\boldsymbol{\theta})$  is defined by the solution of the following ODE

$$\frac{dB}{dt} = rB\left(1 - \frac{B}{K}\right) - FB. \tag{47}$$

The  $I_t$  are assumed independent conditional on q,  $\sigma^2$ , r, K and the ODE model for biomass. Thus the log likelihood can be written as

In this setting, q is fixed at the true value of 0.0005 to focus on the inferential effects

$$\log \mathcal{L}(q, \sigma^2, \boldsymbol{\theta}; I) = -\frac{T}{2} \log(\sigma^2) - \frac{1}{2\sigma^2} \sum_{t} \log\left(\frac{I_t}{qB_t(\boldsymbol{\theta})}\right)^2.$$
 (48)

of model misspecification on biological parameters.  $\sigma^2$ , r, and K are reparameterized into 571 the log scale as  $log(\sigma^2)$ , log(r), and log(K) and fit via MLE.  $\sigma^2$  is allowed to be fit to 572 assess overall model fit. Reparameterization of the parameters into the log scale improves 573 the reliability of optimization in addition to facilitating the use of Hessian information for 574 parameter estimate standard errors. 575 Given that the biological parameters enter the likelihood via a nonlinear ODE, and further 576 the parameters themselves are related to each other nonlinearly, the likelihood function can 577 often be difficult to optimize. A hybrid optimization scheme is used to maximize the log 578 likelihood to ensure that a global MLE solution is found. The R package GA (Scrucca, 2013, 2017) is used to run a genetic algorithm to explore parameter space globally. Optimization occasionally jumps into the L-BFGS-B local optimizer to refine optima within a local mode. 581

The scheme functions by searching globally to iteratively improve hot starts for the local optimizer.

In Appendix A a profile likelihood method for estimating all of the parameters of the 584 model is derived. The profile likelihood technique greatly improves the reliability of local 585 optimizers when fitting the biological parameters alongside additional nuisance parameters. The catchability parameter q has the effect of rescaling biomass which can often function 587 similarly to the role of the carrying capacity parameter K. Thus, the structure of the 588 likelihood may confound q and K, and for some data these parameters may only be weakly 589 identifiable. Posing the model in a Bayesian context provides a convenient mechanism for 590 managing these weak identifiability issues. In a tactful Bayesian formulation q and  $\sigma^2$  may then be marginalized out of the joint posterior to yield fast and reliable inference (Walters 592 & Ludwig, 1994). 593

## <sup>594</sup> 6.6 Gaussian Process Metamodel

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For assessing biological parameters over the simulated grid, as seen in Figure (15), a GP model is used as a flexible, stochastic interpolator over RP space. As previously established, in Section (6.5), the biological parameters of interest are the Schaefer model's log(r) and log(K) parameters. Since the estimates of these parameters are random variables, with variances given by the inverse of the observed fisher information, interpolation of MLEs requires paying additional attention to propagating estimates of uncertainty into the metamodel.

A GP is a stochastic process generalizing the normal distribution to an infinite dimensional analog. GPs are often specified primarily through the choice of a covariance function which defines the relationship between locations in an index set. Typically the index set is spatial for GPs, and in this setting the model is across the reference point space,  $\left(F^*, \frac{B^*}{B(0)}\right)$ , of the three parameter PT data generating model. A GP model implies an n dimensional multivariate normal distribution on the observations of the model and the covariance function fills out the covariance matrix for the observations.

Modeling the estimates of log(r) and log(K) with independent GP models is used to extend analysis of all major biological RP over the simulated grid. Let  $\hat{\mu}$  be the maximum likelihood estimate (MLE) of either log(r) or log(K). Additionally let  $\hat{\omega}$  be the inverted Hessian information of the log likelihood evaluated at  $\hat{\mu}$ .

Each grid location of the simulation produces a single fitted  $\hat{\mu}_i$  at an associate  $\left(F^*, \frac{B^*}{B(0)}\right)$  location with  $i \in \{1, ..., n\}$ .  $\hat{\boldsymbol{\mu}}$  is jointly modeled over the space of reference points as the following GP,

$$\mathbf{x} = \left(F^*, \frac{B^*}{\overline{B}(0)}\right)$$

$$\hat{\mu} = \beta_0 + \beta' \mathbf{x} + f(\mathbf{x}) + \epsilon$$

$$f(\mathbf{x}) \sim \text{GP}(0, \tau^2 R(\mathbf{x}, \mathbf{x'}))$$

$$\epsilon_i \sim \text{N}(0, \hat{\omega}_i). \tag{49}$$

The GP residual variation provides an ideal mechanism for propagating uncertainty from inference in the simulation step into the metamodel.  $\hat{\omega}_i$  is the observed residual variation for the inferred value,  $\hat{\mu}_i$ . This mechanism down weights the influence of each  $\hat{\mu}_i$  in proportion to the inferred sampling distribution uncertainty. This has the effect of smoothing the GP model in a way similar to the nugget effect (Gramacy & Lee, 2012).

