Exploration of Overcompensation and the Spawning Abundance Producing Maximum Sustainable Yield for Upper Cook Inlet Sockeye Salmon Stocks

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Background

Critical to the development of escapement-based management targets for Pacific salmon is quantifying the shape or form of the relationship between spawning abundance and recruitment, and the extent to which that stock-recruitment relationship exhibits compensation and overcompensation (Figure 1). Compensation is the tendency for population productivity (recruits-per-spawner) to decline as spawning abundance increases, resulting in a decrease in potential yield for each additional spawner beyond Smsy. Compensation may be contrasted with overcompensation, or the tendency for recruitment to decrease at high levels of spawning abundance, causing a stock-recruitment relationship to "bend over".

From a management perspective the implication of surplus escapement, escapement in excess of the spawning abundance predicted to produce maximum sustainable yield (Smsy), depends heavily on whether the stock-recruitment relationship exhibits evidence for overcompensation. For a population exhibiting simple compensation, surplus escapement is expected to result in foregone yield in the current year, but no reduction in future recruitment. However, for a population exhibiting overcompensation, surplus escapement may be expected to result in a reduction in future recruitment. As a result, the extent of overcompensation exhibited by a salmon population has very real implications for the expected impact from, and level of risk imposed by, surplus escapement.

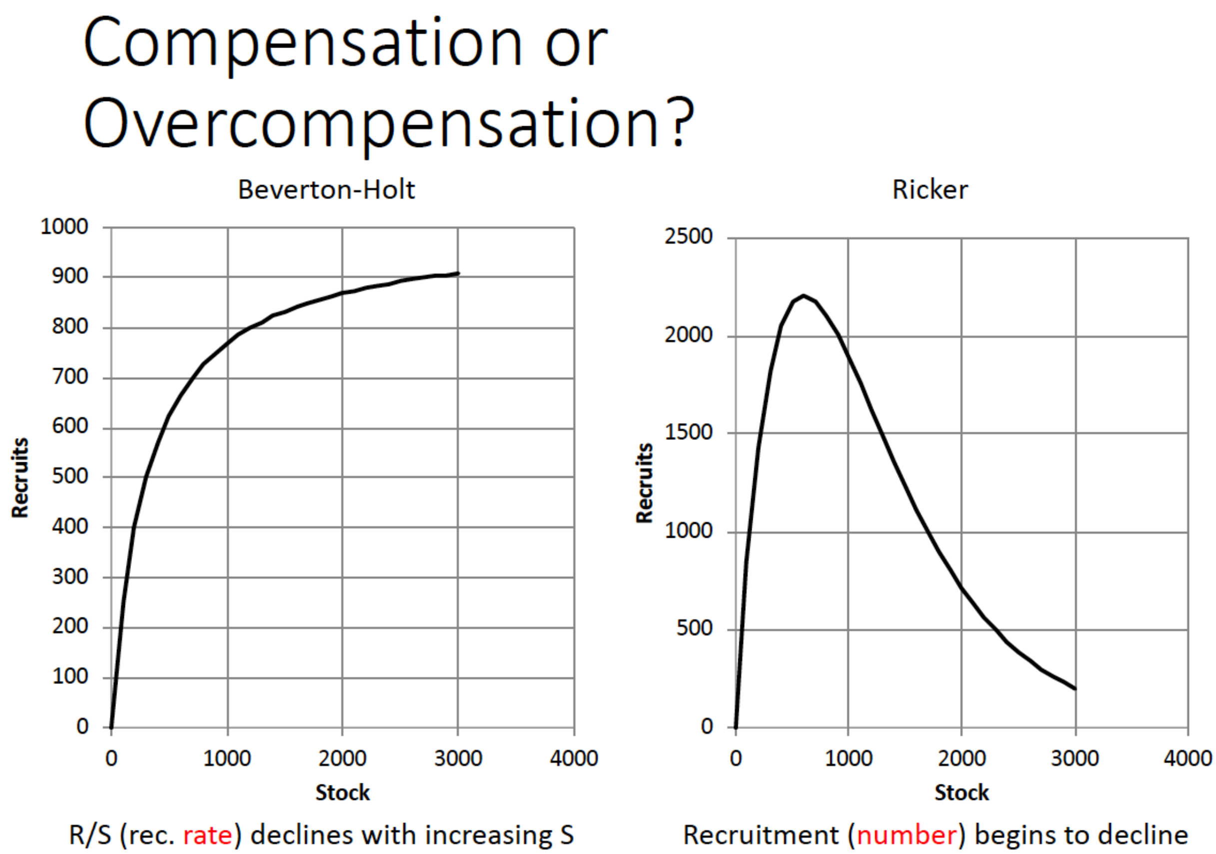

Figure 1. Graphical explanation of the difference between simple compensation and overcompensation in the context of stock-recruitment relationships.

The purpose of this analysis is to explore alternative methods for determining the spawning abundance of sockeye salmon (*Oncorhynchus nerka*) that is expected to produce maximum sustainable yield for the Kenai late-run and Kasilof river sockeye salmon stocks, and from this to quantify the extent to which the stock-recruitment data exhibit evidence for overcompensation, as opposed to simple compensation, within the range of past observations. A broad range of mathematical forms for stock-recruitment relationships have been developed, each with specific properties and meanings for their respective parameters (Hilborn and Walters 1992, Walters and Martell 2004). We explore six alternative stock-recruitment models that are applicable to the Kenai and Kasilof river stocks, compare the statistical evidence supporting each along with differences in their estimated parameters and predictions for maximum sustainable yield (MSY) and the spawning abundance expected to produce MSY (Smsy). In addition, we use two stock-recruitment models that may take either Ricker or Beverton-Holt forms as a proxy for assessing the extent to which overcompensation is evident in these data.

Table 1 contains definitions for common terms and references used throughout this document.

Table 1. Description of symbols, terms, and references.

Name	Definition
MSY	Maximum sustainable yield.
Smsy	The spawning abundance expected to produce MSY.
Recruitment	The number of salmon produced by the spawning stock size in a given (brood) year, returning in subsequent years, and measured as either catch or escapement.
Stock-recruitment Relationship or Spawner-recruit Relationship	The average relationship between spawning abundance and expected recruitment.
Process Error	Random variation in a stock-recruitment relationship.
Productivity	Recruits-per-spawner: The number of recruits (catch + escapement) per unit spawning abundance. Referenced by brood year.
Yield	Surplus production or recruitment of salmon in excess of the amount necessary for escapement, that may be taken as harvest.

Methods

Six alternative stock-recruitment models were fit to data from the Kenai and Kasilof river sockeye salmon stocks. Four of these models: (1) the standard Ricker, brood year interaction Ricker with delayed density-dependent compensation described by either (2) main effects or a (3) statistical interaction term, and (4) autoregressive Ricker, are typical forms routinely evaluated by the Alaska Department of Fish and Game and included in the 2017 escapement goal review by Erickson et al. (2017) for these stocks. Two alternative stock-recruitment models were used to describe the probability that either a Beverton-Holt relationship, which does not permit overcompensation, or a Ricker-type relationship that may allow for overcompensation, have more support from the available data.

Standard Ricker

The Ricker (1954) model is a standard and flexible function often used in the approximation of salmon stock-recruitment relationships. The Hilborn (1985) version of the Ricker model was used because of the easier interpretation of the β parameter and the ability to approximate MSY and Smsy given the model parameters. Under this Ricker formulation:

$$R_t = S_t e^{\alpha(1-S_t/\beta)+\varepsilon_t}$$

R_t is the expected number of recruits arising from a spawning abundance S_t, from a brood year t. The α parameter describes the maximum productivity (recruits-per-spawner) of the population at low spawning abundance and the β parameter describes the equilibrium abundance of the unfished stock. It should be noted that maximum productivity in this form is the exponent of α, or $exp(\alpha)$. Residual process error in brood year t is described by ε_t which is assumed to be normally distributed with mean zero standard deviation σ: $\varepsilon_t \sim Normal(0, \sigma^2)$.

Brood Year Interaction Ricker (main effects)

This model is a modified version of the standard Ricker (1954) that includes two terms (β_1, β_2) describing density-dependence, or the tendency for expected productivity (recruits-per-spawner) to decline with increasing spawning abundance (Ward and Larkin 1964, Larkin 1971, Collie and Walters 1987). In the brood year interaction Ricker model:

$$R_t = S_t e^{\alpha-\beta_1 S_t-\beta_2 S_{t-1}+\varepsilon_t}$$

β_1 describes the effect of spawning abundance in brood year t on population productivity and β_2 describes the lagged or delayed density-dependent effect of spawning abundance in the prior $(t-1)$ brood year.

Brood Year Interaction Ricker (interaction term)

An alternative Ricker model structure intended to capture delayed density-dependent compensation was also explored, which includes a statistical interaction between the spawning abundance in the brood year (t) and the prior brood year $(t-1)$.

$$R_t = S_t e^{\alpha + \gamma S_t S_{t-1} + \varepsilon_t}$$

This model quantifying density-dependence with the statistical interaction term (γ) formed the operating model in simulation analyses for the Kenai River sockeye stock described by Carlson et al. (1999) and has been evaluated as part of recent escapement goal analyses for Upper Cook Inlet sockeye salmon (Clark et al. 2007, Fair et al. 2011, Erickson et al. 2017). Parameters for the density-dependent main effects of spawning abundance in the current (β_1) and prior (β_2) brood years were excluded for model parsimony, as they have routinely been found to not differ from zero when the statistical interaction term is included (Erickson et al. 2017). Although this model has often been used in establishing management reference points for the Kenai River sockeye salmon stock, interpretation of the interaction term is challenging and whether delayed density-dependent effects should be captured by the main effects version of the brood year interaction model (above) is a subject of ongoing discussion.

Autoregressive Ricker

The fourth type of model explored accounts for serial autocorrelation in process error at a lag of one year, under the assumption that these errors may not be fully independent across time. In this autoregressive form of the Ricker model described by Fleischman and Reimer (2017),

$$R_t = \alpha S_t e^{-\beta S_t + \phi v_{t-1} + \varepsilon_t}$$

ϕ describes the effect of the residual in the prior brood year:

$$v_{t-1} = ln(R_{t-1}) - ln(S_{t-1}) - ln(\alpha) + \beta S_{t-1}$$

It should be noted that under this form of the Ricker model the α is not in the exponentiated portion of the equation, and therefore maximum productivity is equal to α and not $ln(\alpha)$.

