

Multiple challenges confront a high-effort inland recreational fishery in decline

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Abstract: Catch-and-release regulations designed to protect fisheries may fail to halt population declines, particularly in situations where fishing effort is high and when multiple stressors threaten a population. We demonstrate this claim using Alberta's Bow River, which supports a high-effort rainbow trout (*Oncorhynchus mykiss*) fishery where anglers voluntarily release >99% of their catch. We examined the population trend of adult trout, which were tagged and recaptured using electrofishing surveys conducted intermittently during 2003–2013. We constructed Bayesian multisession capture–recapture models in Stan to obtain abundance estimates for trout and regressed trend during two periods to account for variation in sampling locations. General patterns from all models indicated the population declined throughout the study. Potential stressors to this system that may have contributed to the decline include whirling disease (*Myxobolus cerebralis*), which was detected for the first time in 2016, notable floods, and release mortality. Because disease and floods are largely uncontrollable from a management perspective, we suggest that stringent tactics such as angler effort restrictions may be necessary to maintain similar fisheries.

Résumé : La réglementation sur la pêche avec remise à l'eau visant à protéger les ressources halieutiques peut ne pas prévenir le déclin de populations, particulièrement dans des situations où l'effort de pêche est grand et de multiples facteurs de stress menacent une population. Nous faisons la démonstration de ce postulat avec l'exemple de la rivière Bow, en Alberta, qui supporte une pêche à la truite arc-en-ciel (*Oncorhynchus mykiss*) à effort élevé dans laquelle les pêcheurs remettent volontairement à l'eau plus de 99 % de leurs prises. Nous avons examiné la tendance démographique de truites adultes qui ont été étiquetées et recapturées dans le cadre de relevés à la pêche électrique menés de manière intermittente de 2003 à 2013. Nous avons construit des modèles bayésiens de capture-recapture à sessions multiples dans le logiciel Stan pour obtenir des estimations de l'abondance pour les truites et obtenu une tendance par régression pour deux périodes pour tenir compte de la variation des lieux d'échantillonnage. Les motifs généraux obtenus de tous les modèles indiquent que la population a baissé tout au long de l'étude. Les facteurs de stress pour ce système qui pourraient avoir joué un rôle dans cette baisse comprennent le tournis des truites (infection à *Myxobolus cerebralis*), qui a été détecté pour la première fois en 2016, des inondations notables et la mortalité après remise à l'eau. Comme il est difficilement possible de contrôler, dans une perspective de gestion, les infections et les inondations, nous suggérons que des mesures draconiennes, comme des restrictions de l'effort des pêcheurs à la ligne, pourraient être nécessaires pour assurer le maintien de ressources halieutiques semblables. [Traduit par la Rédaction]

Introduction

Recreational fisheries can decline and collapse when exploitation rate is high relative to the productivity of the targeted population (Post et al. 2002; Sullivan 2003; Johnston et al. 2007), when environmental conditions are unfavorable (Beamish et al. 1999), or when multiple stressors surpass the compensatory abilities of a given fish population (Hansen et al. 2015). However, declines documented as reductions in catch or abundance are generally multifaceted and subject to much debate (Hilborn and Walters 1992). Failure to achieve scientific consensus on the cause(s) of a decline stems from the fact that data collected by management agencies are observational in nature (Hilborn 2016), extracted from ecosystems with complex dynamics (Sugihara et al. 2012; Glaser et al. 2014), and often lack the experimental manipulations, controls, and replication necessary for causal inference (Jones and Hansen 2014). Consequently, disentangling key factors responsible for a

decline, such as the effects of fishing versus abiotic or environmental stressors, is often difficult (Walters 1986).

