Estimating cross-population variation in juvenile compensation in survival for bull trout (*Salvelinus confluentus*): a Bayesian hierarchical approach

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Abstract: Juvenile compensation in survival, quantified as compensation ratio (CR), is critical for fish population persistence. At present, no estimate of this key parameter exists for bull trout (*Salvelinus confluentus*). This species has a conservation listing and is targeted by recreational angling in portions of its range. Obtaining accurate estimates of CR is crucial to aid recovery efforts and develop sustainable fisheries policies. This investigation develops a hierarchical Bayesian meta-analysis to estimate CR and explore the functional form of stock–recruitment for bull trout. Results show bull trout have high scope for density-dependent compensation evidenced by CR estimates generated herein and by previous research. This demonstrates changes in habitat quality and quantity are likely limiting recovery of many populations. However, owing to lack of data, variance is high. Limitations in available data for this analysis are due to the high cost and operational difficulty of sampling, and high uncertainty in CR estimates. This study highlights the importance of collecting additional paired stock–recruitment data to facilitate future investigations and reduce variance in CR estimates for bull trout.

Résumé : La compensation par les juvéniles, exprimée quantitativement par le rapport de compensation (CR), est indispensable pour assurer la persistance des populations. À l'heure actuelle, aucune estimation de ce paramètre clé n'existe pour l'omble à tête plate (*Salvelinus confluentus*). Cette espèce figure sur les listes d'espèces dont la conservation est préoccupante et est la cible de pêches sportives dans différentes parties de son aire de répartition. L'obtention d'estimations exactes du CR est cruciale pour soutenir les efforts de rétablissement et établir des politiques de pêche durable. L'étude présente une méta-analyse bayésienne hiérarchique utilisée pour estimer le CR et explorer la forme fonctionnelle du recrutement au stock pour les ombles à tête plate. Les résultats montrent que ces derniers présentent un fort potentiel de compensation dépendant de la densité illustré par les valeurs de CR estimées dans le cadre de la présente étude et par des travaux antérieurs. Cela démontre que des changements à la qualité et la quantité des habitats sont susceptibles de limiter le rétablissement de nombreuses populations. Cependant, en raison du manque de données, la variance est forte. Les limites associées aux données disponibles pour cette analyse découlent du coût élevé et de la difficulté de l'échantillonnage, et de la grande incertitude associée aux estimations du CR. L'étude souligne l'importance de recueillir d'autres données jumelées de recrutement au stock pour faciliter les études futures et réduire la variance des estimations du CR pour l'omble à tête plate. [Traduit par la Rédaction]

Introduction

Bull trout (*Salvelinus confluentus*) are endemic to the northwest United States and western Canada and hold designated conservation status across their native range (Post and Johnston 2002; COSEWIC 2013; USFWS 2017). The species expresses four life history types: fluvial, adfluvial, resident, and anadromy. Fluvial and adfluvial forms spawn in tributaries and reside in mainstem rivers (fluvial) or lakes and reservoirs (adfluvial), while stream-resident populations remain within their natal tributary for their entire life (Post and Johnston 2002). The anadromous life history is far less common. Fish expressing this life history spawn in tributaries and spend the remainder of their life cycle within the ocean (Rieman and McIntyre 1993). Life history characteristics (e.g., maturity and growth) vary substantially between bull trout life histories and within life histories across different populations (Rieman and McIntyre 1993; Post and Johnston 2002).

The status of individual populations in different regions varies dramatically. Bull trout were extirpated from much of the southern and eastern portions of their historic range (Rieman and

McIntyre 1993), while populations across the majority of bull trout's current distribution have undergone large-scale reductions in abundance (Haas and McPhail 1991; Post and Johnston 2002; Hagen and Decker 2011). However, within British Columbia, Canada, the story is not the same, with the region considered by some to be the "last stronghold of bull trout on Earth" (Hagen and Decker 2011). The species conservation listing in British Columbia was seen at the time as a precautionary measure, and a more recent systematic assessment of bull trout across the province showed the majority of populations for which data are available to have stable or increasing abundance over the past three decades (MOE 1994; Hagen and Decker 2011). Furthermore, sustainable harvest continues in several adfluvial bull trout populations in the province (Hagen and Decker 2011; FLNRO 2017).

Observed declines in bull trout abundance and distribution are believed to have resulted from habitat degradation and fragmentation, non-native species introductions, and warming water temperatures, combined with highly specific habitat requirements for successful spawning and rearing (Rieman and McIntyre 1993; Post and Johnston 2002). Bull trout are also thought to be highly

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susceptible to overharvest due to a combination of large body size, late maturity, aggressive feeding, and aggregative behaviour (Paul et al. 2000; Post and Johnston 2002; Rees et al. 2012). Bull trout's high susceptibility to anthropogenic impacts and fishing pressure has made it a management priority across jurisdictions to develop and deliver management to protect and recover at-risk bull trout populations and preserve healthy populations (COSEWIC 2013; US Fish and Wildlife Service 2015).

The provision of such management objectives requires estimates of a key population parameter: the Goodyear compensation ratio (CR; Goodyear 1977), comparable to steepness (Martell et al. 2008). This parameter represents the maximum relative increase in juvenile survival rate when a stock's size decreases towards zero (Goodyear 1977; Walters and Martell 2004). Density-dependent compensation in juvenile survival can enable fish populations to persist when stock size is reduced to low abundances (Goodyear 1977; Walters and Martell 2004). Despite observed reductions in population size and geographic range, bull trout appear to have capacity for strong density-dependent compensation in juvenile survival as evidenced by rapid recovery of some populations (Johnston et al. 2007; Erhardt and Scarnecchia 2014). As such, an accurate estimate of bull trout's capacity for density-dependent compensation is an important component in estimating both recovery rates for endangered populations and sustainable harvest rates for fished populations. Despite its importance, density-dependent recruitment compensation potential for bull trout is poorly understood, and the relationship has not been quantitatively explored across the species range.