Here R is the squared exponential correlation function.

$$R(\boldsymbol{x}, \boldsymbol{x'}) = \exp\left(\sum_{j=1}^{2} \frac{-(x_j - x_j')^2}{2\ell_j^2}\right)$$
(50)

R has an anisotropic separable form to allow for differing length scales in the  $F^*$  and  $\frac{B^*}{B(0)}$  axes. The flexibility to model correlations separately in the different RP axes is key due to the differences in the extent of the RP domains marginally.  $\ell_1$  and  $\ell_2$  model the length scales for  $F^*$  and  $\frac{B^*}{B(0)}$  respectively. The metamodel parameters  $\beta_0$ ,  $\beta$ ,  $\tau^2$ ,  $\ell_1$  and  $\ell_2$  are fit via MLE against the observations of  $\hat{\mu}$  and  $\hat{\omega}$  from simulation fits.

Predictive estimates of modeled quantities are obtained via kriging over intermediate values over RP space. Let \*decorate any quantity that is derived for metamodel interpolation.

$$\check{\mu}(\check{s}) = \beta_0 + \boldsymbol{x}(\check{s})\boldsymbol{\beta} + R_{\ell}(\check{s}, s)R_{\ell}^{-1}(s, s) \Big(\hat{\mu}(s) - (\beta_0 + \boldsymbol{x}(s)\boldsymbol{\beta})\Big)$$
(51)

## 7 Results

- chaotic regions
- best hits from Schaffer
- Schnute
- arrow plot
- RP specific plots

While interpolation occurs in the space of either  $\log(r)$  or  $\log(K)$ , these interpolated values are used to build interpolated estimates of major biological reference points. Using the interpolated values  $\log(r)$  and  $\log(K)$  the following transformation are applied to interpolate RP quantities under the Schaefer model,

$$\check{B}^* = \frac{\check{K}}{2} \qquad \check{F}^* = \frac{\check{r}}{2}. \tag{52}$$

Using these interpolated RP quantities, the bias induced by model misspecification is quantified by the following relative measure of bias, similar to a percent error calculation.

Relative Bias = 
$$\frac{\mathring{RP} - RP}{RP}$$
 (53)

Above RP is a stand in for the true value of any of the biological reference points under PT data generation, and  $\check{RP}$  refers to the interpolated estimated RP quantity under the Schaefer model.

# <sup>633</sup> 7 .1 An MSY-Optimal Catch History

When F(t) is held constant at  $F^*$ , B(t) comes to equilibrium as an exponential decay from K to  $B^*$ . Understanding model misspecification bias is simplified in this setting due to the relative simplicity of B(t). However this simplicity is known to poorly inform estimates of r, and thus  $F^*$ , due to the limited range of the production function that is observed (Hilborn & Walters, 1992). This example is a "low contrast" setting.

Figure (16) shows the biases in  $F^*$  and  $\frac{B^*}{B(0)}$  over the space of simulated RPs. The (top-639 right) panel of Figure (16) shows how data generated across a broad space of RPs are mapped 640 onto the limited space of the Schaefer line. Below the Schaefer line, RP estimates are biased 641 by over-estimating  $\frac{B^*}{B(0)}$  and under-estimating  $F^*$ . Above the Schaefer line the vice-versa is 642 true;  $\frac{B^*}{B(0)}$  is under-estimated and  $F^*$  is over-estimated. In the (left) and (bottom) panels of Figure (16) the bias in  $\frac{B^*}{\bar{B}(0)}$  and  $F^*$  are shown component-wise; each panel showing the 644 same patterns, but focusing on only one component of the bias at a time. In these panels red 645 coloring indicates over-estimation of the RP and blue indicates under-estimation. Notice that 646 the region of RPs near the Schaefer line enjoy relatively low bias since model misspecification 647 is minor in this region. 648

Notice that under the Schaefer model  $B^*$  is necessarily half of K. Since  $\frac{B^*}{\overline{B}(0)}$  is always under the Schaefer model, the bias in  $\frac{B^*}{\overline{B}(0)}$  (as seen in Figure (16)) simply measures the distance from the data generating location vertically to the Schaefer line.

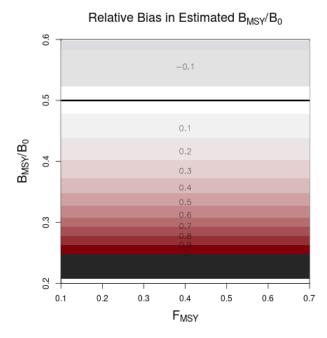
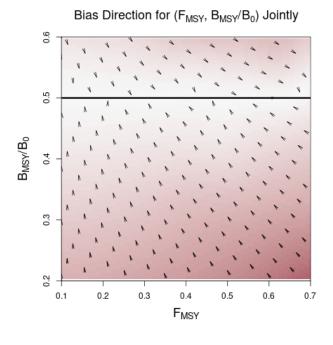
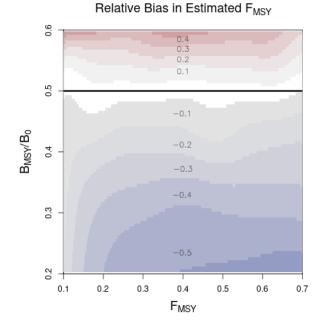


Figure 16: Heatplots showing the bias in RP estimation induced by model misspecification. In all cases the restricted RP-space of the Schaefer model is shown as a horizontal black line at  $\frac{B^*}{B(0)} = 0.5$ . (left) Relative bias in  $\frac{B^*}{B(0)}$ . (top-right) Bias in RP-space shown directionally. Arrows point from the location where data is generated, toward the location in on the Schaefer line where MLE projects. The intensity of color shows the absolute error as a distance in RP-space. (bottom) Relative bias in  $F^*$ .