The four model alternatives described above are consistent with the standard models the Alaska Department of Fish and Game has previously used to estimate potential yield for the Kenai and Kasilof sockeye salmon stocks in the most recent escapement goal review (Erickson et al. 2017). The two models described below were used to quantify the likelihood that overcompensation (decreasing recruitment for escapements in excess of Smsy) or simple compensation is supported by these two datasets. We used the relative support from the data for a Ricker-type model that permits overcompensation, relative to the level of support for a Beverton-Holt model (no overcompensation possible), as a proxy for the extent to which overcompensation is reflected in the data.

Ricker Beverton-Holt Mixture

The first model used to quantify support for the overcompensation hypothesis is a mixture of both Beverton-Holt and Ricker models. A state (δ) parameter is sampled from a Bernoulli distribution with a prior probability of 0.5, taking a value of 0 or 1 in each posterior sample. If $\delta = 1$, the stock-recruitment relationship has a Ricker form (potential overcompensation), while if $\delta = 0$ the relationship has a Beverton-Holt form (no possible overcompensation).

$$R_t = \left[\delta\left(S_t e^{\alpha_R(1-S_t/\beta_R)}\right) + (1-\delta)\left(\frac{\alpha_B S_t}{1+\frac{\alpha_B S_t}{\beta_B}}\right)\right] e^{\varepsilon_t}$$

Separate productivity (α_R, α_B), density-dependent (β_R, β_B), process error standard deviation (σ_R,σ_B) parameters are estimated for each model type, given their different values and meanings. After estimation, the proportion of time the model spends as a Ricker function as opposed to Beverton-Holt function can be calculated as the proportion of posterior samples where δ has a value of 1 or 0 respectively. In general terms, the more time the model spends as Beverton-Holt may be interpreted as less evidence for the overcompensation hypothesis.

Deriso-Schnute

The second model used to quantify support for the overcompensation hypothesis is the Deriso-Schnute model. The Deriso-Schnute is a generalized stock-recruitment model that can take the shape of either a Beverton-Holt or Ricker model depending on the value of a shape parameter c.

$$R_t = \alpha S_t (1 - c\beta S_t)^{\frac{1}{c}} e^{\varepsilon_t}$$

If $c = -1$, the model has the Beverton-Holt form, while if $c = 0$ it takes the shape of a Ricker model (Figure 2). This generalized stock-recruitment model was originally introduced by Deriso (1980) and further developed by Schnute (1985). The estimated value of the shape parameter may be interpreted as evidence for a Ricker or Beverton-Holt function describing the stock-recruitment data and by extension may be a way to quantify evidence regarding the overcompensation hypothesis.

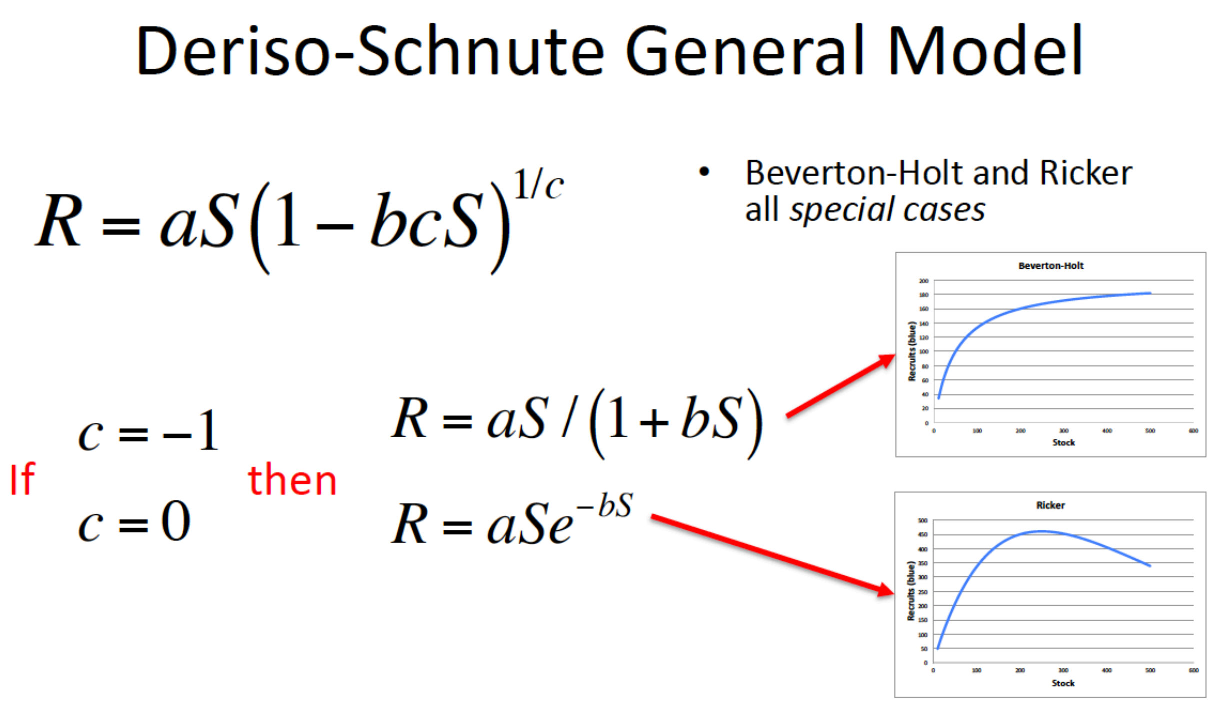

Figure 2. Visual description of the Deriso-Schnute stock-recruitment model.

Estimation Methods

All models were fit to available stock-recruitment data for the Kenai River late-run and Kasilof River sockeye salmon stocks using Bayesian methods, by minimizing the difference between the natural log of observed and predicted recruitment for a given brood year's spawning abundance and estimating the σ parameter describing the residual error. Bayesian posterior samples were generated with JAGS software (Plummer 2013) implemented using the R2jags package in R (Su and Yajima 2015). Three chains with random starting values were run for 2 million iterations, saving 1 in every 100 samples to reduce posterior correlation. The first 50% of the chain was discarded as a burn-in period leaving a total of 30,000 posterior samples.

Standard diagnostics were used to assess model convergence, including potential scale reduction factors ($\hat{R}$) and effective sample sizes for model parameters. Traceplots and the extent of autocorrelation at lags up to 20 were also evaluated. No significant convergence difficulties were observed, although under the Ricker Beverton-Holt mixture model posteriors for the Ricker parameters were less well defined because the model on average spent less time exploring this state for both stocks.

Prior probability distributions for estimated model parameters were either uninformative or mildly informative (Table 2). Mildly informative priors included those for the process error standard deviation of each model (σ), which were normally distributed with mean zero and variance equal to one, and was constrained between 0 and 2. In reality all estimates of process error standard deviations were far below two and sensitivity tests indicated this choice of prior did little aside from constrain extremely unrealistic jumps in model parameters. The shape parameter in the Deriso-Schnute model (c) was constrained between -1 and 0 as per our goal of quantifying evidence for Beverton-Holt and Ricker forms of this model. Finally, the prior probability for the different states in the mixture model was fixed at $p = 0.5$ for the Bernoulli draw in each posterior sample, thus representing equal prior belief in each model type.

A mild sensitivity of the Ricker Beverton-Holt mixture model to the specified prior for density dependent parameters (β_R, β_B) was observed, wherein the mixture probability for the Ricker model was slightly lower for the Kasilof River stock when the prior on these parameters was more broadly distributed.

Table 2. Full model equations and priors for each model parameter. Normal distributions are presented with the mean and variance $Normal(mean, variance)$. [min,max] indicates truncation of the full prior distribution across a range (min-max).

Name	Equation	Priors
Ricker	$R_t = S_t e^{\alpha(1-S_t/\beta)+\varepsilon_t}$	$\alpha \sim ln(Uniform(1e-3{,}20))$ $\beta \sim Uniform(1{,}1e7)$ $\sigma \sim Normal(0{,}1)[1e-3{,}2]$
Brood Year Interaction Ricker (main effects)	$R_t = S_t e^{\alpha-\beta_1 S_t-\beta_2 S_{t-1}+\varepsilon_t}$	$\alpha \sim ln(Uniform(1e-3{,}20))$ $\beta_{1,2} \sim Uniform(0{,}1e-3)$ $\sigma \sim Normal(0{,}1)[1e-3{,}2]$
Brood Year Interaction Ricker (interaction term)	$R_t = S_t e^{\alpha+\gamma S_t S_{t-1}+\varepsilon_t}$	$\alpha \sim ln(Uniform(1e-3{,}20))$ $\gamma \sim Normal(0{,}1e-2)$ $\sigma \sim Normal(0{,}1)[1e-3{,}2]$
Autoregressive Ricker	$R_t = \alpha S_t e^{-\beta S_t+\phi v_{t-1}+\varepsilon_t}$ $v_{t-1} = ln(R_{t-1}) - ln(S_{t-1}) - ln(\alpha) + \beta S_{t-1}$	$\alpha \sim Uniform(1e-3{,}20)$ $\beta \sim Unform(0{,}1)$ $\phi \sim Normal(0, \sqrt{10})$ $v_0 \sim Normal\left(0, \frac{\sigma^2}{1-\phi^2}\right)$ $\sigma \sim Normal(0{,}1)[1e-3{,}2]$
Ricker Beverton-Holt Mixture	$R_t = \left[\delta\left(S_t e^{\alpha_R(1-S_t/\beta_R)}\right) + (1-\delta)\left(\frac{\alpha_B S_t}{1+\frac{\alpha_B S_t}{\beta_B}}\right)\right] e^{\varepsilon_t}$	$\alpha_R \sim ln(Uniform(1e-3{,}20))$ $\alpha_B \sim Uniform(1e-3{,}20)$ $\beta_R \sim Normal(0,(1e7)^2)[0,]$ $\beta_B \sim Normal(0,(1e7)^2)[0,]$ $\sigma_R \sim Normal(0{,}1)[1e-3{,}2]$ $\sigma_B \sim Normal(0{,}1)[1e-3{,}2]$
Deriso-Schnute	$R_t = \alpha S_t(1-c\beta S_t)^{\frac{1}{c}} e^{\varepsilon_t}$	$\alpha \sim Uniform(1e-3{,}20)$ $\beta \sim Uniform(0{,}1)$ $c \sim Uniform(-1{,}0)$ $\sigma \sim Normal(0{,}1)[1e-3{,}2]$

Simulation of Potential Yield

Potential yield was simulated across a range of trial spawning abundances for each stock, under each of the alternative stock-recruitment models. Spawning abundance was increased iteratively in steps of 1,000 spawners across a suitable range, and at each level of spawning abundance potential yield was calculated for each of the 30,000 samples from the joint posterior distribution of model parameters. Correction for the log-normal process error distribution was achieved by using the appropriate bias correction for model parameters in the case of the standard and autoregressive Ricker models (Hilborn 1985, Fleischman and Reimer 2017), or multiplying expected recruitment from each posterior sample by $e^{\sigma^2}/2$ for each trial spawning abundance.