Several policy options are available to managers seeking to offset the effects of fishing-related mortality in inland recreational fisheries. Traditionally, fishing mortality has been managed using passive regulations such as bag or length limits (Lester et al. 2003), seasonal or area closures (Welcomme 2008), and gear restrictions (Rahel 2016). Such regulations either (i) manipulate the catch or harvest rate of individual anglers by decreasing catchability or vulnerable fish population size or (ii) indirectly control total angling effort through voluntary choices by anglers. Thus, the ability of these passive regulations to offset issues related to high angling effort remains tenuous (Cox et al. 2003; Pereira and Hansen 2003). For example, minimum length limits may fail to prevent recruitment overfishing when angler effort is unresponsive to declines in fishery quality (Allen et al. 2013). Similarly, catch-and-release regulations (i.e., zero harvest) may fail

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to achieve management objectives or maintain fish populations in situations where effort is high or when release mortality is present (Post et al. 2003). Despite the potential for problems in high-effort situations, catch-and-release regulations are generally the most stringent regulations enacted by inland recreational fisheries managers in North America (Hubert and Quist 2010).

Anthropogenic stressors such as fishing-related mortality reduce a population's ability to offset stochastic natural disturbances or disease outbreaks (Holling 1973). For example, severe floods may reduce fish density through direct mortality or downstream displacement (Warren et al. 2009). Pathogens may also alter population dynamics through reductions in growth (Johnson et al. 2004) or competitive ability (Godwin et al. 2015), changes in behavior (Barber et al. 2000), or through direct mortality events (Hatai and Hoshiai 1992). For instance, viral hemorrhagic septicemia virus resulted in mass mortality events in freshwater drum (*Aplodinotus grunniens*) (Lumsden et al. 2007) and muskellunge (*Esox masquinongy*) (Elsayed et al. 2006) within the Laurentian Great Lakes. The importance of pathogen-induced mortality was also illustrated throughout the intermountain-west region of the United States, where whirling disease (*Myxobolus cerebralis*) reduced salmonid abundance by up to 90% in some watersheds (Nehring and Walker 1996; Vincent 1996). While stochastic events and disease outbreaks influence fish population dynamics, biologists have few direct tools for managing stressors such as these.

A central challenge facing recreational fisheries managers is how to mitigate the combined effects of anthropogenic and stochastic environmental threats, as freshwater systems appear particularly vulnerable to the effects of multiple stressors (Ormerod et al. 2010). Unfortunately, traditional fisheries management approaches rarely incorporate the effects of multiple, potentially changing stressors on population sustainability (Lynch et al. 2016; Paukert et al. 2016). Thus, approaches that explicitly recognize management trade-offs among key stressors may be useful. For example, S.R. Carpenter et al. (2017) developed a multidimensional sustainable safe operating space (i.e., "SOS") that distinguished among stressors that were controllable (e.g., harvest) and largely uncontrollable (e.g., environmental change or disease outbreaks) by fisheries managers. These authors suggested that managers may need to offset the effects of uncontrollable variables with those they can influence to maintain a quality fishery within a particular SOS (S.R. Carpenter et al. 2017).

The Lower Bow River (LBR) rainbow trout (*Oncorhynchus mykiss*) fishery highlights the challenges of managing inland recreational fisheries in the presence of multiple stressors. The LBR is reputed as a world-class rainbow trout fishery (Post et al. 2006; Askey et al. 2007) and experiences high angling effort in part because of its proximity to a large city (Calgary, Alberta; 1.2 million people; Rhodes 2005; Statistics Canada 2016). Notable floods occurred in 2005 and 2013 (i.e., 1/10 and 1/100-year flood events, respectively; Veiga et al. 2015). Furthermore, whirling disease was detected in the LBR for the first time in 2016, although it is unknown when the disease arrived (Canadian Food Inspection Agency 2017). Given that the potential for these threats to impact rainbow trout in the LBR appears high, our objectives were to determine (i) abundance of rainbow trout ≥ 250 mm fork length (FL) and (ii) assess trends in abundance during 2003–2013. Results from this study are then used to demonstrate the potential importance of effort restrictions as an inland recreational fisheries management tool, particularly when angling effort is high and the remaining stressors cannot easily be controlled.

Methods

Study area

The Bow River originates in the Rocky Mountains of southwestern Alberta and is a major tributary of the South Saskatchewan River (Fig. 1). Our study occurred in the LBR, which designates a

224 km section of the river beginning at the Bearspaw Dam and flowing eastward through Calgary, Alberta, to the Bassano Dam (Fig. 1). The LBR receives substantial nutrient inputs from wastewater effluent as it flows through Calgary (Sosiak 2002), which increases production of top trophic levels in the system (Askey et al. 2007).