Estimates of CR are obtained through analysis of stock–recruitment data. Such analyses have high data needs and are only possible when reliable measures of both spawning stock size and resulting recruitment exist (Hilborn and Walters 1992). In addition, analysis of stock–recruitment data are strongly limited by two types of error known as "errors in variables" and "time-series bias", which can introduce large bias into resulting parameter estimates (e.g., alpha — slope at the origin — and thus CR), which can mask trends in data (Hilborn and Walters 1992). Bias introduced by both error types can only be limited if collected data has high contrast in spawning stock size. That is, when data sets contain observations of spawner abundance over a broad range of spawning stock size, including estimates near carrying capacity and at very low abundances (Hilborn and Walters 1992). Collecting such data are highly challenging. As a result, the prevalence of uninformative data, in combination with structural and observational uncertainties, continue to present major challenges within the estimation of key fisheries statistics surrounding population productivity and persistence, including the estimation of CR (Walters and Martell 2004).

One approach to limiting the impacts of bias and improving parameter estimates in stock–recruitment analyses is the use of meta-analytic approaches (Gelman et al. 2014). Such analyses can improve estimates of stock–recruitment data through their ability to pool multiple data sets with various ranges of spawning stock abundance within a single model (Gelman et al. 2014). Bayesian hierarchical approaches are typically utilized to conduct meta-analyses of stock–recruitment and have been shown to improve estimation of stock–recruitment parameters in data-limited situations, demonstrating the approach's feasibility when investigating populations of species such as bull trout, where limited stock–recruitment data are available (Liermann and Hilborn 1997; Myers et al. 1999; Forrest et al. 2010). Use of a Bayesian approach also facilitates characterization of uncertainty in model structure and key parameters and permits estimation of posterior predictive distributions, which provide predictions of key parameters (e.g., CR) for unsampled populations (Gelman et al. 2014).

In this study, we attempt to estimate stock–recruitment parameters for bull trout using a Bayesian hierarchical meta-analysis, with focus on characterizing cross-population variability in bull trout's CR (Goodyear 1977; Walters and Martell 2004). This research provides the first attempt to characterize the scope for compensation in bull trout. Though paired data on spawning stock size and resulting recruitment exist for several isolated populations of bull trout of varied life history, data quantity is limited for most populations, suggesting a robust statistical treatment is necessary. This species-level prediction of CR for bull trout is invaluable, as many regions do not collect data on both spawner and juvenile densities. As such, any preliminary information on CR, which describes the scope for improvements in juvenile survival at small population size, will benefit regional-level management and conservation efforts.

Methods

Data

Spawner and juvenile abundance estimates were compiled from regional management reports, peer-reviewed literature, and personal communication with experts for 41 populations of fluvial and adfluvial bull trout. Of the data acquired, 27 populations were excluded from this analysis due to short time series duration (<5 years), incomplete information for either spawner or recruitment estimates, or when substantial changes in productivity or carrying capacity occurred in the system (e.g., strong anthropogenic or natural perturbations and (or) enhancement activities). Available data was largely limited to adfluvial fish and streams within British Columbia, Canada. A total of 14 populations were included in this investigation with a median length of time-series data of 7 years. Data were available for three fluvial populations, with the remaining 11 data sets coming from adfluvial populations. A description of each data set utilized in this analysis is provided in Table 1.

Estimates of the total number of eggs produced by each population in each year were taken to represent the index of spawning stock abundance used within the hierarchical meta-analysis. The majority of spawner data obtained for this study came in the form of redd counts. These data were converted to total number of eggs produced by each population using the following procedure. First, a hierarchical meta-analysis of length-at-age information for each of the 14 populations was conducted to generate estimates for the parameters (L_∞, K, and t_0) of the von Bertalanffy growth function. Model code for this analysis is provided in the online supplementary information[1], while a list of all model parameters and their description for both the stock–recruitment and length-at-age analyses are given in Table 2. Age-specific incidence functions for length-at-age, maturity-at-age, and fecundity-at-age were then calculated (Table 3). The resulting fecundity estimate for age 7 fish in each population was then multiplied by the redd count data to generate the estimated number of eggs produced by each population per year, which were then used as the spawner index data within our system.

For the purpose of this investigation, a recruit was defined as an age 1+ fish. Estimates of recruit abundance for each population (excluding the Metolis Basin, Kaslo River, and Keen Creek) came in the form of electrofishing depletion estimates. Recruit abundance estimates from Metolius Basin were measured from smolt trap counts, while those from the Kaslo River and Keen Creek were measured from snorkel surveys. Estimates from electrofishing depletion in subsections of each stream for each population were expanded by best estimates of available stream habitat to come to

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Table 1. Description of bull trout stock–recruit and length-at-age data sets utilized in analysis.

System	Province or state	Life history	Data range	Data series length (years)	Sample size (no. of fish)	Data range (years)	Source*
Eunice Creek	Alberta	Fluvial	1971, 1973–1978, 1982, 1983	9	NA	NA	1
Attichika Creek	British Columbia	Adfluvial	2001–2007	7	34	1	2
South Pass	British Columbia	Adfluvial	2001–2007	7			2
Tributary 4 Mainstem	British Columbia	Adfluvial	2001–2007	7			2
Tributary 4 Fishway	British Columbia	Adfluvial	2002–2007, 2009–2014	12			2
Tributary 4 Icefalls	British Columbia	Adfluvial	2003, 2007, 2009, 2010, 2012–2015	8			2
Tributary 12	British Columbia	Adfluvial	2001–2007	7			2
Tributary 16	British Columbia	Adfluvial	2001–2007	7			2
Smith-Dorrien Creek	Alberta	Adfluvial	1993–2000	8	9684	13	1
Line Creek	British Columbia	Fluvial	1991–1999	9	63	4	3
Kaslo River	British Columbia	Adfluvial	2008–2013	6	2591	16	3
Keen Creek	British Columbia	Adfluvial	2008–2013	6			3
Lynx Creek	Alberta	Fluvial	1995–2001	7	51	5	3
Metolius Basin	Oregon	Adfluvial	1999–2013	15	NA	4	2

Note: Length-at-age data are provided as length–age key. Source for all length-at-age information comes from personal communication with authors of stock–recruitment reports and publications.

*Sources: 1, journal; 2, research document; 3, personal communication.

Table 2. Notation of parameter and indices for estimation models used within each population.