Description of Data

Data used for analysis of stock-recruitment relationships and potential yield were provided by the Alaska Department of Fish and Game (February, 2019). The average return abundance of the 2.4 and 3.3 age classes was assumed for this small component of the return from the 2012 brood year (which will return in 2019) in order to include this additional data point.

Table 3. Data used for stock-recruitment analysis.

	Kenai River		Kasilof River	
Brood Year	**Spawning Abundance**	**Total Return**	**Spawning Abundance**	**Total Return**
1968	115,545	960,169	90,958	145,853
1969	72,901	430,947	46,964	110,919
1970	101,794	550,923	38,797	168,239
1971	406,714	986,397	91,887	295,083
1972	431,058	2,547,851	115,486	372,639
1973	507,072	2,125,986	40,880	341,734
1974	209,836	788,067	71,540	342,896
1975	184,262	1,055,373	48,884	321,500
1976	507,440	1,506,012	142,058	691,693
1977	951,038	3,112,620	158,410	610,171
1978	511,781	3,785,040	119,165	695,679
1979	373,810	1,321,039	155,527	783,821
1980	615,382	2,673,295	188,314	1,082,721
1981	535,524	2,464,323	262,271	1,853,442
1982	755,672	9,587,700	184,204	1,287,592
1983	792,765	9,486,794	215,730	1,008,308
1984	446,297	3,859,109	238,413	766,694
1985	573,761	2,587,921	512,827	369,740
1986	555,207	2,165,138	283,054	674,252
1987	2,011,657	10,356,627	256,707	887,782
1988	1,212,865	2,546,639	204,336	665,176
1989	2,026,619	4,458,679	164,952	512,385
1990	794,616	1,507,693	147,663	501,812
1991	727,146	4,436,074	233,646	946,237
1992	1,207,382	4,271,576	188,819	815,919
1993	997,693	1,689,779	151,801	521,361
1994	1,309,669	3,052,634	218,826	765,529
1995	776,847	1,899,870	202,428	530,599
1996	963,108	2,261,757	264,511	751,566

1997	1,365,676	3,626,402	263,780	682,580
1998	929,090	4,465,328	259,045	792,308
1999	949,276	5,755,063	312,481	1,158,888
2000	696,899	7,058,333	263,631	1,388,432
2001	738,229	1,697,957	318,735	1,627,669
2002	1,126,616	3,628,712	235,732	1,250,022
2003	1,402,292	1,919,813	353,526	1,560,304
2004	1,690,547	3,236,600	523,653	1,491,097
2005	1,654,003	4,804,018	360,065	878,678
2006	1,892,090	5,006,280	389,645	744,647
2007	964,243	4,378,678	365,184	484,387
2008	708,805	3,380,397	327,018	873,640
2009	848,117	3,809,455	326,283	1,035,630
2010	1,038,302	3,625,388	295,265	1,377,594
2011	1,280,733	4,513,815	245,721	686,373
2012	1,212,921	1,490,134	374,523	509,565

General Results

Model Selection

The range of models evaluated in this analysis provided very similar fits to the stock-recruitment data for the Kenai and Kasilof river sockeye salmon stocks (Figure 3). The exception is the Kasilof River stock for which the predictions from the autoregressive Ricker model better matched low recruitments at the beginning of the time series and higher recruitments observed in the late 1970s and early 1980s.

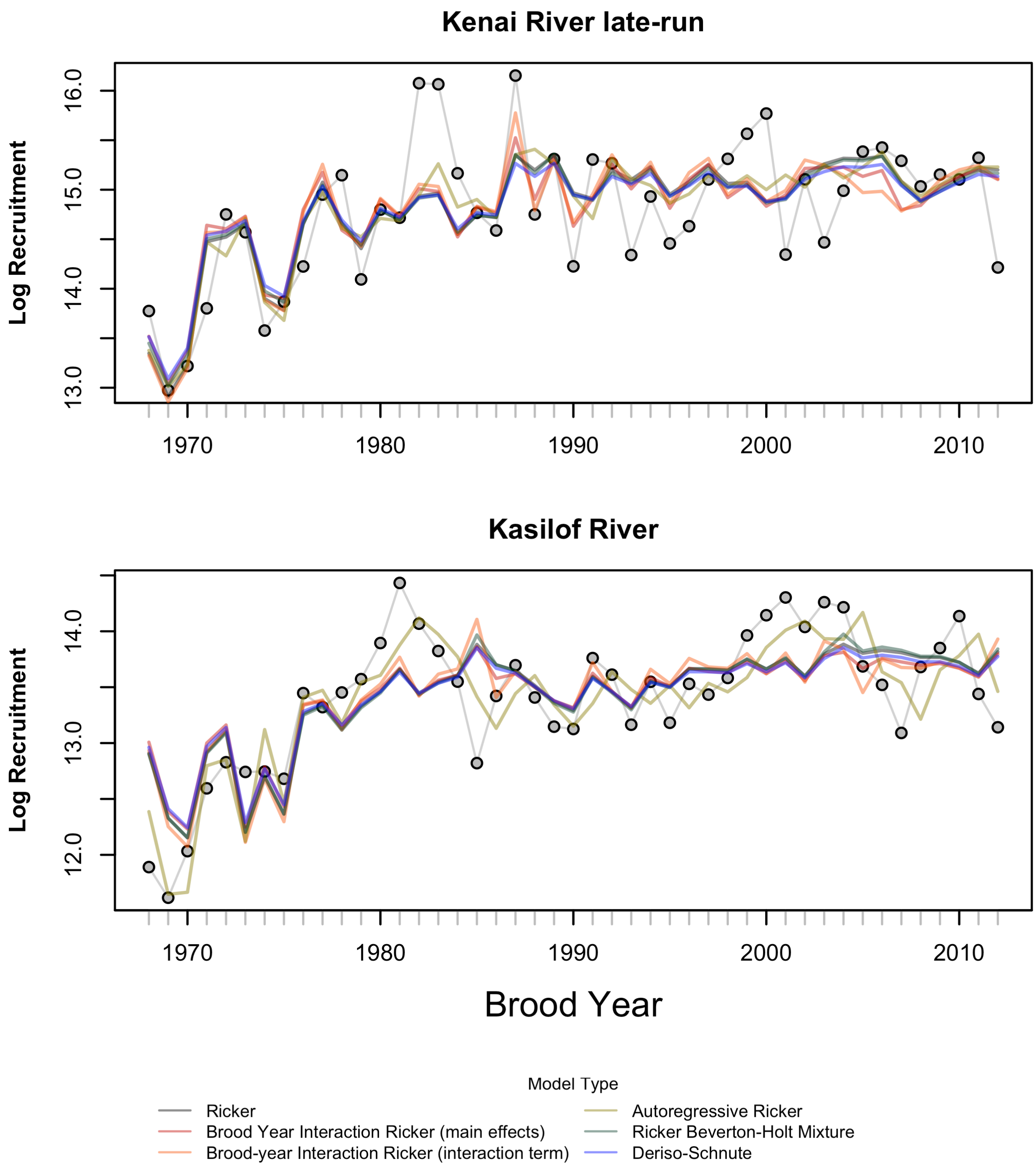

Figure 3. Predicted recruitment from the six model alternatives for the Kenai and Kasilof river sockeye salmon stocks. Lines are posterior median values for predicted recruitment in log space and points are the observed recruitments in log space, by brood year.

To evaluate support for alternative models in a Bayesian context, estimates of out-of-sample prediction error through cross-validation (Table 4) have been recommended (Gelman et al. 2014). The Watanabe-Akaike information criterion (WAIC) is an approximation to cross-validation and serves as a metric for model selection in a Bayesian context as it is calculated from the posterior predictive distribution (Hooten and Hobbs 2015). In general terms lower WAIC values indicate a better fit by the model to the data.

Table 4. WAIC values for each model fitted to each stock. Green colors indicate lower WAIC values and therefore preferred models.

Model	Kenai River	Kasilof River
Basic Ricker	67.06	55.80
Brood Year Interaction (main effects)	66.04	56.38
Brood Year Interaction (interaction term)	63.75	56.37
Autoregressive Ricker	68.02	35.10
Ricker Beverton-Holt Mixture	66.41	56.58
Deriso-Schnute	66.55	55.34

Comparison of WAIC values for the range of models evaluated indicates that for the Kenai River stock there is relatively equal support for all model types, however a slight preference for the brood year interaction Ricker that includes the statistical interaction term. The difference in WAIC between all candidate models for the Kenai River stock was less than 3.31, indicating limited evidence for the brood year interaction model with the statistical interaction term being vastly superior to alternatives from a WAIC perspective. Conversely, for the Kasilof River stock a substantially lower WAIC value was found for the autoregressive Ricker model. These preferred models are consistent with findings in the most recent ADF&G escapement goal review for these stocks (Erickson et al. 2017).

Overcompensation

The strength of evidence for the overcompensation hypothesis, that escapements in excess of Smsy are predicted to result in reduced future recruitment, was evaluated using two models that attempt to quantify the probability of a Ricker or Beverton-Holt model better representing the observed stock-recruitment relationship. While a model-based preference for the Ricker model does not necessarily indicate that overcompensation is present, given the flexibility of this model to describe relationships with and without overcompensation, a preference for the a Beverton-Holt like model indicates there is limited evidence for overcompensation as this model allows for recruitment to asymptote but not decline at high spawning abundances (i.e. overcompensation). In this way one can consider the potential for overcompensation under Ricker to be the null hypothesis and a model-based preference for a Beverton-Holt stock-recruitment relationship to be evidence for rejecting this null hypothesis. More generally, a model-based preference for the Beverton-Holt model would indicate limited evidence for overcompensation across the range of observed spawning abundances.

Results from the Ricker Beverton-Holt mixture model indicate that the majority of posterior samples were generated under the Beverton-Holt model (Figure 4). For the Kasilof River sockeye salmon stock, 40.3% of posterior samples were generated from the Ricker model while 59.7% of samples were generated from the Beverton-Holt model. For the Kenai River late-run stock, 23.0% of posterior samples were generated from the Ricker model while 77.0% of samples were generated from the Beverton-Holt model. The relative proportions of posterior samples generated from each model suggest that a Beverton-Holt model better represents the underlying stock-recruitment relationship for the Kenai River stock, and as such there is limited evidence for overcompensation across the range of observed spawning abundances. For the Kasilof River stock there is a moderate preference for the Beverton-Holt relative to the Ricker model from the mixture sampling probabilities.