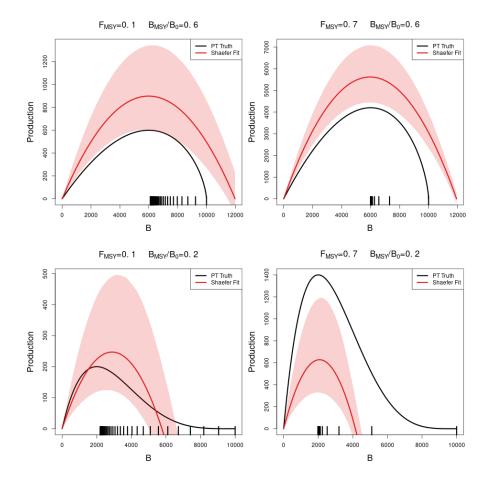


Figure 17: A comparison of the true PT production function (in black) and the estimated logistic curve (in red) with 95% CI shown. The examples shown represent the four corners of maximum model misspecification in the simulated RP-space. Observed biomasses are plotted in the rug plots below the curves.

Figure (17) shows four of the most misspecified example production function fits as compared to the true data generating PT production functions. In the rug plots below each set of curves the observed biomasses demonstrate the exponential decay from K to  $B^*$  in each case. In particular, notice how only biomasses greater than the PT  $B^*$  are observed. Due to the leaning of the true PT curves, and the symmetry of the logistic parabola, the logistic curve only observes information about its slope at the origin from data observed on the right portion of the PT curves. Above the Schaefer line PT is steeper on the right of  $B^*$  than it is on the left, and so the the logistic curve over-estimates r, and thus  $F^*$ , for data generated above the Schaefer line. Below the Schaefer line the vice versa phenomena occurs. Below the Schaefer line PT is shallower to the right of  $B^*$  than it is on the left and so the logistic parabola estimate tends to under estimate  $F^*$ .

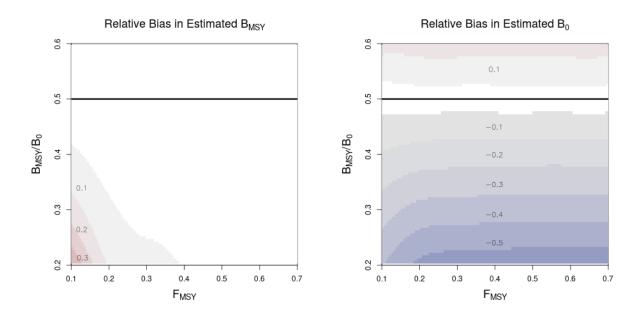


Figure 18: MLE Bias surfaces for  $B^*$  (left) and K (right) individually.

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Figure (17) also gives some examples of the relative behavior of  $B^*$  and K. In Figure (16)

it is clear that the bias behavior of  $\frac{B^*}{B(0)}$  is locked in a fixed pattern under the Schaefer model. 664 Figure (17) indicates that the individual biases of  $B^*$  and K may behave quite differently. 665  $B^*$  appears to be estimated fairly accurately while K does not. Figure (18) teases apart  $\frac{B^*}{\overline{B}(0)}$  into individual bias surfaces for  $B^*$  and K respectively. 667 Interestingly  $B^*$  enjoys a large region of RP-space with relatively low bias. Given that  $B^*$ 668 has relatively consistently low bias, K maintains the expected inverse relationship with  $\frac{B^*}{B(0)}$ 669 bias. Since the parabolic structure of the logistic function ties the ratio of  $B^*$  and  $\bar{B}(0)$  to 670  $\frac{1}{2}$ , their is only one degree of freedom shared between  $B^*$  and  $\bar{B}(0)$  so that their ratio is maintained at  $\frac{1}{2}$ . In this setting it appears that  $B^*$  estimation is largely conserved at the 672 cost of K.

## 7.2 More Informative Catch Histories

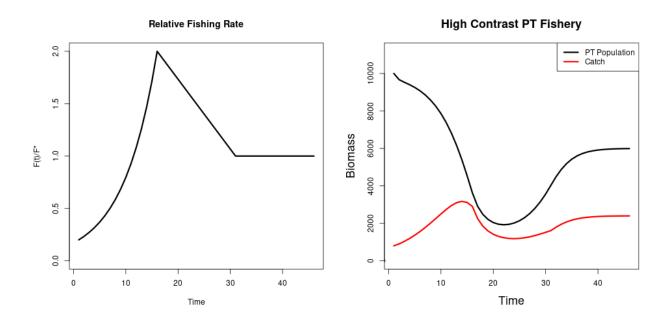
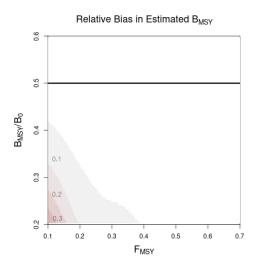


Figure 19: (left) Relative fishing specified so as to induce contrast. (right) Population biomass and catch demonstrating contrast in a PT population with  $F^* = 0.4$  and  $\frac{B^*}{B(0)} = 0.6$ .