Index or parameter	Value	Description
Indices		
t	$(1, 2, \ldots, T)$	Time (in years)
a	$(1, 2, \ldots, A)$	Age (in years)
A	17	Maximum age (in years)
i	$(i, \ldots, I)$	Population index
Model parameters		
CR	++	Goodyear compensation ratio
α	++	Slope of the stock–recruit function at the origin
β	++	Scaling parameter of the stock–recruit function
R_0	++	Unfished recruitment potential
φ_E	++	Fecundity incidence function: mean eggs produced at age
$\mathbf{lx}_a$	++	Survivorship-at-age
M	++	Instantaneous natural mortality rate (year^{-1})
$\mathbf{f}_a$	++	Fecundity-at-age (eggs)
s	$1.72e^{-3}$	Scaler parameter of length–egg relationship
δ	2.31	Exponent parameter of length–egg relationship
$\mathbf{L}_a$	++	Length-at-age
L_∞	++	Asymptotic length at which growth equals zero
k	++	von Bertalanffy metabolic coefficient
t_0	++	Hypothetical age when length is zero
$\mathbf{m}_a$	++	Maturity-at-age
Υ	++	Slope of length–maturity schedule
L_{50}	++	Length at 50 percent maturity as a proportion of L_∞
cv	++	Coefficient of variation in length-at-age
τ_t	16.00	Precision of time varying process error for the Ricker and Beverton–Holt stock–recruitment functions
$\tau_{recruits}$	++	Precision of observation error for recruitment
Ω	++	Time-varying process error

Note: The symbol ++ indicates parameters that are estimated.

a total recruitment estimate for each year for each population. Estimates of juvenile abundance from the smolt trap were converted to estimates of age 1+ abundance by the following procedure. A length–age key for the population was first used to assign an age to all fish captured in the smolt trap. Survival rate of these juvenile fish (age 1+ to age 3+) was then calculated by taking the average survival for age 1+ and age 2+ fish as estimated by Bowerman and Budy (2012). We then back-calculated the number of age 1+ recruits based on both estimated age and survival rates. All data sets of recruit abundance were then back-shifted through time by 2 calendar years to assign each cohort of recruits to the correct spawner abundances (to account for egg incubation prior to hatching; Johnston et al. 2007).

Model structure

A hierarchical Bayesian meta-analysis was used to estimate the magnitude of recruitment compensation (CR) exhibited by bull trout as a species and its variation among populations. As the functional form of the stock–recruitment relationship that best represents bull trout is not known, estimates of CR were calculated under the assumption of either the Ricker or Beverton–Holt stock–recruitment functions (Ricker 1954; Beverton and Holt 1957). This permitted exploration of variation in CR between the two models and a preliminary investigation of the functional form of the stock–recruitment relationship for the species.

Analysis of stock–recruitment data served to jointly estimate unfished growth, survivorship, maturity, and fecundity incidence

Table 3. Calculations of age-specific incidence functions used in model.

Parameter	Equation
Length-at-age (L_a)	$L_a = L_\infty\{1 - \mathrm{e}^{[-K(a-t_0)]}\}$
Survivorship-at-age (lx_a)	$lx_a = \begin{cases} 1 & a = 1 \\ lx_{a-1}\mathrm{e}^{-M} & 1 < a < A \\ \dfrac{lx_{A-1}}{1 - \mathrm{e}^{-M}} & a = A \end{cases}$
Maturity-at-age (m_a)	$m_a = \begin{cases} 0 & a \leq 3 \\ \dfrac{1}{1 + \mathrm{e}^{\left\{\frac{-[L_a - (L_{50} \cdot L_\infty)]}{\alpha}\right\}}} & a > 3 \end{cases}$
Fecundity-at-age (f_a)	$f_a = \begin{cases} 0 & a \leq 3 \\ \mathrm{stL}_a^\delta & a > 3 \end{cases}$

Table 4. Derivation of recruitment parameters of the Ricker and Beverton–Holt stock–recruit functions.

Stock–recruitment function	Parameter	Equation
Ricker	β	$\beta = \dfrac{\log(\alpha\varphi_E)}{R_0 \cdot \varphi_E}$
Beverton–Holt	β	$\beta = \dfrac{\alpha\varphi_E - 1}{R_0 \cdot \varphi_E}$
Ricker and Beverton–Holt	α	$\alpha = \dfrac{\mathrm{CR}}{\varphi_E}$
Ricker and Beverton–Holt	φ_E	$\varphi_E = \sum\limits_{a=1}^{A} lx_a m_a f_a$

functions, as well as the parameters of either the Ricker or Beverton–Holt models. Model code for this analysis can be found in the online supplementary information[1]. Both models were parameterized using unfished recruit potential (R_0) and the Goodyear CR using the incidence functions described in Table 3 (Botsford 1981*a*, 1981*b*). Calculated recruitment parameters were then used to predict recruitment in each system based on the observed spawner index in each year (given as total number of eggs) and model fits of each recruitment function to data for each of the 14 populations (Table 4). Equations for the Ricker (eq. 1) and Beverton–Holt recruitment (eq. 2) functions are given by

$$(1) \qquad R_{i,t} = \alpha E_{i,t}\mathrm{e}^{\beta_1 E_{i,t} + \Omega_t}$$

$$(2) \qquad R_{i,t} = \frac{\alpha E_{i,t}}{1 + \beta_2 E_{i,t}}\mathrm{e}^{\Omega_t}$$

Hierarchical hyperparameter and prior selection

Within the hierarchical model framework, parameters are assumed to come from probability distributions that are shared by all populations (the prior distribution; Parent et al. 2013). Hyperparameters can then be used to describe the distribution of each of these priors (Parent et al. 2013). In this framework, hyperparameters are assumed to represent all populations, and parameters for individual populations are jointly estimated. Within the model structure, the parameters of the von Bertalanffy growth equation (L_∞, K, and t_0) and Goodyear CR were assumed to be sampled from a common population distribution, conditional on hyperparameters. Hyperparameter and prior distributions used in this investigation are provided in Table 5.