Rainbow trout were introduced into the LBR by stocking between 1933 and 1947 (Gilmour 1950) and are now naturalized (Rhodes 2005). Rainbow trout are the most sought-after species in the LBR fishery, and most fish are caught via fly-fishing during August. This system supports the highest effort fishery in Alberta (mean 161 angler hours per hectare annually; Council and Ripley 2006), has been functionally catch and release since at least 2006 (e.g., 0.005% of captured rainbow trout were kept by anglers; Council and Ripley 2006), and is worth CAN\$24.5 million per year (Crowe-Swords 2016).

Field sampling

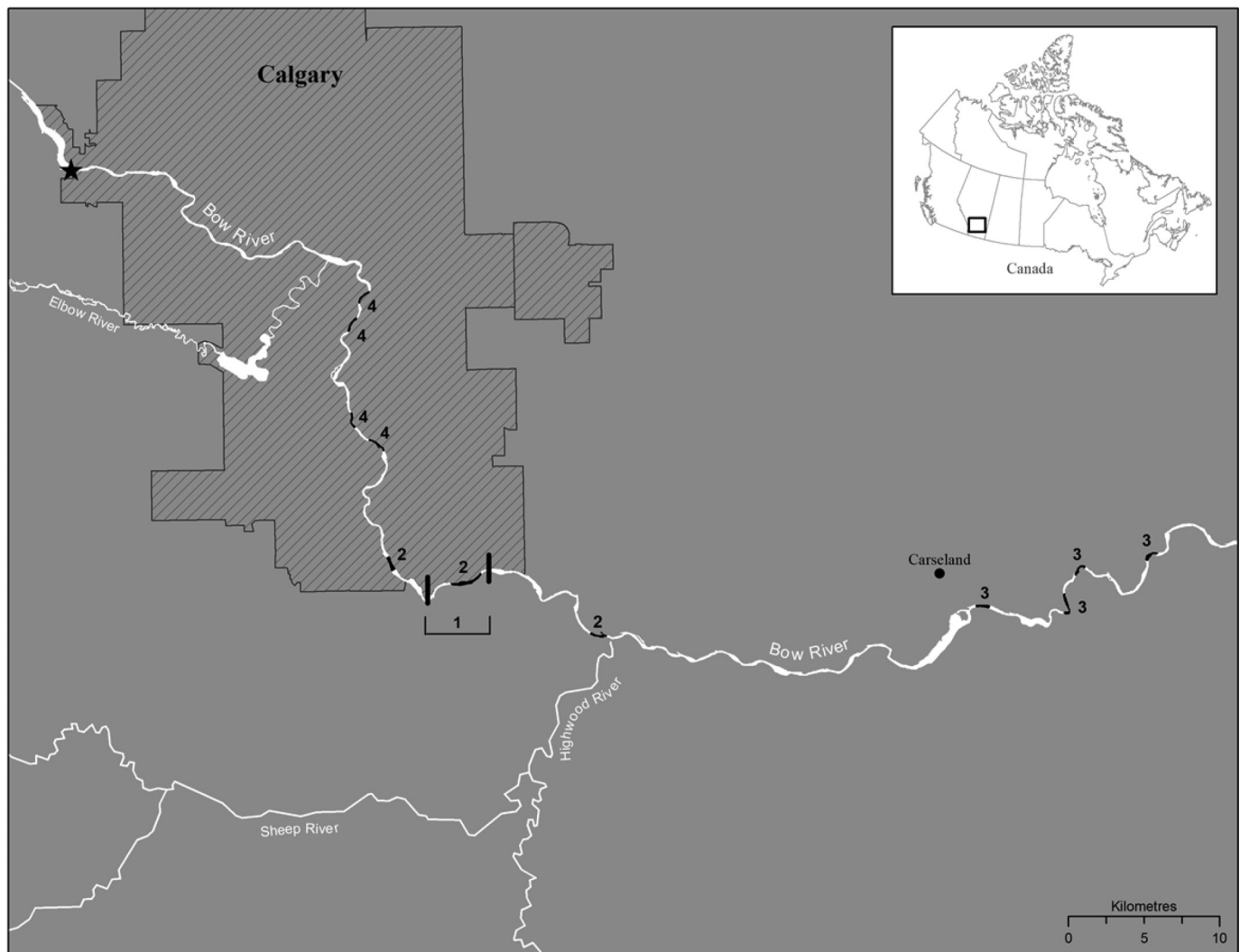
Alberta Environment and Parks biologists conducted seven multiday capture–recapture surveys during 2003–2013 to assess trout population trends in the LBR. A contiguous 4.32 km section of the river was sampled in 2003, 2005, 2007, and 2008 (Fig. 1). During 2011–2013, sampling occurred at four randomly selected 1 km sections (Fig. 1). In all years, fish were sampled using two Smith-Root 5.0 or 7.5 Generator Powered Pulsators and jet-powered boom electrofishers on four consecutive days during late August to early September. Boats fished opposite banks in the downstream direction, and fish were transferred to tubs until the end of the section was reached. Rainbow trout ≥ 250 mm FL were tagged behind the dorsal fin using individually numbered Floy anchor tags, and fish were released in the center of the section they were captured in.