The setting of constant relative fishing rate is a useful simplification for building understanding of the dynamics that induce bias, but in practice constant fishing rate is a somewhat oversimplified setting. Consider a hypothetical stock where fishing rate accelerates as technology and fishing techniques improve rapidly until management practices are applied. Figure (19) demonstrates this more realistic, while still idyllic, fishing behavior. This population is exposed to a variety of fishing rates, which induce contrast in the generated indices and allows the fitting model to observe a decrease in the population followed by a rebuild of the stock. This represents a "high contrast" setting that is widely thought to better inform growth rate parameters, such as r.

Figure (20) shows the relative bias surfaces for  $B^*$  and  $F^*$  under 45 epochs of data in the high contrast setting. On the one hand, notice the relative lack of bias in  $F^*$  over a large swath of RPs far from the Schaefer line. On the other hand, notice that bias in  $B^*$  increases here relative to the low contrast setting. The pattern of bias in  $B^*$  maintains a similar pattern, and overall scale, as the low contrast setting seen in Figure (18), however



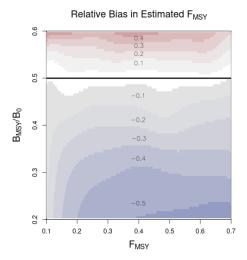
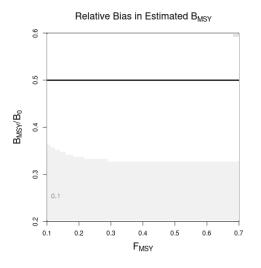


Figure 20: MLE Bias surfaces for  $B^*$  (left) and  $F^*$  (right) with relative fishing rate as specified in Figure (19)

a smaller region of RP-space enjoys low bias here. Due to the expanded pattern of  $B^*$  bias here, as compared with the low contrast setting, and the constrained relationship with  $\frac{B^*}{\overline{B}(0)}$ , the bias surface for K maintains the same general inverse relationship with  $\frac{B^*}{\overline{B}(0)}$ .

If the data are augmented so that the fishing rate is held at  $F^*$  for an additional 45 time epochs (90 epochs total), so that slower growing stocks may observe more data near  $B^*$ , Figure (21) shows the updated bias surfaces. The scale of bias in  $B^*$  is reduced, but the general patterns of bias remains similar for both RPs. While the bias behavior of  $B^*$  estimates are diminished,  $F^*$  biases are generally magnified.



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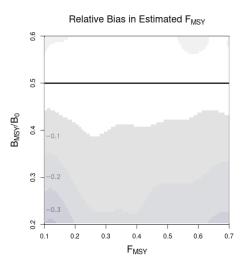


Figure 21: MLE Bias surfaces for  $B^*$  (*left*) and  $F^*$  (*right*) with relative fishing rate augmented with additional observations near equilibrium.

## 8 Discussion

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Results presented here generally agree with what is known about estimating growth rate parameters (Lee et al., 2012; Conn et al., 2010; Magnusson & Hilborn, 2007), in this case r, and thus  $F^*$ . In the presence of contrast  $F^*$  estimation can enjoy very low bias even for a wide range of poorly specified models; conversely in the absence of contrast  $F^*$  estimation can suffer very large bias even for slightly misspecified models. In all cases when model misspecification is removed, even with weakly informative data,  $F^*$  estimation is unbiased. Model misspecification is thus a necessary but not sufficient condition for inducing bias.

While it is established that growth rate parameters require contrast to estimate, the 705 implications of these biases jointly across a variety of RPs have not received as much at-706 tention. When considering  $B^*$  alongside  $F^*$  in varying contrast environments, it becomes 707 clear that different data informs different parts of the production function differently. In 708 low contrast environments  $B^*$  is estimation is remarkably unbiased across all but the most 709 challenging instances of model misspecification. However in the presence of contrast, while  $F^*$  enjoys better estimation,  $B^*$  estimation experiences substantial bias for only modestly 711 misspecified models. Further, by augmenting contrasting data with an additional period of 712 low contrast data this pattern begins to reverse with  $B^*$  bias receding toward more poorly 713 specified models and  $F^*$  bias encroaching toward only modestly misspecified models as seen 714 in Figure (21).

The behavior of bias in estimating  $B^*$  and  $F^*$  suggests that the limited parameter space 716 of the Schaefer model induces a trade off in estimating these parameters. In practice, when 717 the true model is not known and the Schaefer model is unlikely to be correctly specified, 718 one should at best expect to only estimate either  $B^*$  or  $F^*$  correctly depending on the 719 particular degree of model misspecification. The observed contrast then serves to distribute 720 the available information among  $B^*$  and  $F^*$ . Increasing the flexibility of the production 721 function by moving toward curves with additional parameters could release these structural 722 limitations (Mangel et al., 2013). Punt and Cope (2019) considers a suite of possible three 723 parameter curves which could be used instead of current two parameter curves. 724

This study only explores the compatibility of the possible productivity shapes exhibited

by the PT and Schaefer models. While the PT and Schaefer models are instructive for a variety of dome shaped production behaviors, it is possible that under different modeling assumptions, for example BH production or age structured models, different bias patterns will emerge. Extending this work to be able to make claims in those settings is necessary for developing more generally extensible claims.