The hierarchical meta-analysis of length-at-age data discussed in the Data section above also served to generate informative priors for the parameters of the von Bertalanffy growth function (L_∞, K, and t_0) for each population for use within the stock–recruitment model. This process was integral to our analysis, as generation of candidate stock–recruitment models was conditional on population-specific growth rates. Informative hyperparameters for the mean and precision of the prior probability distributions of CR were based on species-specific CR estimates provided in Myers et al. (1999). The hyperparameter for mean of CR was assumed normally distributed and based on the mean and precision of log-transformed species-level CRs reported in Myers et al. (1999) to provide a conservative estimate of CR. The hyperparameter for the precision of CR was transformed from an estimate of the standard deviation of CR. This standard deviation estimate was assumed to be lognormally distributed based on population-level CRs reported in Myers et al. (1999).

The parameter D_0 was assumed to be lognormally distributed, with mean and precision estimated from observed densities of recruits in various streams (with minimal fishing effort) reported

by in Decker and Hagen (2007). To account for low but unknown fishing effort, we expanded precision for this prior by 1.5 times what was presented in Decker and Hagen (2007). The prior for unfished abundance (R_0) was obtained by multiplying D_0 by estimates of accessible spawning habitat (stL; in kilometres) obtained for each system.

Choice of nonhierarchical priors and parameter values

Estimates of natural mortality rates (M) and length–maturity schedules (Υ) for bull trout have not yet been reported in the published literature. We generated a prior for M following both the methodology employed by Post et al. (2003), which used observations from the Lower Kananaskis Lake bull trout population (see Johnston et al. 2007), as well as estimates of M for a similar species, lake trout (*Salvelinus namaycush*). For this investigation, we calculated maturity as a logistic function with median L_{50} and slope Υ. Length of 50% maturity (L_{50}) was calculated as the product of asymptotic length (L_∞) and an estimated proportion of asymptotic length at 50% maturity (p_{50}), which was given as an informative beta prior with shape parameters of 500 and 1000. This prior was chosen to be consistent with age-at-maturity reported in Johnston et al. (2007). The prior for Υ was determined using a visual examination of Johnston et al. (2007). The beta distribution for p_{50} was chosen to constrain values of L_{50} to be positive. Finally, the scalar parameter of the length–egg relationship (Γ) and the exponent parameter of the length–age relationship (δ) were set as reported by Johnston (2005).

Time-varying process error (Ω) was assigned a normal distributed prior with mean of 0 and precision τ_t of 16. Observation error (τ_{recruits}) for the Ricker and Beverton–Holt models was assigned an uninformative gamma prior. Time-varying process error for the von Bertalanffy growth equation τ_{vbk} was assigned a beta distribution with shape parameters of 1.5 and 1.5.

Posterior calculation

Posterior density functions for parameters of interest were approximated using the Markov chain Monte Carlo (MCMC) algorithm implemented using JAGS software (Just Another Gibbs Sampler; available from http://mcmc-jags.sourceforge.net/) implemented through R utilizing the R2jags package (Yu-Sung and Yajima 2015; Plummer 2016; R Core Team 2016). Three chains were run for 100 000 iterations after a burn-in of 90 000, and the final posterior estimates were thinned by 10. Convergence was evaluated using the Gelman–Rubin diagnostic tool (Brooks and Gelman 1998) and visual inspection of trace plots of the Markov chains for each parameter.

Bayesian approach to model uncertainty

In this investigation, formal comparison of the stock–recruitment models under the alternative assumptions of the Ricker and Beverton–Holt stock–recruit functions was not conducted. However, the deviance information criterion (DIC) was calculated to provide some information regarding goodness of fit (Spiegelhalter et al. 2002). The computed DIC results were not used

Table 5. Hyperparameter and prior distributions of parameters utilized within the analysis of stock–recruitment and length-at-age.

Estimated parameter	Prior	Hyperparameter
Compensation ratio (CR)	$L(\mu CR, \tau CR)$	$\mu CR \sim N(2.287, 0.893)$ sdreck $\sim L(0.274, 210.786)$ $\tau CR = $ sdreck^{-2}
Asymptotic length at which growth equals zero (L_∞)	$N(\mu L_{\infty,i}, \tau L_{\infty,i})^{*,\dagger}$	
von Bertalanffy (Brody) growth coefficient (k)	$N(\mu k_i, \tau k_i)^{*,\dagger}$	
Hypothetical age when length is zero (t_0)	$N(0, 0.25)^*$	
Unfished recruit density (D_0)	$L(2.87, 0.439)$	
Unfished recruitment potential (R_0)	$R_0[i] = D_0[i] \cdot stL[i]$	
Slope of length–maturity schedule (Υ)	$L(\log_e(40), 100)$	
Length at 50 percent maturity as a proportion of L_∞ (L_{50})	$B(1000, 600)$	
Natural mortality (M)	$L(\log_e(0.2), 100)$	
Precision of observation error for recruitment ($\tau_{recruits}$)	$\Gamma(0.001, 0.001)$	
Time-varying process error (Ω)	$N(0, \tau_t)$	
Coefficient of variation in length-at-age (cv)	$B(1.5, 1.5)$	

Note: Priors, hyperparameters, and likelihood functions are given abbreviated distribution names as follows: L = lognormal (mean, precision), N = Normal (mean, precision), B = Beta (shape parameters), and Γ = Gamma (shape and scale parameters). Mean and precision in text are abbreviated to μ and τ, respectively.

*Prior presented in table was utilized within hierarchical analysis of stock–recruitment.

†Prior was constrained to be greater than 0.01.

for model selection, as there is no formal quantitative measure of what scale of difference in DIC values between models should direct model choice and as the statistically "best" model may still not be the most beneficial for management and policy decisions (Spiegelhalter et al. 2002; Richards 2005; Carruthers et al. 2010).

Sensitivity analyses

A key assumption in the use of hierarchical Bayesian meta-analyses is the concept of exchangeability of data sets (Parent et al. 2013; Gelman et al. 2014). That is, each population-specific parameter (e.g., CR) is considered an independent sample from a common distribution, which may be indexed by hyperparameters (Gelman et al. 2014). To test this assumption for the posterior predictive distribution of CR, we ran the hierarchical analyses of the Ricker and Beverton–Holt functions an additional 14 times each, systematically excluding one data set in each subsequent run to explore its impacts on the posterior density functions.