Analysis

Multisession capture–recapture models were constructed to obtain derived abundance estimates of rainbow trout ≥ 250 mm FL, which were regressed through time to estimate the population trend during 2003–2008 and 2003–2013 to account for sampling changes (described above). Multisession capture–recapture models generalize a simple closed capture–recapture model to multiple sessions or years and are useful for combining data from multiple years into a single analysis (Converse and Royle 2012; Kéry and Royle 2015). Our models estimated capture probabilities for each day within each year to account for imperfect detection of fish in our surveys. Data were modeled in an integrated Bayesian framework. The integrated approach propagated uncertainty through the abundance analysis and ultimately into estimates of population trend, rather than analyzing the outputs of models as data (Maunder and Punt 2013; Paul 2013). Additionally, we elected to use the Bayesian framework because it offered more modeling flexibility and allowed for the accounting of the full range of uncertainties related to all models and parameter values (Punt and Hilborn 1997). Standard open population models were not fit because surveys were not conducted in consecutive years throughout the study.

A statistical approach known as data augmentation was used to simplify Bayesian abundance estimation. Data augmentation reparameterizes a standard closed capture–recapture model into an occupancy-style model (Royle 2009; Kéry and Schaub 2012). This parameterization removes the abundance parameter N from the model as an estimated parameter, which is useful because it fixes the dimension of the parameter space and thus enables the use of approaches such as Markov chain Monte Carlo (MCMC; Royle and Dorazio 2008). Data augmentation removes N from the model by marginalizing over a $\text{Bin}(M, \psi)$ prior distribution for N , where M is an arbitrarily large number of unobserved individuals with all-zero capture histories, and ψ is an inclusion probability to be estimated from the data (Royle 2009). The capture histories of

Fig. 1. Map showing locations sampled via multipass electrofishing in the Lower Bow River during 2003–2013 (upper insert: location of the study area in Alberta, Canada). Note that sampling locations in 2003, 2005, 2007, and 2008 were identical and are represented by the section of river delineated with vertical black bars (sampling location “1”). Sampling locations were subsequently changed to stratified random locations: 2011 = “2”, 2012 = “3”, 2013 = “4.” The Bearspaw Dam is indicated by a star (★).



individuals observed in the field are then augmented by the capture histories of the all-zero “potential” individuals, which are said to be present in the population according to a Bernoulli prior with inclusion probability ψ . This approach implies that the marginal prior for N is Uniform(0, M) and hence that the expectation of N can be recovered as the derived variable ψM through the estimation of ψ , any relevant capture probabilities, and a Bernoulli latent variable (Royle et al. 2014).