Given the role that catch plays in understanding where the production function is in-731 formed, it is clear that good estimates of catch are important for contextualizing modeling 732 inferences. While the production model treats catches as known without uncertainty, upon 733 inspection of Figure (12, right) this assumption is clearly suspect. Results presented here 734 only consider very deterministic catch histories. More work is needed to understand how 735 jittery catch may affect RP estimation. A smoothing model of catch may be preferable 736 for estimation, but results of this study suggest that even improvements to the contextual 737 understanding of catch will be important for interpreting model inferences correctly. 738

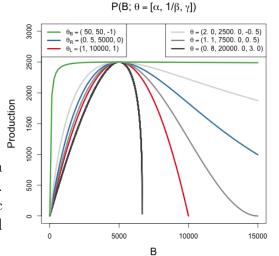
# 739 A Proposal: Productivity & Growth Extensions

The Deriso production function presents a convenient three parameter form that is capable of representing many of the most common two parameter production functions as special cases (Deriso, 1980). The BH and Logistic production functions arise when  $\gamma$  is fixed to -1 or 1 respectively, and the Ricker model is a limiting case as  $\gamma \to 0$  (J. Schnute, 1985).

$$\frac{dB}{dt} = P(B;\theta) - (M+F)B$$

$$P(B; [\alpha, \beta, \gamma]) = \alpha B(1 - \beta \gamma B)^{\frac{1}{\gamma}}$$

Figure 22: The Deriso production function plotted across a variety of parameter values. The special cases of BH, Ricker, and Logistic production are shown in green, blue, and red respectively.



Using the Deriso model as a data generating model across a wide range of RP-space, similarly as described in Section (6 .3), presents an ideal setting for extending the above study of RP biases across a broad range of productivity assumptions. Under the Deriso model inverting the relationship between RPs and model parameters is not fully analytically possible (J. T. Schnute & Richards, 1998). Numerical inversion of the nonlinear system seen in Eq (54) is required for determining parameter values for data generation. Notice for a given  $\gamma$  value,  $\alpha$  and  $\beta$  can be solved analytically.

$$\frac{B^*}{\bar{B}(0)} = \frac{\left(\frac{\alpha}{M+F^*}\right)^{\frac{1}{\gamma}} - 1}{\left(\frac{\alpha}{M}\right)^{\frac{1}{\gamma}} - 1}$$

$$\alpha = (M+F^*) \left[1 - \frac{1}{\gamma} \left(\frac{F^*}{M+F^*}\right)\right]^{-\gamma}$$

$$\beta = \frac{1}{\gamma \bar{B}(0)} \left(1 - \left(\frac{\alpha}{M}\right)^{\frac{1}{\gamma}}\right)$$
(54)

$$P_{\mathrm{BH}}(B; [\alpha, \beta, -1]) = \frac{\alpha B}{(1 + \beta B)}$$

$$\frac{B^*}{\bar{B}(0)} = \frac{1}{\frac{F^*}{M} + 2}$$

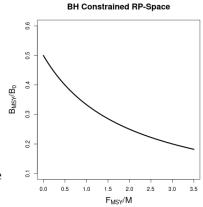


Figure 23: The restricted RP-space under the BH production function.

Inference under the BH model is of particular interest due to its overwhelming popularity in stock assessment. Similar to the limited RP-space of the Schaefer model the two parameter BH model also has a limited RP-space as shown in Figure (23). While the BH constrained RP space is more complicated than the Schaefer model, analogy to the results obtained under the PT-Schaefer simulation setting, and the flexible GP metamodel, should expedite the analysis of BH inference.

## 57 Individual Growth

Models that include individual growth and maturity dynamics are another important prac-758 tical setting for extending the understanding of how productivity model misspecification can 759 bias RPs estimation. The Deriso-Schnute delay-difference (DD) model provides a compact 760 representation of simple age-structured dynamics (Deriso, 1980; J. Schnute, 1985, 1987). 761 While various modeling strategies may be considered for including effects of age-structure 762 in the population, the Deriso-Schnute DD model presents an ideal model for the simulation 763 setting presented here. The compact representation of the Deriso-Schnute DD model via 764 delay-differential equations accounts for the effects of individual growth and maturity while 765 maintaining relatively fast computation.

The DD model is derived directly from an assumption of Von Bertalanffy growth (Von Bertalanffy, 1938) in weight, as seen in Eq (58). In this setting Von Bertalanffy growth relates individual age to individual weight by assuming linear instantaneous growth (as parameterized by the growth parameters  $\kappa$  and  $w_{\infty}$ ). The DD model expands the idea of biomass production into the processes of recruitment, individual growth, and maturity. This formu-

lation separates the number of individuals in the population (N) from the biomass of the population (B). The dynamics of N, as seen in Eq (56), are very similar to that of the Deriso production model presented above, however the role of the production function is now filled by a "recruitment" function which describes how new individuals are added to the numbers equation. The B dynamics, can then be seen to describe biomass by an account of 1) biomass of new recruits, 2) the net growth of existing biomass, and 3) biomass lost due to mortality. The model accounts for maturity as knife-edge maturity at the instant an individual reaches age  $a_0$ .