Results

Evaluation of both hierarchical models (Ricker and Beverton–Holt) using Gelman–Rubin statistics and trace plots showed both models approached convergence. Posterior estimates were found to be insensitive to initial conditions, and there was little to no observed autocorrelation after thinning in the posterior MCMC chains for either model. Overall, fits of both models adequately described the mean relationship between spawning stock size and recruit abundance (Fig. 1). DIC for the Ricker and Beverton–Holt models were 390.9 and 386.0, respectively. This suggests that the Beverton–Holt model is supported by the analyzed bull trout data based on rule of thumb in Burnham and Anderson (1998).

Fits to stock–recruit data obtained for each of the 14 populations under the assumption of Ricker and Beverton–Holt stock–recruit functions are provided in Fig. 1, while Fig. 2 shows median marginal probability distributions for CR for each population estimated using the Ricker (top panel) and Beverton–Holt (bottom panel) models. Values obtained for median CR with 95% confidence intervals are given in Table 6. Median estimates for the Beverton–Holt model were considerably higher than those obtained for the Ricker model. Further, data sets from several stocks were more informative at estimating CR than others. No discernable relationship was observed between life history (adfluvial or

fluvial) or geographic origin of the stock–recruit data and the estimated values for CR. Median marginal probability distributions for unfished recruitment potential (R_0) for each population estimated using the Ricker (Fig. 2a) and Beverton–Holt (Fig. 2b) models are provided in Table 7. The posterior predictive distribution for CR suggests a median of 384.03 (Beverton–Holt) or 121.45 (Ricker) (Table 8). Assessment of the possible impacts of hyperparameter choice on the posterior predictive estimate of CR found the informative priors did not have undue influence on the posterior estimate (Fig. 3). Finally, posteriors for steepness (Mace and Doonan 1988), which can be calculated directly from CR, were 9.30 (1.04–77.45) for the Ricker and 480.04 (28.69–8295.29) for the Beverton Holt (Martell et al. 2008).

Exchangeability of the data sets was explored by running each of the stock–recruit models (Ricker and Beverton–Holt) an additional 14 times, systematically excluding one population in each run. Posterior predictive distribution for CR with each population removed was not noticeably different from the predictive distribution obtained with all populations included. This suggests that none of the populations were substantially different from the others and did not unduly influence the results of the hierarchical analysis. It was therefore concluded that the assumption of exchangeability within the analysis was met (Fig. 4).

Discussion

Outcomes

Observed large-scale reductions in bull trout abundance and distribution throughout much of their range, in addition to evidence of bull trout's susceptibility to anthropogenic impacts, has raised conservation concerns surrounding the future of the species (Post and Johnston 2002; Hagen and Decker 2011; Rees et al. 2012). Obtaining an accurate estimate of bull trout's capacity for density-dependent compensation, and thus their ability to respond to population declines, is a crucial step towards evaluating sustainable harvest rates for fished populations and estimating recovery rates and targets for at-risk populations (Walters and Martell 2004; Pine et al. 2013). Through the use of a hierarchical Bayesian approach, this research provides the first characterizations of CR for bull trout while accounting for uncertainty within the parameter estimate.

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Fig. 1. Fits to stock–recruit data obtained for 14 bull trout stocks under the assumption of Ricker (continuous lines) and Beverton–Holt (broken lines) stock–recruitment functions.
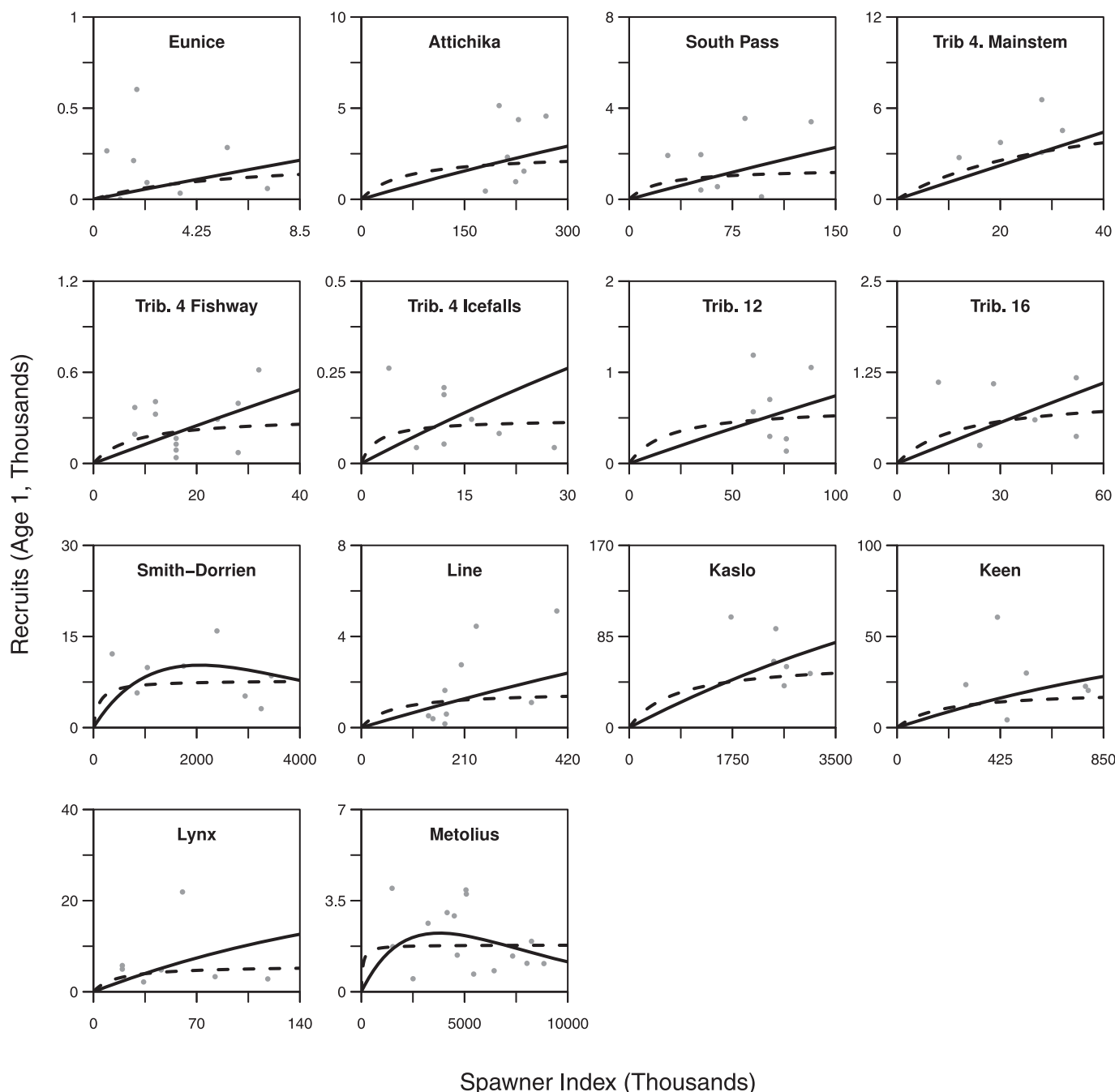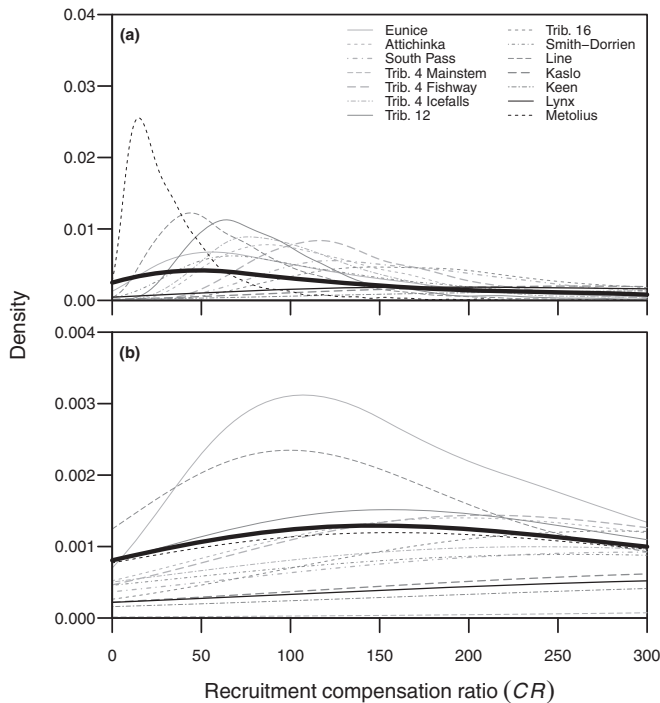