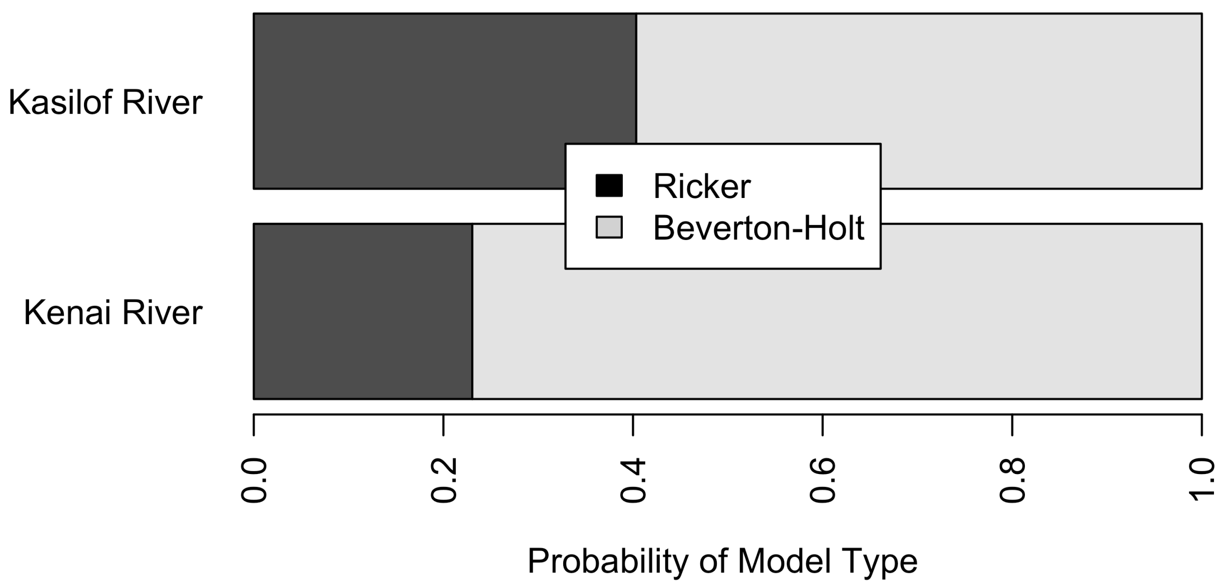

Figure 4. Probability of the Ricker or Beverton-Holt model representing stock-recruitment relationships for each sockeye salmon stock, from the mixture Ricker model. Each bar describes the proportion of time the model spent sampling as Ricker or Beverton-Holt, as defined by the proportion of posterior samples in which the state was $\delta = 1$ or $\delta = 0$, respectively.

Results from the Deriso-Schnute model with respect to overcompensation are more mixed. For the Kenai River stock the posterior distribution for the shape parameter indicates substantially higher probability for a value of -1, indicating more evidence for a Beverton-Holt type relationship (Figure 5). Given that a Beverton-Holt function does not provide for overcompensation, this indicates limited evidence for the overcompensation hypothesis with respect to the Kenai River late-run sockeye salmon stock. Conversely, when the Deriso-Schnute model was fit to stock-recruitment data from the Kasilof River the posterior distribution for the shape parameter was more uniform with a marginally higher probability for a value of -1 (Figure 5). This results suggests nearly equal evidence for Ricker and Beverton-Holt relationships representing the data for this stock. However, this result does not indicate overcompensation is present, merely that we cannot reject the overcompensation hypothesis for the Kasilof River stock under this model.

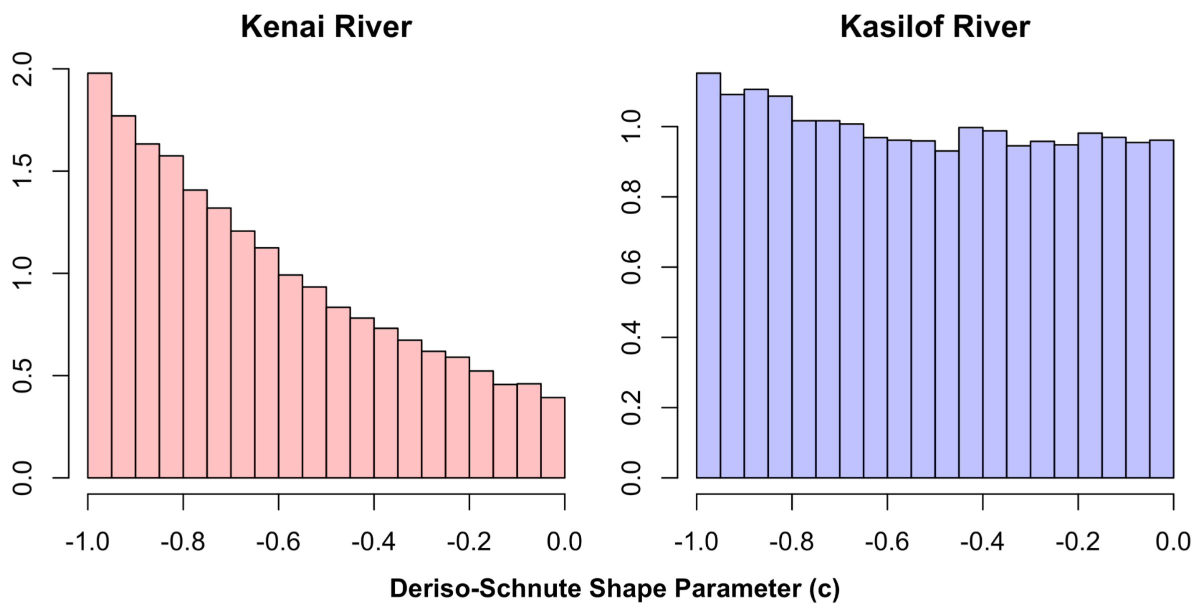

Figure 5. Evidence for a Ricker or Beverton-Holt like model better representing the data for each stock based on the Deriso-Schnute model. The Deriso-Schnute shape parameter controls whether the underlying relationship is more consistent with one of the two model types. A shape parameter value of -1 is similar to Beverton-Holt, while a shape parameter value of 0 indicates a Ricker-like form where overcompensation is possible. Histograms are the marginal posterior distributions for the shape parameters estimated for each stock.

Specific Results

In the following section model-specific parameter estimates and projections for potential yield as a function of spawning abundance are presented. Potential yield was simulated based on the posterior distribution for model parameters, which after appropriate log-normal correction represent the expected potential yield and estimation uncertainty in potential yield.

Model parameter estimates were consistent with those identified by Erickson et al. (2017) where specific model comparison was possible. With respect to simulation results, the spawning abundances expected to produce maximum potential yield and estimated maximum potential yield generally agreed with findings in the most recent ADF&G escapement goal review for Upper Cook Inlet sockeye (Erickson et al. 2017).

In the case of the Kenai River late-run sockeye stock, estimates of the spawning abundance expected to produce maximum sustainable yield (Smsy) ranged from 1.03 – 1.78 million sockeye, with maximum potential yield (MSY) ranging from 2.97-3.55 million sockeye across candidate models. Data for the Kenai River stock showed a marginal preference based on WAIC for the brood year interaction model parameterized with the statistical interaction term. The estimate of the spawning abundance (escapement) producing maximum potential yield from this model was 1.03 million sockeye, with a potential yield of 3.14 million sockeye. However, it should be noted that the small difference in WAIC values ($\Delta WAIC < 3.31$) across candidate models fit to the Kenai River data indicates relatively equal support for these alternatives.

For the Kasilof River sockeye stock the autocorrelated Ricker was the WAIC-preferred model, and predicted maximum potential yield could be obtained by an escapement of 235,000 sockeye and is expected to produce a potential yield of 629,000 sockeye.

Considerations Regarding Kenai River late-run Sockeye Salmon

Although the brood year interaction model that approximates delayed density-dependent compensation with a statistical interaction term exhibited the lowest WAIC value for the Kenai River stock, there are several important considerations in developing management reference points based on this model. First, despite this model exhibiting the lowest WAIC value, the difference in WAIC among all candidate models is quite small with a maximum difference of only 3.31 units. The relatively small differences in WAIC among candidate models suggest there is at best marginal evidence for the superiority of the brood year interaction model with the statistical interaction term in representing this stock-recruitment relationship, and inference from other candidate models should not be ignored.

Second, there is empirical evidence for delayed density-dependent effects on the growth (Ruggerone and Rogers 2003) and survival (i.e. intense grazing of *Cyclops* copepods in years of high fry abundance in one year reducing the biomass of available copepod biomass the following spring for emergent fry leading to reduced survival, see Edmundson et al. 2003) of Kenai River sockeye. However, it is unclear why this hypothesis would be better represented by a model including the statistical interaction $R_s = S_t exp(\alpha + \gamma S_t S_{t-1} + \varepsilon_t)$ term proposed by Carlson et al. (1999), as opposed to a model describing delayed density dependence as main effects $R_s = S_t exp(\alpha - \beta_1 S_t - \beta_2 S_{t-1} + \varepsilon_t)$. It should be noted that representing delayed density dependence with the main effects version of the brood year interaction model is generally more common within the literature (Eggers and Rogers 1987, Walters and Staley 1987, Welch and Noakes 1990). Finally, it is somewhat unclear whether the interpretation of the statistical interaction term aligns with the hypotheses proposed to describe delayed density-dependent effects on the productivity of the Kenai River stock.

To further explore the actual form and implications of this statistical interaction, a generalized additive model (GAM) of the form $ln\left({R_t}/{S_t}\right) \sim \alpha + f(S_t, S_{t-1})$ was fit to Kenai River sockeye stock-recruitment data 1969-2012, where $f(S_t, S_{t-1})$ is a smoothed (thin plate regression spline) approximation of the statistical interaction term (Figure 6). This smoothed approximation of the interaction suggests: 1) high spawning abundances in current and prior brood years is associated with low productivity (log recruits-per-spawner), 2) maximum productivity appears to be associated with low spawning abundance in the brood year and spawning abundances near 1 million in the prior brood year, and 3) spawning abundances either above or below this level in the prior brood year are associated with reduced population productivity.