The single-year data augmentation scheme described above was expanded to a multisession framework by introducing a year-specific subscript t to all parameters and values (e.g., ψ_t , M_t , and N_t). Abundance in each year N_t was assumed to be Poisson-distributed with year-specific mean λ_t :

$$(1) \quad N_t \sim \text{Poisson}(\lambda_t)$$

This multisession framework and Poisson assumption formed the basis for three separate models, as the models could either be used to estimate year-specific abundances (as in eq. 2 below; model 1) or regress the population trend by fixing the trend on the first year of data (as in eqs. 3 and 4 below; models 2 and 3, respectively). Two trend models were fit to account for potential issues

with field sampling: model 2 estimated a trend for years when the surveys occurred in identical locations (i.e., 2003–2008), while model 3 regressed a trend across the entire study period.

Model 1 was parameterized as a generalized linear model of the form

$$(2) \quad \lambda_t = e^{\beta_{0t}}$$

where β_{0t} are fixed effects that represent independent abundance estimates for each year (i.e., 2003, 2005, 2007, 2008, 2011, 2012, and 2013; Royle et al. 2014). Model 2 regressed a trend through abundance estimates during the first 4 years of data collection (i.e., 2003, 2005, 2007, and 2008):

$$(3) \quad \lambda_t = e^{\beta_0 + \beta_1(t-t^*)}$$

where β_0 was fixed at a single intercept, β_1 is a coefficient describing the log-linear abundance trend, and t^* is a baseline year that centers the trend. Model 3 regressed a trend term through abundance estimates during 2003–2013:

$$(4) \quad \lambda_t = e^{\beta_0 + \beta_1(t-t^*) + \beta_2 \text{length}_t}$$

where β_2 is a covariate controlling for the total length (km) of the river sampled in each year. Additionally, all models featured constraints between the year-specific inclusion parameters ψ_t and intercept terms (i.e., β_0 , or β_0), and ψ_t can be fixed as

$$(5) \quad \psi_t = \frac{\lambda_t}{M_t}$$

so that the intercepts are estimable (Royle et al. 2014; Kéry and Royle 2015).

Capture probabilities (p) were modeled using a generalized linear mixed model of the same form for all three models. For each year t , four occasion-specific capture probabilities j and i individual random effects (i.e., $p_{i,j,t}$) were modeled. Capture probabilities were modeled as additive fixed effects based on the capture occasion (i.e., $\beta_{j,t}$) and the addition of a random logistic-normal term that represented individual heterogeneity in capture probability, $\alpha_{i,t}$:

$$(6) \quad \text{logit}(p_{i,j,t}) = \beta_{j,t} + \alpha_{i,t}$$

where

$$(7) \quad \alpha_{i,t} \sim \text{Normal}(0, \text{SD} = \sigma_t \times \sigma_{\text{raw},i,t})$$

$$(8) \quad \sigma_t \sim \text{Normal}(0, 1.25)$$

$$(9) \quad \sigma_{\text{raw},i,t} \sim \text{Normal}(0, 1)$$

Thus, σ_t is a year-specific random effect on capture probability drawn from an informative prior distribution. The specific prior values of σ_t were not of primary interest to this study, but these priors did alter the variance around the abundance estimates. Data did not contain enough information to allow use of an uninformative prior for σ_t (e.g., $\sigma_t \sim \text{Normal}(0, 10)$), and simpler versions of these models without individual heterogeneity terms failed to pass goodness-of-fit tests because of overdispersion in the individual encounter history data. Consequently, we were left with the choice to use simpler but potentially ill-fitting models or to employ an informative prior and obtain models that passed goodness-of-fit tests. The latter approach was chosen, as it seemed precautionary to err on the side of incorporating more uncertainty in the models. Values for the informative priors ensured that capture probabilities did not go to zero and that N_t did not go to infinity, so that the upper limits of the derived density estimates (abundance-km⁻¹) corresponded to densities observed in other fluvial wild stock rainbow trout fisheries (Vincent 1996). Lastly, $\sigma_{\text{raw},i,t}$ altered the individual random effects to a noncentered parameterization, which manipulated the geometry of the posterior and improved numerical performance (Betancourt and Girolami 2013; Monnahan et al. 2017).