$$\frac{dB}{dt} = \underbrace{w(a_0)R(B;\theta)}^{\text{Recruitment Biomass}} + \underbrace{\kappa\left[w_{\infty}N - B\right]}^{\text{Net Growth}} - \underbrace{(M+F)B}^{\text{Mortality}}$$
(55)

$$\frac{dN}{dt} = R(B;\theta) - (M+F)N \tag{56}$$

$$R(B; [\alpha, \beta, \gamma]) = \alpha B(t - a_0) (1 - \beta \gamma B(t - a_0))^{\frac{1}{\gamma}}$$

$$(57)$$

$$w(a) = w_{\infty}(1 - e^{-\kappa a}) \tag{58}$$

For the purpose of inference the parameters  $\kappa, w_{\infty}, a_0$  and M are typically fixed at values determined by the population of study. Thus the primary inferential goal of the DD model is 768 again focused on learning the recruitment parameters. Using the Deriso-Schnute DD model 769 as a data generating model across a wide range of RP-space, and fitting those data under a 770 BH restriction of the DD model, further extends the simulation study of RP bias to include the effects of individual growth.

#### Summary 773

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My dissertation will include extensions of the metamodeling analysis of RP bias, as pre-774 sented in Sections (5 - 8), in the context of the Deriso-BH simulation setting. Additionally 775 my dissertation will include further extensions into the analysis of RP bias under model misspecification of the DD model's recruitment function. The Deriso production/recruitment 777 function presents numerical challenges that require careful numerics and a different handling 778 of the simulation design, but allows for extensions into all of the most widely used models 779 of productivity. Furthermore, the DD model allows for an efficient extension of results into 780

 $_{781}$   $\,$  to context of maturity and growth dynamics.

# References

- Beverton, R. J., & Holt, S. J. (1957). On the dynamics of exploited fish populations (Vol. 11).

  Springer Science & Business Media.
- Conn, P. B., Williams, E. H., & Shertzer, K. W. (2010). When can we reliably estimate the productivity of fish stocks? Canadian Journal of Fisheries and Aquatic Sciences, 67(3), 511–523.
- Deriso, R. B. (1980, February). Harvesting Strategies and Parameter Estimation for an Age-Structured Model. Canadian Journal of Fisheries and Aquatic Sciences, 37(2), 268–282. Retrieved 2020-05-13, from https://www.nrcresearchpress.com/doi/abs/
- 10.1139/f80-034 doi: 10.1139/f80-034
- DeYoreo, M. (2012). Integrating catchability out of the likelihood.
- Fox Jr., W. W. (1970). An Exponential Surplus-Yield Model for Optimizing
  Exploited Fish Populations. Transactions of the American Fisheries So-
- Exploited Fish Populations. Transactions of the American Fisheries Society, 99(1), 80–88. Retrieved 2022-02-17, from https://onlinelibrary
- .wiley.com/doi/abs/10.1577/1548-8659%281970%2999%3C80%3AAESMF0%3E2
- .O.CO%3B2 (\_eprint: https://onlinelibrary.wiley.com/doi/pdf/10.1577/1548-
- <sup>798</sup> 8659%281970%2999%3C80%3AAESMFO%3E2.0.CO%3B2) doi: 10.1577/
- 1548-8659(1970)99 < 80:AESMFO > 2.0.CO;2
- Gramacy, R. B. (2020). Surrogates: Gaussian process modeling, design, and optimization for the applied sciences. Chapman and Hall/CRC.
- Gramacy, R. B., & Lee, H. K. (2012). Cases for the nugget in modeling computer experiments. Statistics and Computing, 22(3), 713–722. (Publisher: Springer)
- Hilborn, R. (2010). Pretty good yield and exploited fishes. *Marine Policy*, 34(1), 193–196. (Publisher: Elsevier)
- Hilborn, R., & Mangel, M. (1997). The Ecological Detective: Confronting Models with Data.
   Princeton University Press.
- Hilborn, R., & Walters, C. J. (1992). Quantitative Fisheries, Stock Assessment: Choice

  Dynamics, and Uncertainty Chapman and Hall. New York.
- Kingsland, S. (1982). The refractory model: the logistic curve and the history of population