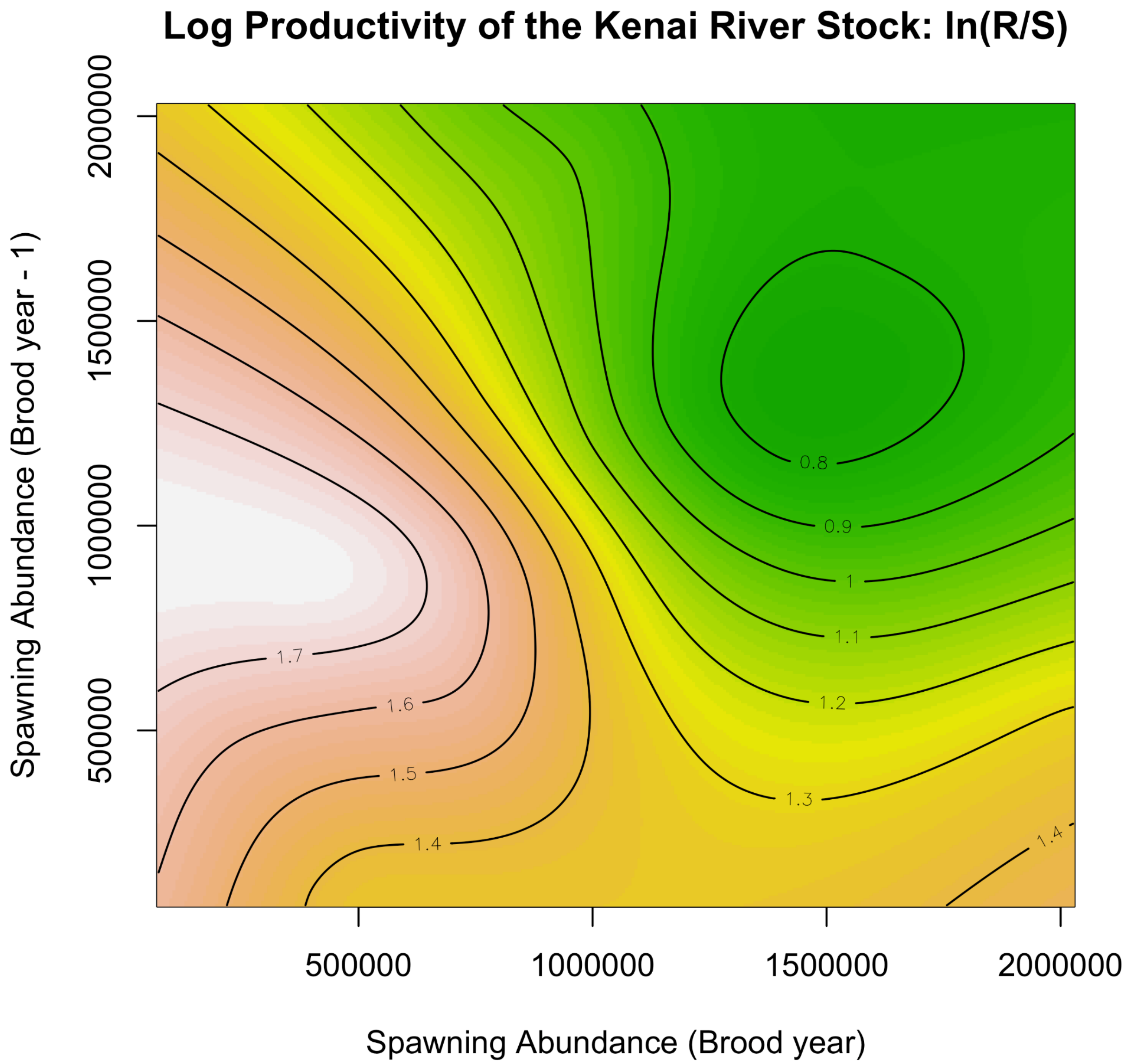

Figure 6. Smoothed approximation of the statistical interaction term representing delayed density dependence. Smoothed approximation estimated as the interaction of thin plate splines in a generalized additive model.

Standard Ricker

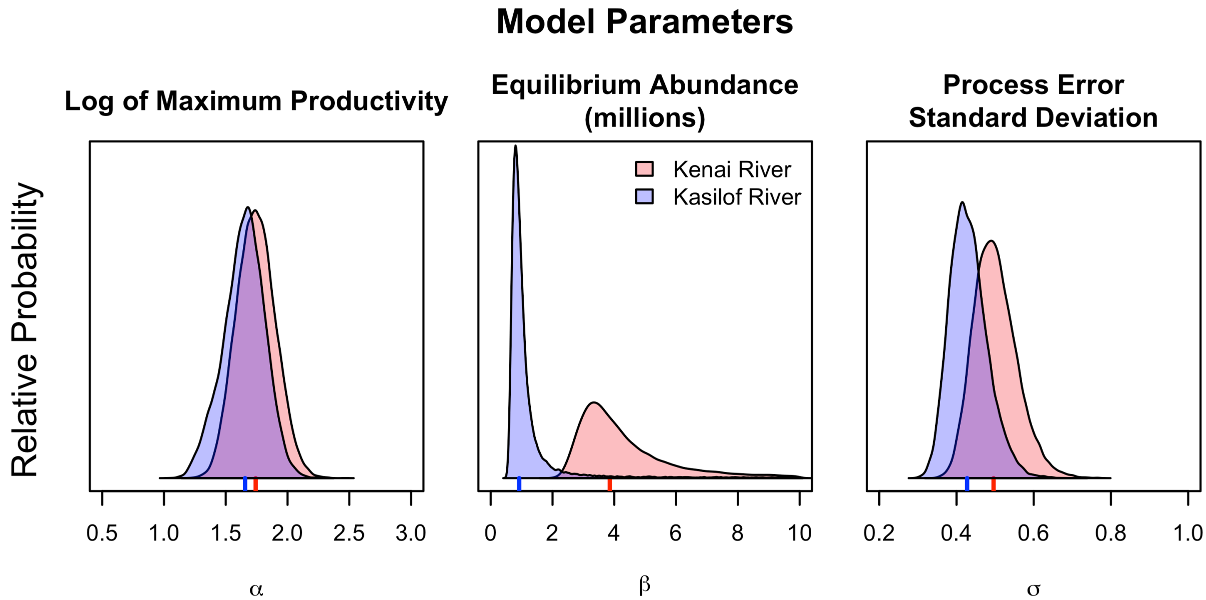

Figure 7. Posterior distributions for Ricker model parameters. The highest point on each distribution indicates the parameter value with the highest posterior probability density given the data. Vertical colored lines on the x-axis highlight the posterior median parameter value for each population.

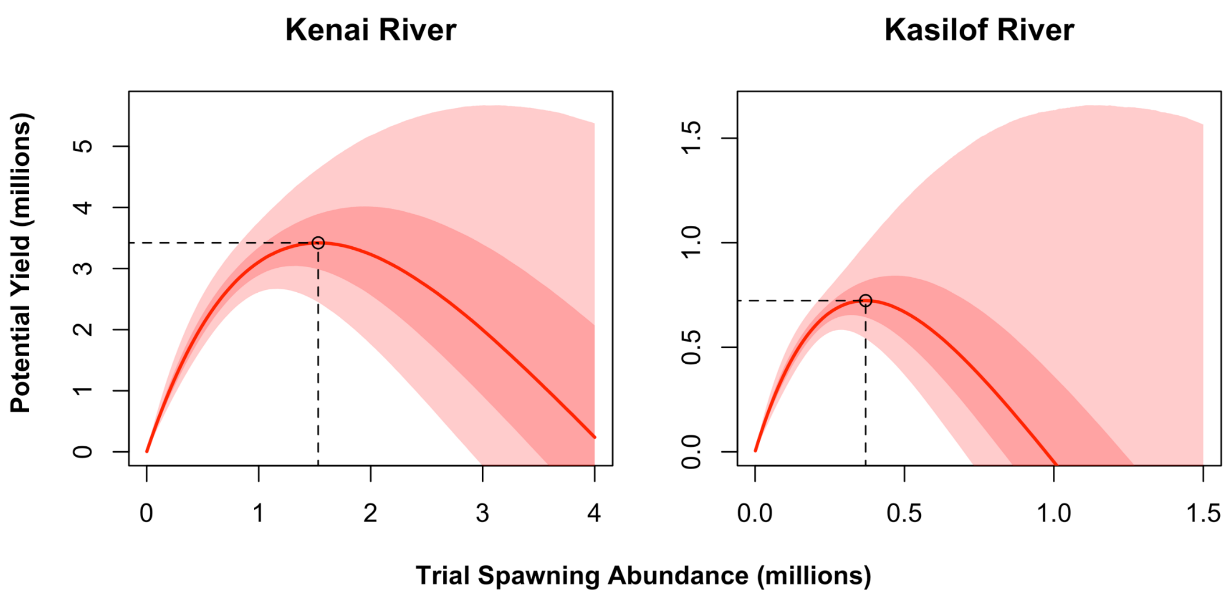

Figure 8. Simulated potential yield for the standard Ricker model across a range of trial spawning abundances. The red line indicates the median expectation, while the dark and light shaded regions indicate the 50% and 95% credible intervals for predictions. Dashed lines describe predicted Smsy and MSY for each stock.

Brood Year Interaction Ricker (main effects)