The marginal posterior probabilities for CR estimated for each population demonstrate that bull trout have large scope for improvements in juvenile survival at low stock size. This finding is supported by both anecdotal information, which has suggested the recovery of multiple unmonitored bull trout stocks following harvest reduction (Hagen and Decker 2011), as well as by work by Fraley and Shepard (1989) in the Flathead River basin, Johnston et al. (2007) in Lower Kananaskis Lake, and Erhardt and Scarnecchia (2014) in the Clearwater Basin. High juvenile compensation has also been found in closely related brook trout (*Salvelinus fontinalis*) (de Gisi 1994). The imprecise nature of both the marginal posterior distributions and the median posterior predictive distribution for CR is not surprising. The majority of data sets used in this analysis were relatively uninformative in that they are characterized by short duration time series and limited range of stock abundances over the length of available time series. Only two data sets (Smith-Dorrien Creek and Metolius Basin) had wide variation in spawner abundances, yet the short time series meant there was still substantial uncertainty in posterior estimates of CR for these systems.

The high estimates of CR obtained in this investigation, and evidence of rapid recovery of trout populations (Johnston et al. 2007; Erhardt and Scarnecchia 2014), suggest the bottleneck for bull trout population recovery is likely habitat quality and quantity, which is assessed through the stock–recruitment β parameter, rather than the compensatory response. Bull trout's complex life history and highly specific habitat requirements put them at high risk of population reductions or decreased population persistence as a result of anthropogenic impacts on key habitat (Haas

Fig. 2. Marginal posterior probability distributions of compensation ratio obtained for the 14 stocks under (*a*) Ricker and (*b*) Beverton–Holt hierarchical stock–recruitment models. The posterior predictive distribution for compensation ratio (thick black line) is also shown.
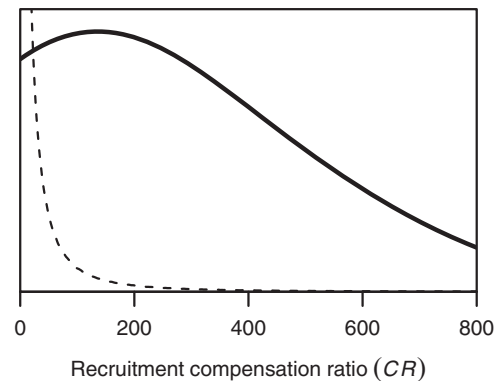

Fig. 3. Hyperparameter choice for compensation ratio (dashed line) with posterior predictive estimate (solid line) superimposed to show potential influence of prior choice on posterior estimate.

and McPhail 1991; Post and Johnston 2002; Hagen and Decker 2011). A detailed examination of how habitat quality and quantity specifically influence juvenile bull trout survival remains warranted and necessary to inform future management and recovery efforts focused on habitat improvements and maintenance (Haas and McPhail 1991; Post and Johnston 2002; Hagen and Decker 2011).

Estimating compensation in juvenile survival within population dynamics models is inherently difficult due to high data needs and confounding of compensation with other parameters (i.e., R_0). When estimating such parameters, it is important to remember to include uncertainty, as use of fixed parameter estimates (even if the value is deemed conservative) can result in incorrect conclusions within recovery planning and development of sustainable harvest rates, leading to failures in management (Hilborn and Liermann 1998; Morris et al. 2015). Though this investigation was not able to provide a precise estimate of compensation for specific populations, the posterior predictive estimate developed herein establishes a distribution for compensation for bull trout that excludes biologically unrealistic values.