- ecology. The Quarterly Review of Biology, 57(1), 29–52. (Publisher: Stony Brook Foundation, Inc.)
- 813 Lee, H.-H., Maunder, M. N., Piner, K. R., & Methot, R. D. (2012, August). Can
- steepness of the stock-recruitment relationship be estimated in fishery stock as-
- sessment models? Fisheries Research, 125-126, 254-261. Retrieved 2022-01-29,
- from https://linkinghub.elsevier.com/retrieve/pii/S0165783612001099 doi:
- 10.1016/j.fishres.2012.03.001
- Magnusson, A., & Hilborn, R. (2007). What makes fisheries data informative? Fish and
- Fisheries, 8(4), 337–358. (Publisher: Wiley Online Library)
- Mangel, M. (2006). The Theoretical Biologist's Toolbox: Quantitative Methods for Ecology and Evolutionary Biology..
- Mangel, M., MacCall, A. D., Brodziak, J., Dick, E., Forrest, R. E., Pourzand, R., & Ralston,
- S. (2013, April). A perspective on steepness, reference points, and stock assessment.
- Canadian Journal of Fisheries and Aquatic Sciences, 70(6), 930–940. Retrieved 2019-
- 07-03, from https://www.nrcresearchpress.com/doi/10.1139/cjfas-2012-0372
- doi: 10.1139/cjfas-2012-0372
- Maunder, M. N. (2003). Is it time to discard the Schaefer model from the stock assessment scientist's toolbox? *Fisheries Research*, 61(1-3), 145–149.
- Pearson, D. E., & Erwin, B. (1997). Documentation of California's commercial market sampling data entry and expansion programs.
- Pella, J. J., & Tomlinson, P. K. (1969). A generalized stock production model. *Inter-*\*\*American Tropical Tuna Commission Bulletin, 13(3), 416–497.
- Prager, M. H. (2002). Comparison of logistic and generalized surplus-production models
- applied to swordfish, Xiphias gladius, in the north Atlantic Ocean. Fisheries Research,
- 58(1), 41–57. (Publisher: Elsevier)
- Prager, M. H. (2003, March). Reply to the Letter to the Editor by Maunder. Fisheries
- Research, 61(1), 151-154. Retrieved 2022-01-30, from https://www.sciencedirect
- . com/science/article/pii/S0165783602002746 doi: 10.1016/S0165-7836(02)
- 839 00274-6
- Punt, A. E., Butterworth, D. S., Moor, C. L. d., Oliveira, J. A. A. D., & Haddon, M. (2016).

```
Management strategy evaluation: best practices. Fish and Fisheries, 17(2), 303–334.
841
         Retrieved 2018-12-13, from https://onlinelibrary.wiley.com/doi/abs/10.1111/
842
         faf.12104 doi: 10.1111/faf.12104
843
   Punt, A. E., & Cope, J. M. (2019, September). Extending integrated stock assessment mod-
844
         els to use non-depensatory three-parameter stock-recruitment relationships. Fisheries
845
         Research, 217, 46-57. Retrieved 2019-07-19, from http://www.sciencedirect.com/
846
         science/article/pii/S0165783617301819 doi: 10.1016/j.fishres.2017.07.007
847
   Radhakrishnan, K. (1993). Description and Use of LSODE, the Livermore Solver for Ordi-
848
         nary Differential Equations., 124.
849
   Ramasubramanian, K., & Singh, A. (2017). Machine learning using R (No. 1). Springer.
850
   Rankin, P. S., & Lemos, R. T. (2015, October). An alternative surplus production
851
         model. Ecological Modelling, 313, 109–126. Retrieved 2022-02-11, from https://
852
         www.sciencedirect.com/science/article/pii/S0304380015002732 doi: 10.1016/
853
         j.ecolmodel.2015.06.024
854
   Ricker, W. E. (1954). Stock and recruitment. Journal of the Fisheries Board of Canada,
855
         11(5), 559–623. (Publisher: NRC Research Press Ottawa, Canada)
856
   Schnute, J. (1985, March). A General Theory for Analysis of Catch and Effort Data.
857
         Canadian Journal of Fisheries and Aquatic Sciences, 42(3), 414–429. Retrieved 2020-
858
         05-13, from https://www.nrcresearchpress.com/doi/abs/10.1139/f85-057
859
         10.1139/f85-057
860
   Schnute, J. (1987). A general fishery model for a size-structured fish population. Canadian
861
         Journal of Fisheries and Aquatic Sciences, 44(5), 924–940. (Publisher: NRC Research
862
         Press Ottawa, Canada)
863
   Schnute, J. T., & Richards, L. J. (1998, February). Analytical models for fishery reference
864
         points. Canadian Journal of Fisheries and Aquatic Sciences, 55(2), 515–528. Retrieved
865
         2020-01-14, from https://www.nrcresearchpress.com/doi/abs/10.1139/f97-212
866
         doi: 10.1139/f97-212
867
   Scrucca, L. (2013, April). GA: A Package for Genetic Algorithms in R. Journal of Sta-
868
         tistical Software, 53, 1-37. Retrieved 2022-01-17, from https://doi.org/10.18637/
869
         jss.v053.i04 doi: 10.18637/jss.v053.i04
870
```

Scrucca, L. (2017). On Some Extensions to GA Package: Hybrid Optimisation, Parallelisation and Islands EvolutionOn some extensions to GA package: hybrid optimi-872 sation, parallelisation and islands evolution. The R Journal, 9(1), 187–206. Re-873 trieved 2022-01-17, from https://journal.r-project.org/archive/2017/RJ-2017 874 -008/index.html 875 Von Bertalanffy, L. (1938). A quantitative theory of organic growth (inquiries on growth 876 laws. II). Human biology, 10(2), 181–213. (Publisher: JSTOR) 877 Walters, C., & Ludwig, D. (1994). Calculation of Bayes posterior probability distributions 878 for key population parameters. Canadian Journal of Fisheries and Aquatic Sciences, 879 51(3), 713–722. (Publisher: NRC Research Press Ottawa, Canada) 880

# Appendix A: Profile Likelihood MLE

Given that q has the effect of rescaling the mean function, a naive handling of q has the potential to interfere with the inference on  $\theta$ . While the parameter q is typically identifiable, it can introduce lesser modes which complicate naive inference.