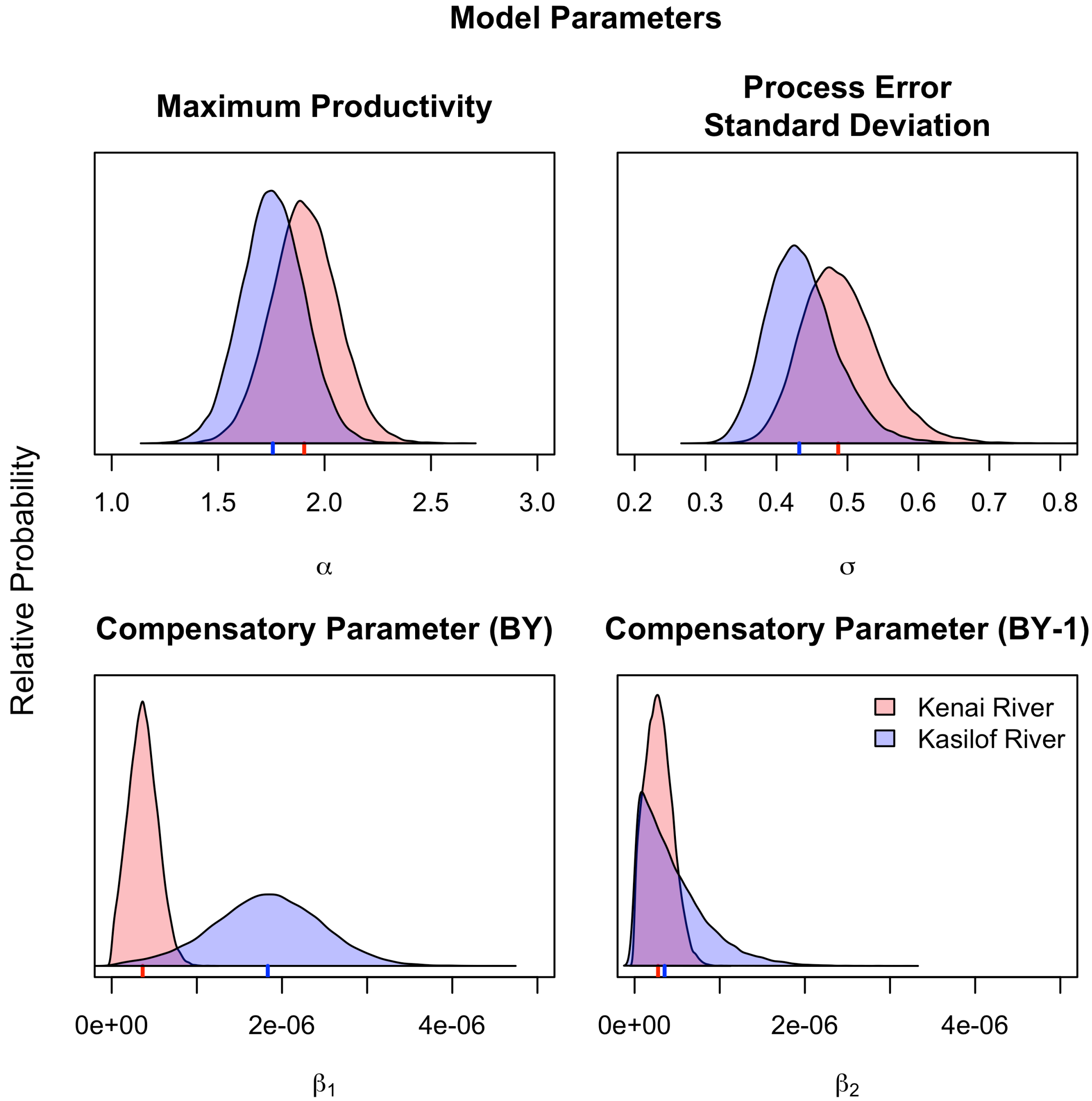

Figure 9. Posterior distributions for brood year interaction Ricker (main effects version) model parameters. The highest point on each distribution indicates the parameter value with the highest posterior probability density given the data. Vertical colored lines on the x-axis highlight the posterior median parameter value for each population.

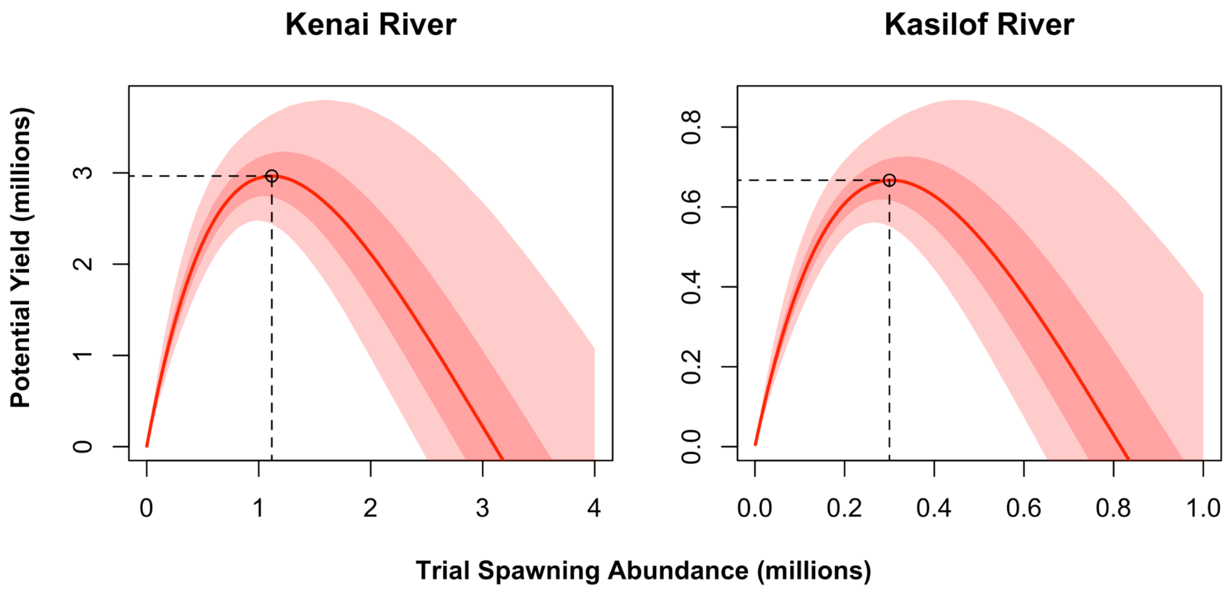

Figure 10. Simulated potential yield for the brood year interaction Ricker (main effects version) model across a range of trial spawning abundances. The red line indicates the median expectation, while the dark and light shaded regions indicate the 50% and 95% credible intervals for predictions. Dashed lines describe predicted Smsy and MSY for each stock.

Brood Year Interaction Ricker (interaction term)

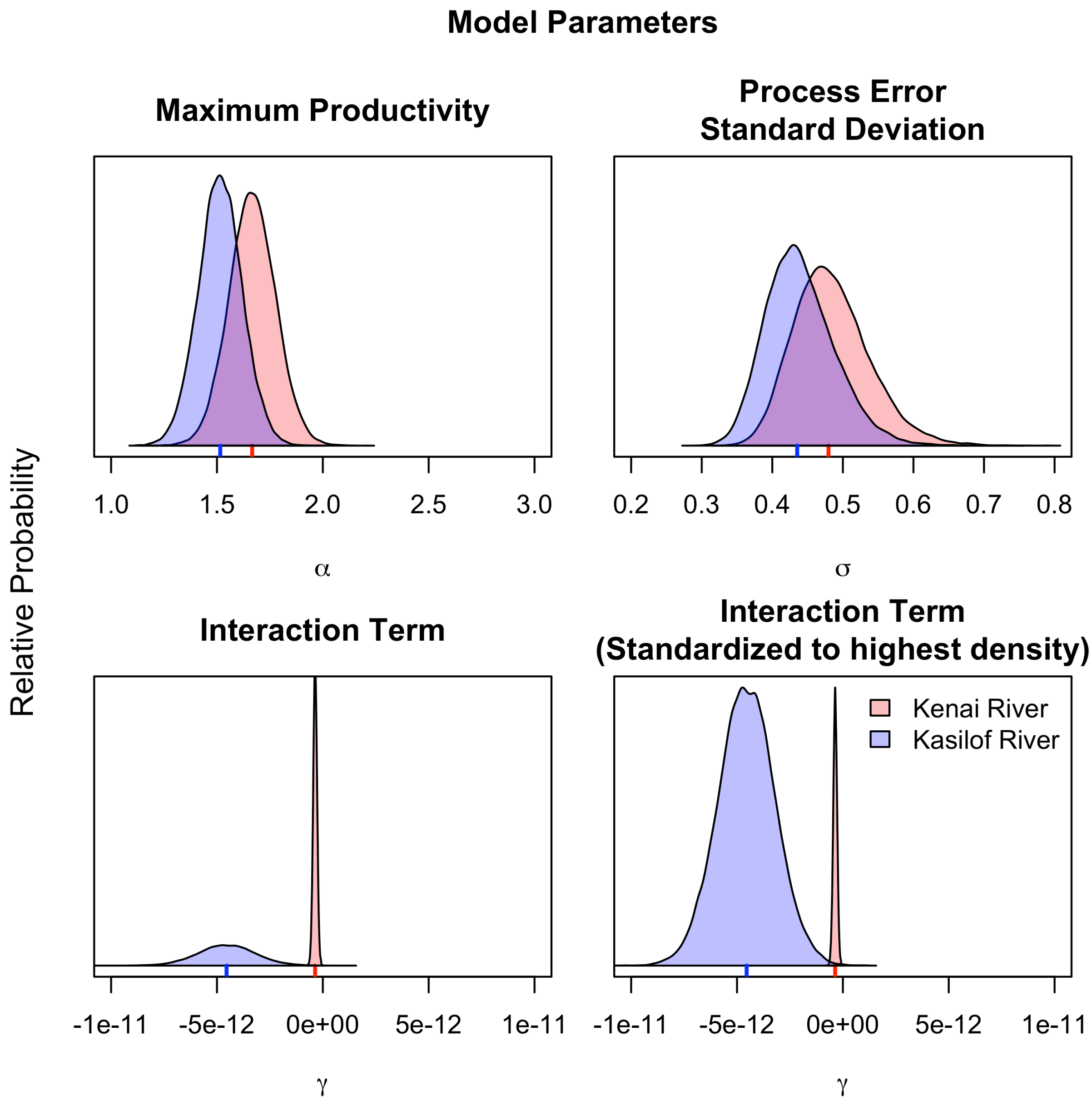

Figure 11. Posterior distributions for brood year interaction Ricker (interaction term version) model parameters. The highest point on each distribution indicates the parameter value with the highest posterior probability density given the data. Vertical colored lines on the x-axis highlight the posterior median parameter value for each population. Note: bottom panels display the same information for γ, but probability distributions in the bottom-right panel have been standardized relative to the highest probability density for easier comparison.

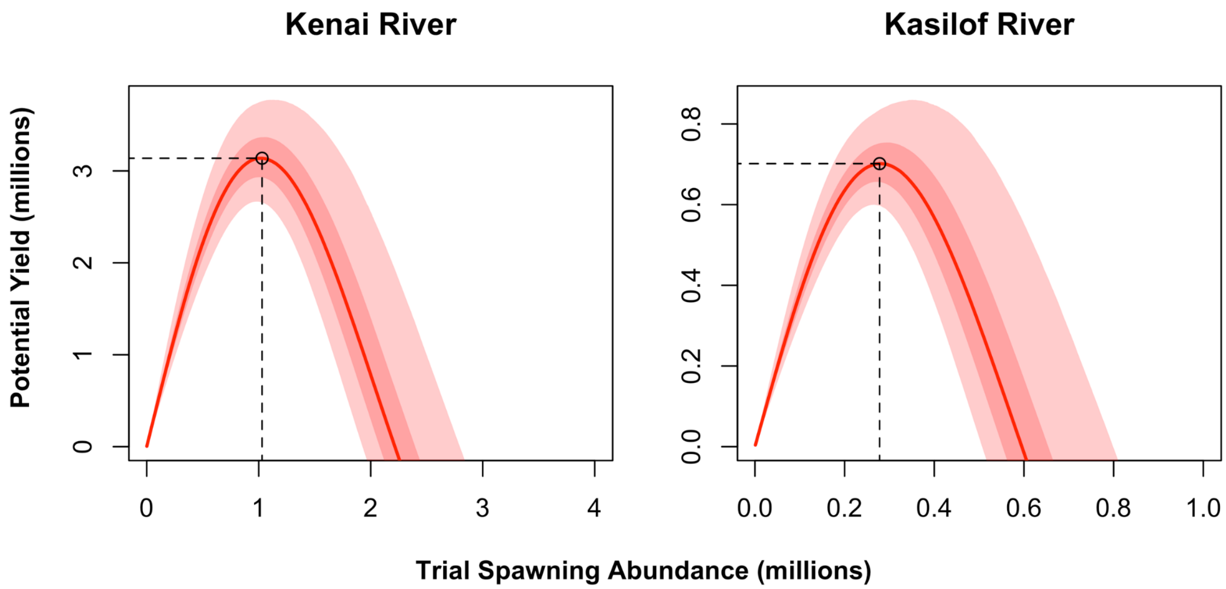

Figure 12. Simulated potential yield for the brood year interaction Ricker (interaction term version) model across a range of trial spawning abundances. The red line indicates the median expectation, while the dark and light shaded regions indicate the 50% and 95% credible intervals for predictions. Dashed lines describe predicted Smsy and MSY for each stock.