Estimates of abundance N_t were derived as

$$(10) \quad N_t = n_t + \theta_t$$

where n_t is the number of individual fish captured in year t , and θ_t represents the sum of M_t independent Bernoulli trials with trial-specific success probability equal to

$$(11) \quad \frac{\psi_t \prod_{j=1}^4 (1 - p_{i,j,t})}{\psi_t \prod_{j=1}^4 (1 - p_{i,j,t}) + (1 - \psi_t)}$$

Phrased differently, abundance of fish in each year was calculated as the sum of the number of fish captured in that year and the sum of M_t Bernoulli random deviates describing fish that were present in that year, but never physically captured. A standardized index of rainbow trout density among years (N_{km_t}) was computed by dividing the estimates of N_t by the length (km) of river sampled in year t . Lastly, the percent decline per year for models 2–3 was derived as

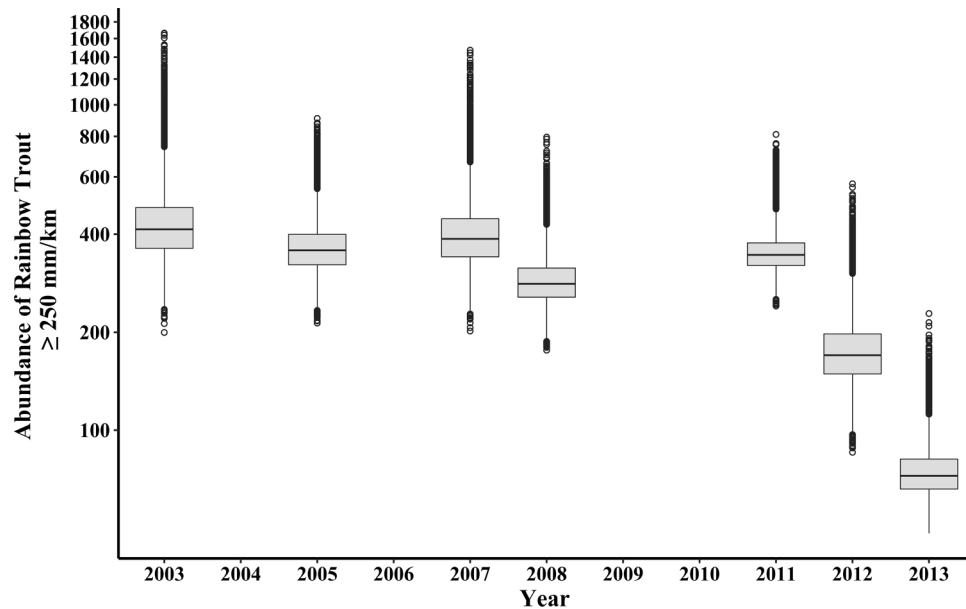
$$(12) \quad \text{Trend}(\%) = (e^{\beta_1} - 1) \times 100$$

where the Trend term represents the per year percent change in N_t during 2003–2008 and 2003–2013 (denoted as Trend_s and Trend_p, respectively).

Priors for all additional parameters were set at vague or weakly informative values, and the sensitivity of the results to priors was tested during model development. All predictor variables were centered and standardized prior to analysis (Gelman 2008). For each model, each year's observed capture history data was augmented by $M_t = 8000$, which implied $N_t \sim \text{Uniform}(0, 8000)$ priors, and visual inspection of the results showed this bound was sufficiently large so as to not influence estimates of abundance or the corresponding derived densities (see also Royle et al. 2014). Occasion-specific capture probabilities for all models were given flat $\text{logit}(\beta_{j,t}) \sim \text{Uniform}(0, 1)$ priors. For all three models, intercept terms (β_0 , β_0) were given normal priors centered at zero, with a prior standard deviation (SD) of 10 to represent a substantial amount of ignorance regarding the values of λ_t on the log scale. The remaining regression coefficients (β_1 for models 2 and 3, β_2 for model 3) were given normal priors centered at zero with an SD of 1. Priors for these remaining regression coefficients were weakly informative, as our predictor variables were also on the unit scale (Gelman et al. 2015), and while these priors did not truncate estimates of β_1 and β_2 for either model, they did substantially improve the numerical performance. Final model versions were arrived at after fitting several alternative models that either (i) failed to pass posterior predictive checks and (or) (ii) provided identical (or nearly identical) posterior distributions for key parameters. Specifically, we fit models that assumed abundances were distributed as a negative binomial random variable, but these models produced nearly identical results for abundances and the trend term as the simpler Poisson model. We also fit simpler mark-recapture models that featured a single capture probability for each year and models that featured occasion-specific capture probabilities for each year without individual heterogeneity terms, and while these models produced equivalent results as our final models, they did not pass our posterior predictive checks (see below).