The posterior predictive estimate of CR calculated here can be used as an informative prior in future Bayesian models for the species. It serves to restrict the parameter space of this key parameter to one that is biologically realistic for the species, reduce uncertainty, and improve inference for populations where stock–recruitment data are scarce or nonexistent or where available data lack the contrast necessary to adequately estimate parameters of a population's stock–recruitment relationship. Any future work of this type, which utilizes additional data sets, can build on this investigation and will further increase precision of the posterior predictive estimate of CR provided.

Model comparison was conducted using DIC, which provides a formal system to compare the fit of each hierarchical stock–recruitment model to the available bull trout data (Spiegelhalter et al. 2002). DIC supported the model choice of the Beverton–Holt function. This was not expected ecologically, as bull trout behav-

ior, notably evidence of cannibalism of juveniles and superimposition of redds coupled with size-dependent predation, would suggest the Ricker function should provide a better fit (Hilborn and Walters 1992). However, statistically, the finding is expected based on the lack of variation in the available spawner index data. It should be noted that the systems for which highly variable stock–recruit data were available (Smith-Dorrien Creek and the Metolius Basin) show a pattern consistent with the Ricker function upon visual inspection of Fig. 1. DIC, however, does not provide a direct mechanism to compare the overall plausibility of each model structure given the data (Michielsens and McAllister 2004). Therefore, despite the results of DIC, neither functional form should be ruled out, and model uncertainty should be carried forward into any future bull trout stock assessment work.

This analysis was negatively impacted by three main factors: a limited quantity of available data sets, a limited range of spawner abundance within most data sets, and a limited time series within most data sets. During data collection, it became evident that there is a general lack of stock–recruitment data for bull trout. As well, the majority of available information is not at the scale or temporal duration necessary to be used in stock–recruitment analysis (in the form of paired spawning stock biomass and resulting recruit abundance estimates). Twenty-seven populations had to be excluded from this analysis due to factors including short time series (<5 years) and incomplete information in spawner and (or) recruit abundance estimates. Of systems that were able to be included, the average length of data set was 7 years. Despite our best efforts, our resulting estimates of compensation are understandably uncertain. One key outcome of this work is the need to continue collecting information on both stock and recruitment indices from as many bull trout populations as possible to improve these CR estimates and therefore improve predictability of models that rely on them.

Data obtained from different regions (i.e., US or Canada and individual state or province) also lacked consistency in data collection approaches. It appears that different regions consistently collect different abundance indices (e.g., redd counts, juvenile estimates, smolt counts, or a combination of these), but rarely collect paired indices of spawners and recruits together over time. This prohibited a more thorough investigation of juvenile compensation across the species range. Gaining an understanding of the recovery potential for bull trout is a key step in fish recovery planning and population management. Therefore, more rigorous and standardized data collection of bull trout stock–recruitment data across the species range should be a priority.

Only data from two systems (Smith-Dorrien Creek and the Metolius Basin) had high contrast in spawning stock abundance through time, with spawner abundance estimates ranging from near collapse to near carrying capacity. Generally, data were avail-

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Table 6. Population-specific posterior median (95th percentiles) estimates of CR obtained from the baseline hierarchical models for the Ricker and Beverton–Holt stock–recruitment functions.

System	Ricker	Beverton–Holt
Eunice Creek	90.98 (14.05–357.82)	182.54 (28.52–1 472.00)
Attichika Creek	112.03 (43.09–366.2)	388.55 (70.95–5 585.95)
South Pass	165.26 (62.84–445.81)	507.47 (99.24–6 970.61)
Tributary 4 Mainstem	1 098.66 (421.52–2 787.85)	1 966.12 (613.79–11 177.10)
Tributary 4 Fishway	129.15 (57.07–297.73)	400.13 (89.35–10 334.80)
Tributary 4 Icefalls	101.14 (38.94–374.73)	506.22 (74.55–8 602.46)
Tributary 12	80.99 (31.12–266.45)	294.83 (48.26–5 503.27)
Tributary 16	189.92 (73.77–480.40)	478.98 (115.52–5 250.12)
Smith-Dorrien Creek	111.79 (29.45–522.81)	518.85 (66.68–7 957.60)
Line Creek	60.11 (15.61–198.91)	210.07 (27.68–7 773.40)
Kaslo River	348.70 (71.57–1 424.88)	852.16 (117.05–8 137.27)
Keen Creek	488.83 (105.17–1 948.47)	1 069.74 (146.87–10 191.67)
Lynx Creek	314.42 (43.18–1 449.36)	949.82 (115.69–7 405.72)
Metolius Basin	25.91 (5.72–130.06)	357.94 (26.27–5 149.55)

Table 7. Population-specific posterior median (95th percentiles) estimates of R_0 obtained from the baseline hierarchical models for the Ricker and Beverton–Holt stock–recruitment functions.

System	Ricker	Beverton–Holt
Eunice Creek	269.19 (15.70–5 219.43)	209.13 (40.06–4 065.47)
Attichika Creek	1 024.70 (103.69–15 166.82)	2 615.08 (981–17 947.29)
South Pass	919.29 (62.64–17 173.69)	1 530.25 (533.76–13 314.03)
Tributary 4 Mainstem	1 481.58 (96.41–29 984.90)	6 777.90 (1 899.87–56 076.50)
Tributary 4 Fishway	361.55 (19.06–5 720.44)	321.60 (125.78–4 521.42)
Tributary 4 Icefalls	107.31 (5.78–3 905.50)	130.98 (54.16–880.52)
Tributary 12	560.63 (38.22–14 405.86)	700.45 (243.09–8 004.71)
Tributary 16	937.69 (48.34–15 567.56)	1 054.79 (337.96–10 139.42)
Smith-Dorrien Creek	1 203.63 (542.82–24 679.94)	8 104.24 (3 486.26–22 514.32)
Line Creek	1 493.79 (158.14–19 049.16)	1 666.29 (618.31–23 747.06)
Kaslo River	7 684.20 (1 030.49–119 263.05)	62 684.65 (23 111.74–282 875.57)
Keen Creek	1 733.70 (259.88–30 340.19)	20 755.43 (7 445.98–91 079.27)
Lynx Creek	1 039.69 (117.02–15 546.98)	6 025.15 (2 217.04–26 684.33)
Metolius Basin	841.84 (381.61–7 775.83)	1 824.28 (1 013.68–3 460.57)