Autoregressive Ricker

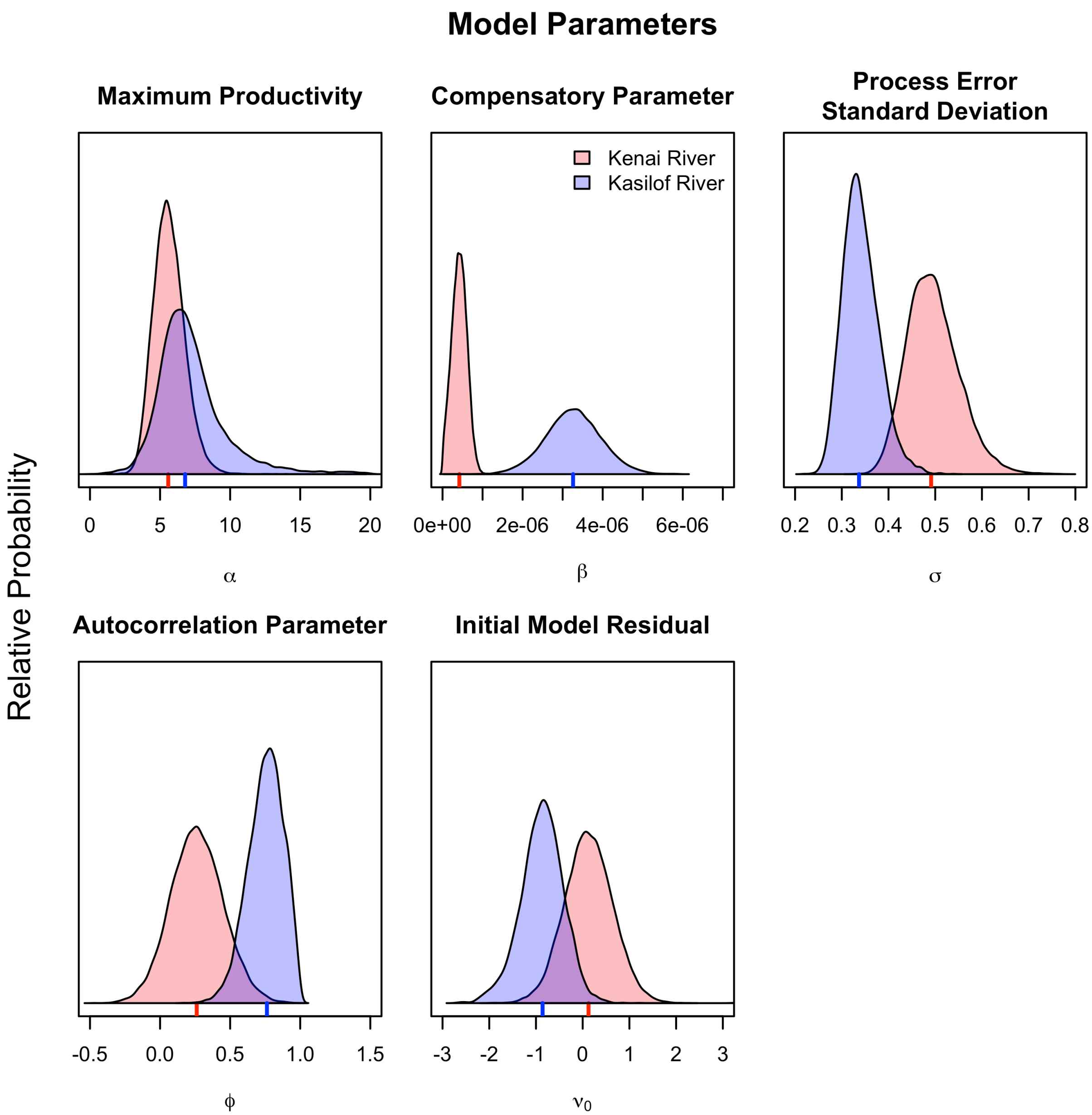

Figure 13. Posterior distributions for autoregressive Ricker model parameters. The highest point on each distribution indicates the parameter value with the highest posterior probability density given the data. Vertical colored lines on the x-axis highlight the posterior median parameter value for each population.

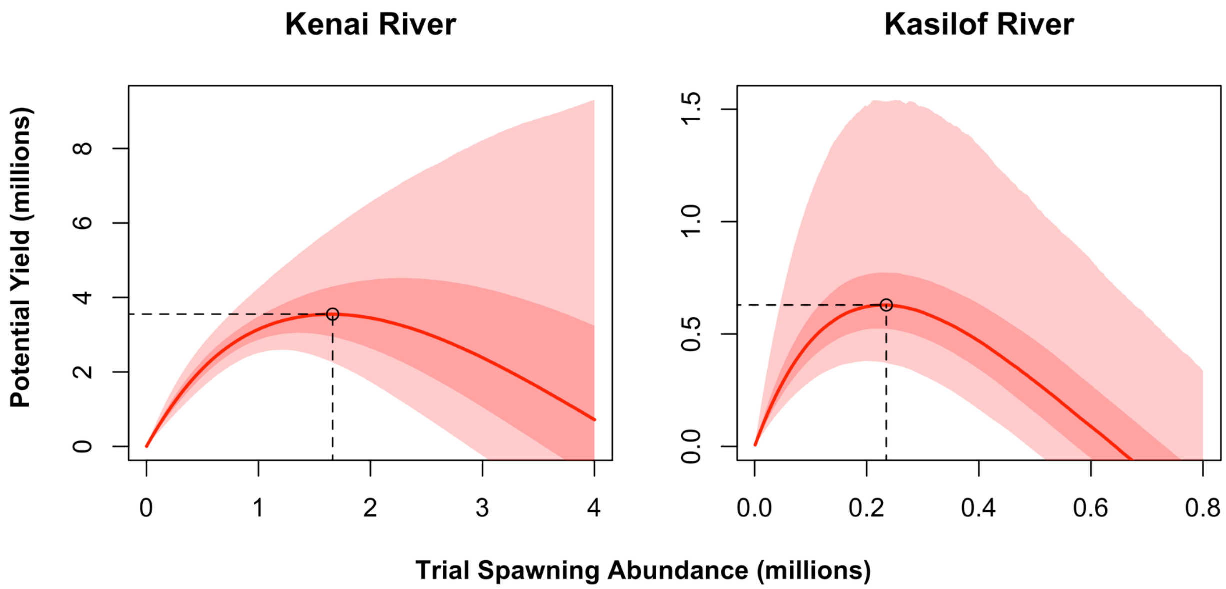

Figure 14. Simulated potential yield for the autoregressive Ricker model across a range of trial spawning abundances. The red line indicates the median expectation, while the dark and light shaded regions indicate the 50% and 95% credible intervals for predictions. Dashed lines describe predicted Smsy and MSY for each stock.

Ricker Beverton-Holt Mixture

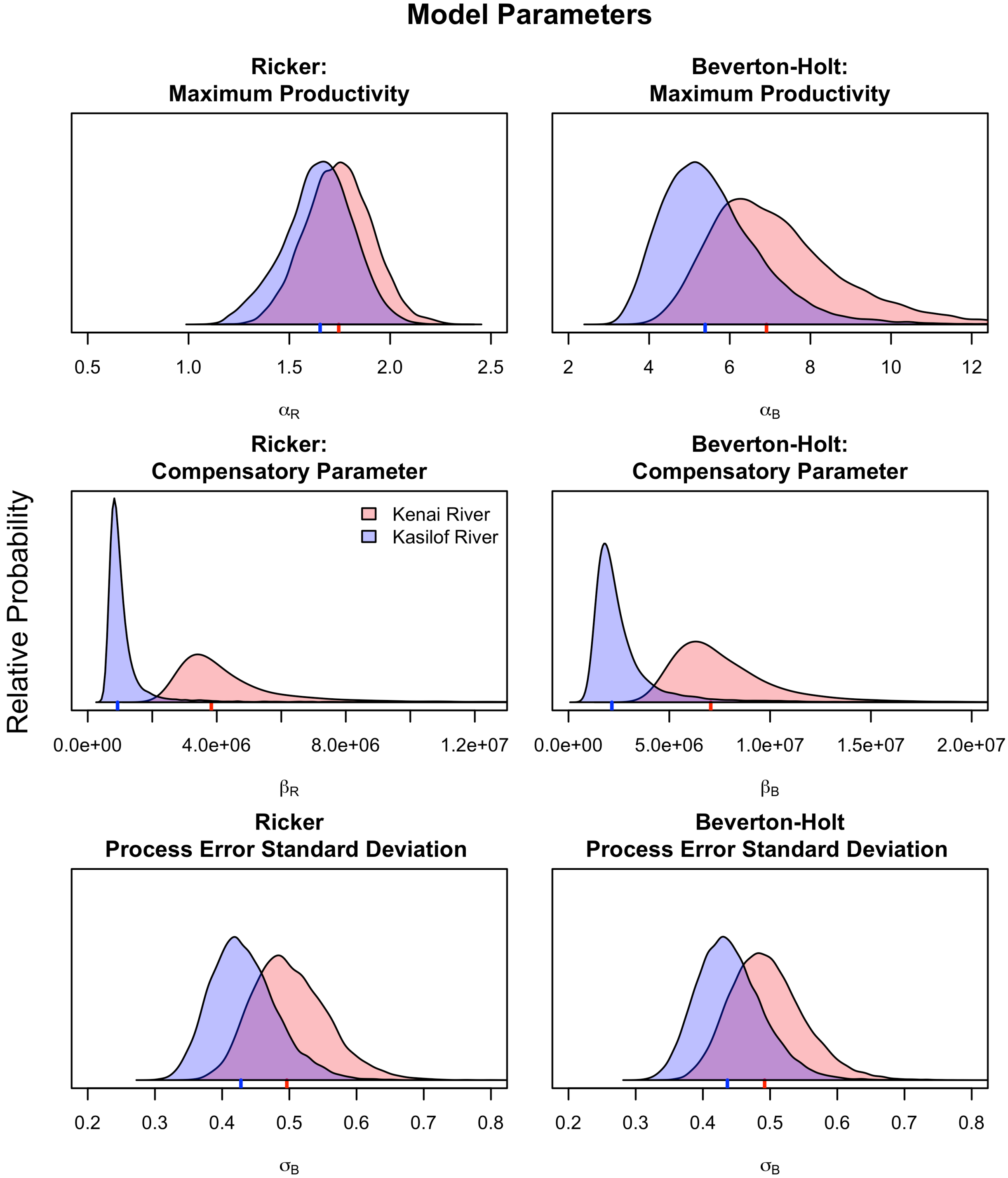

Figure 15. Posterior distributions for Ricker Beverton-Holt mixture model parameters. The highest point on each distribution indicates the parameter value with the highest posterior probability density given the data. Vertical colored lines on the x-axis highlight the posterior median parameter value for each population.