Below I outline a profile likelihood method for MLE inference on q and  $\sigma^2$ . However if posed in a Bayesian context, q and  $\sigma^2$  may be marginalized out of the joint posterior to yield a direct sampling scheme for q and  $\sigma^2$  which factors the posterior into the form  $p(q, \sigma^2, \boldsymbol{\theta}|I) = N(\log(q)|\sigma^2, \boldsymbol{\theta}, I)IG(\sigma^2|\boldsymbol{\theta}, I)p(\boldsymbol{\theta}|I)$  (Walters & Ludwig, 1994; DeYoreo, 2012)

The joint likelihood on the log scale can be written as,

$$\log \mathcal{L}(q, \sigma^2, \boldsymbol{\theta}; I) = -\frac{T}{2} \log(\sigma^2) - \frac{1}{2\sigma^2} \sum_{t} \log\left(\frac{I_t}{qB_t(\boldsymbol{\theta})}\right)^2.$$
 (59)

First Eq (59) is maximized with respect to q by partial differentiation of Eq (59) with respect to q,

$$\frac{\partial \log \mathcal{L}}{\partial q} = -\frac{1}{q\sigma^2} \left( \sum_{t} \log \left( \frac{I_t}{B_t(\boldsymbol{\theta})} \right) - T \log(q) \right)$$
 (60)

The maximum of the likelihood in the q direction is attained when  $\frac{\partial \log \mathcal{L}}{\partial q} = 0$ . By setting  $\frac{\partial \log \mathcal{L}}{\partial q}$  to 0 and solving for q, the MLE of q in terms of  $\theta$  can be written as

$$q(\boldsymbol{\theta}) = e^{\frac{1}{T} \sum_{t} \log \left( \frac{I_{t}}{B_{t}(\boldsymbol{\theta})} \right)} = \left( \prod_{t} \frac{I_{t}}{B_{t}(\boldsymbol{\theta})} \right)^{\frac{1}{T}}.$$
 (61)

Notice that  $\hat{q}(\boldsymbol{\theta})$  is the geometric mean of the empirical scaling factors between the observed index and modeled biomass at each time. This form is emblematic of the interpretation of the q parameter as the proportionality constant between the observed index and the modeled biomass. Additionally notice that  $\hat{q}$  is a function of  $\boldsymbol{\theta}$ , so that achieving the global maximum of the likelihood function still requires maximization over  $\boldsymbol{\theta}$ . Furthermore,  $\hat{q}(\boldsymbol{\theta})$  is only a function of  $\boldsymbol{\theta}$  and that  $\sigma^2$  does not enter the expression. This will be helpful in further maximization of the likelihood with respect to  $\sigma^2$ .

Now to maximize in the  $\sigma^2$  direction Eq (59) is differentiated with respect to  $\sigma^2$ ,

$$\frac{\partial \log \mathcal{L}}{\partial \sigma^2} = -\frac{T}{2\sigma^2} + \frac{1}{2(\sigma^2)^2} \sum_{t} \log \left( \frac{I_t}{qB_t(\boldsymbol{\theta})} \right)^2.$$
 (62)

The maximum of the likelihood in the  $\sigma^2$  direction is attained when  $\frac{\partial \log \mathcal{L}}{\partial \sigma^2} = 0$ . Setting  $\frac{\partial \log \mathcal{L}}{\partial \sigma^2}$  to 0 and solving for  $\sigma^2$  produces the following MLE as a function of  $\boldsymbol{\theta}$ ,

$$\sigma^{2}(\boldsymbol{\theta}) = \frac{1}{T} \sum_{t} \log \left( \frac{I_{t}}{q(\boldsymbol{\theta}) B_{t}(\boldsymbol{\theta})} \right)^{2}$$
 (63)

Notice that the conditionally MLE of  $\sigma^2$  is not only a function of  $\boldsymbol{\theta}$  but also a function of q.

As previously noted,  $q(\boldsymbol{\theta})$  is only a function of  $\boldsymbol{\theta}$ , and so to achieve a global maximum of the joint likelihood,  $\sigma^2(\boldsymbol{\theta})$  is written entirely in terms of  $\boldsymbol{\theta}$  by replacing q by  $q(\boldsymbol{\theta})$  as seen above.

By combining Eq (61) and Eq (63) the MLEs of q and  $\sigma^2$  can be written entirely in terms of  $\theta$ . Furthermore, this realization allows the joint maximization of the likelihood to be reduced to the following profile log-likelihood,

$$\log \mathcal{L}(\boldsymbol{\theta}; I) = -\frac{T}{2} \log (\sigma^2(\boldsymbol{\theta})) - \frac{1}{2\sigma^2(\boldsymbol{\theta})} \sum_{t} \log \left( \frac{I_t}{q(\boldsymbol{\theta})B_t(\boldsymbol{\theta})} \right)^2.$$
 (64)

This profile log-likelihood is maximized numerically over  $\boldsymbol{\theta}$ , and the estimates for q and  $\sigma^2$  are given by evaluating Equations (61) and (63) at  $\hat{\boldsymbol{\theta}}$ .

$$\hat{\boldsymbol{\theta}} = \operatorname*{argmax}_{\boldsymbol{\theta}} \log \mathcal{L}(\boldsymbol{\theta}; I) \tag{65}$$

$$\hat{\sigma}^2 = \sigma^2(\hat{\boldsymbol{\theta}}) \tag{66}$$

$$\hat{q} = q(\hat{\boldsymbol{\theta}}) \tag{67}$$

This profile formulation via  $\hat{q}(\boldsymbol{\theta})$  and  $\hat{\sigma}^2(\boldsymbol{\theta})$  reduces the computational complexity of this numerical optimization, while also avoiding the multimodality issues induced by q.