Table 8. Posterior median (95th percentiles) estimates of CR obtained from the baseline hierarchical models for the Ricker and Beverton–Holt stock–recruitment functions.

| Estimated parameter	Ricker	Beverton–Holt
μCR	4.75 (3.96–5.02)	5.94 (4.88–7.17)
τCR	0.59 (0.46–0.76)	0.57 (0.43–0.75)
CR posterior predictive	121.45 (7.86–1717.90)	384.03 (22.95–6636.23)

able for only small ranges of variation in spawning stock size. Data of this kind is challenging to incorporate within stock–recruit analyses, as such information contributes to biases ("errors in variables" and "time series bias"), which make it difficult to ascertain the true stock–recruit relationship (Hilborn and Walters 1992). The inclusion of additional data sets, specifically ones that have large variation in spawner abundances that extend from very low abundance to near carrying capacity (i.e., high contrast) and longer than 20 years duration, would serve to improve estimates of recruitment parameters including CR and reduce uncertainty in these estimates (Hilborn and Walters 1992). These data sets are understandably rare and difficult to capture by accident, suggesting a need for an adaptive management experiment on bull trout recruitment. Our hierarchical model was the most appropriate approach to deal with such data, allowing us to estimate reasonable hyperparameters for CR, which in turn informed the analysis. But as additional data become available, particularly if there is high variation in spawner density, this will improve on posterior predictive estimates over time.

At present, most of what we know about bull trout's capacity for recovery comes from research on adfluvial fish in Lower Kananaskis Lake, Alberta, where detailed stock and recruit sampling was conducted over a 10-year period and over a population ranging in size from near collapse to nearly carrying capacity (Johnston et al. 2007). Within this investigation, every attempt was made to obtain data across bull trout's migratory life history types and spatial distribution. Despite this, data available for this study were primarily from British Columbia, Canada, with only three systems available from one other Canadian province (Alberta) and only one system from bull trout's range within the United States (Oregon). No difference in CR would be expected as a result of geography because of the similarity in conditions required for bull trout recruitment across systems (Post and Johnston 2002).

In addition, the majority of available data (11 of 14 systems) were for adfluvial bull trout, with only three systems representing the fluvial life form, and zero data for anadromous or resident life histories. Although bull trout life histories vary significantly in their maximum size, migration patterns, as well as other key statistics, all bull trout life history types rear in similar habitats (Post and Johnston 2002; Rees et al. 2012). Therefore, factors affecting juvenile survival are likely similar, implying findings here are still relevant. Certainly, we did not detect a noticeable difference between the two life history types examined.

Findings of this investigation provide a key first step in establishing a precise estimate of recruitment compensation potential for bull trout. The posterior predictive estimate of CR obtained within this study has broad applications within the management

Fig. 4. Median and quantiles of posterior predictive probability distributions of compensation ratio obtained for the 14 stocks under (*a*) Ricker and (*b*) Beverton–Holt hierarchical stock–recruitment models excluding one population from the analysis at a time. Median estimates are shown as a black bar inside the box showing the interquartile range. Outliers are shown as circles.
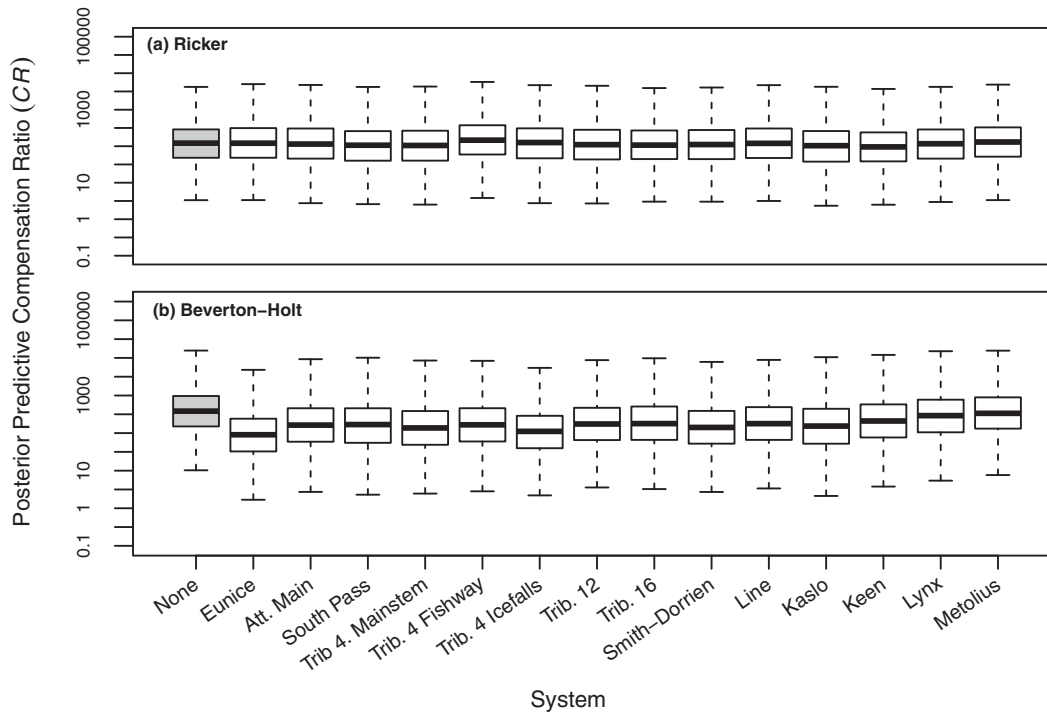
of bull trout across the species range. Notably, our estimate for CR can be used to establish conservation thresholds for bull trout populations where recreational fishing opportunities exist (e.g., in the development of spawning potential ratios) and in calculating recovery potential for populations of conservation concern (Pine et al. 2013). There is still substantial uncertainty in CR; however, this work has begun the process of constraining the range of CR to one that is biologically realistic for bull trout and verifies that the species is indeed capable of incredible recovery potential if adequate conditions exist.

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