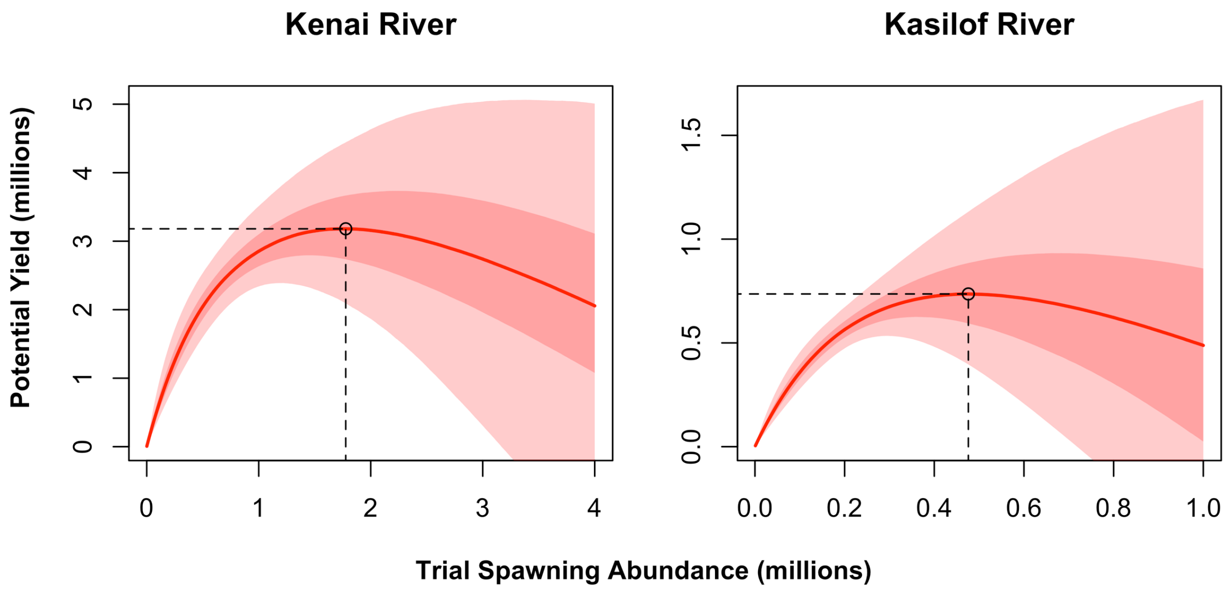

Figure 16. Simulated potential yield for the Ricker Beverton-Holt mixture model across a range of trial spawning abundances. The red line indicates the median expectation, while the dark and light shaded regions indicate the 50% and 95% credible intervals for predictions. Dashed lines describe predicted Smsy and MSY for each stock.

Deriso-Schnute

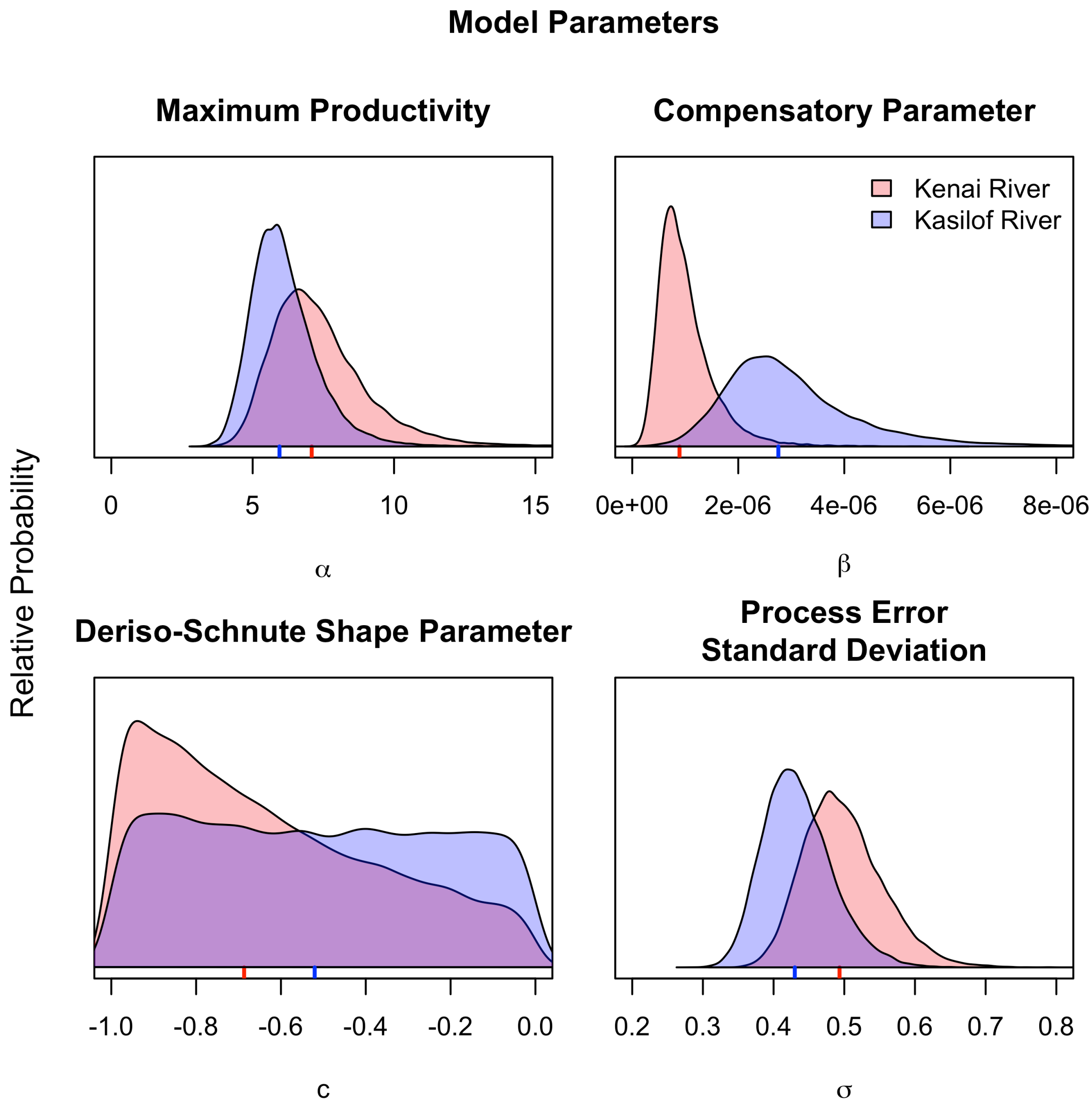

Figure 17. Posterior distributions for Deriso-Schnute model parameters. The highest point on each distribution indicates the parameter value with the highest posterior probability density given the data. Vertical colored lines on the x-axis highlight the posterior median parameter value for each population.

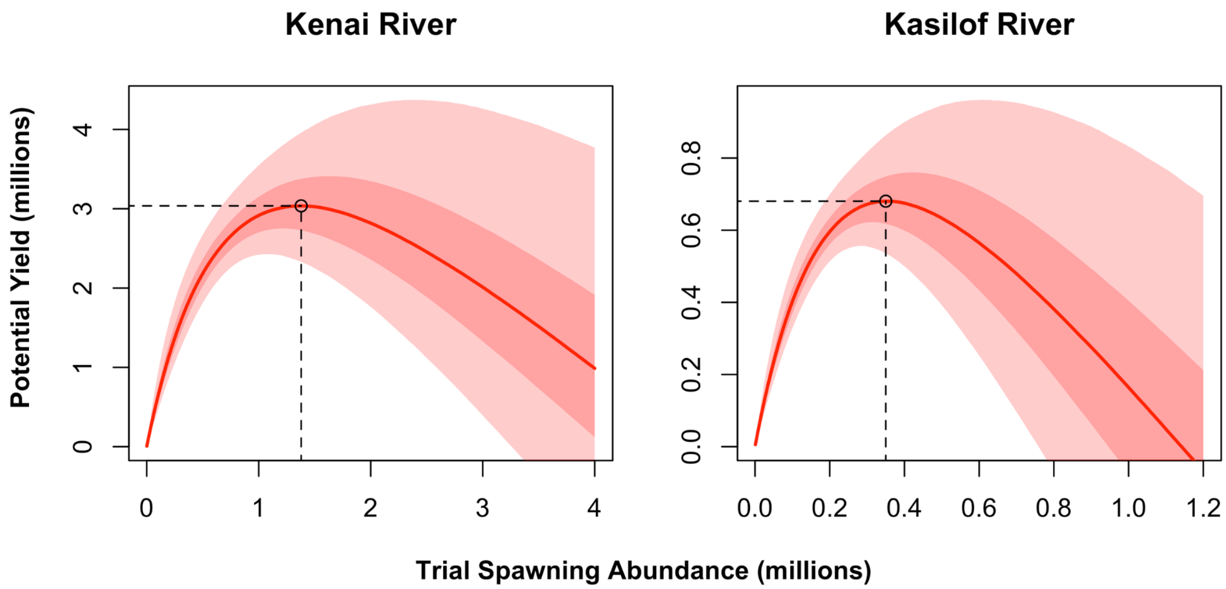

Figure 18. Simulated potential yield for the Deriso-Schnute model across a range of trial spawning abundances. The red line indicates the median expectation, while the dark and light shaded regions indicate the 50% and 95% credible intervals for predictions. Dashed lines describe predicted Smsy and MSY for each stock.

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