Our models were challenging to fit using traditional Bayesian methods. For example, we originally attempted to fit our models in JAGS (Plummer 2003), but MCMC chains mixed poorly and simulations were slow. We circumvented these issues by fitting models in Stan, which employs an efficient class of MCMC algorithms based on Hamiltonian Monte Carlo (Stan Development Team 2016). Stan proved useful for this analysis and data set when coupled with the noncentered parameterization of the random effects (see also Monnahan et al. 2017) and was more efficient than analogous programs run in Jags (i.e., judged as the number of effective samples per unit time). Thus, we echo Monnahan et al. (2017) and recommend Stan as a powerful tool for ecological modeling.

Fig. 2. Posterior distributions of rainbow trout density in the Lower Bow River, Alberta, Canada, during 2003–2013. Results are from model 1. Boxplots designate the median (horizontal black line), the 25th and 75th percentiles (lower and upper box boundaries), the upper and lower whiskers that extend to 1.5 times the interquartile range, and any remaining “outliers” (circles). Note that floods occurred in 2005 and 2013.



Bayesian models were implemented using RStan in R (B. Carpenter et al. 2017; Stan Development Team 2016; R Core Team 2017), and we provide both R and Stan code to simulate and analyze data for model 3 at the lead author’s personal website (available from <https://github.com/ChrisFishCahill/MultiSessionTrend>). We ran ten chains for each model, discarded the first 5000 draws as burn-in, and retained the next 5000 draws with a thinning rate of 1 to summarize posterior distributions. Starting values were jittered for each model, and chains were started at different random number seeds. Additionally, chains were inspected visually for mixing, Gelman–Rubin statistics (\hat{R}) were used to test for convergence to a stable distribution among chains, and tree-depth plots were explored to evaluate step size and performance of the no-U-turn sampler using ShinyStan (Gelman et al. 2014; Gabry 2015). We also ensured that models featured no divergent transitions during sampling, which is a diagnostic that indicates whether results from Stan are valid (Betancourt and Girolami 2013; Monnahan et al. 2017). Model fit was evaluated using posterior predictive p values (Kéry and Royle 2015), the development of which is described in Appendix A.

Results

Results from all three models suggest that the abundance of rainbow trout ≥ 250 mm FL declined during 2003–2013. Model 1 showed that while year-specific estimates of abundance (i.e., N_t) and derived values of density (i.e., N_{km_t}) were highly variable, both declined during 2003–2008 and 2003–2013 (Table A1 and Fig. 2, respectively). Density values from the independent intercepts model declined more sharply during 2011–2013 than during 2003–2008 (Fig. 3). The highest derived values for rainbow trout density occurred in 2003 (median = 414 fish·km⁻¹; 95% credible interval (CRI): 290–713 fish·km⁻¹), while the lowest density estimates occurred in 2013 (median = 72 fish·km⁻¹; 95% CRI: 57–111 fish·km⁻¹; Fig. 2). Trend_s was highly variable, but 88% of the posterior mass for this derived variable was < 0 (median = -5.5% per year; CRI: -14.2% to 4.3% per year; upper panel Fig. 4). Values of Trend_t (2003–2013) were less variable than those of Trend_s (2003–2008), but featured a similar median estimate for the percent change per year, and 99% of the posterior mass was < 0 (median = -6.6% per year; CRI: -10.5% to -2.6% per year; lower panel Fig. 3).

Posterior predictive checks indicated that no major deviations from the modeling assumptions existed for all models (i.e., posterior predictive p values 0.18–0.33; Fig. 4), and \hat{R} statistics suggested convergence to a stable distribution among chains for all parameters in each model (i.e., all $\hat{R} = 1$; Tables A1–A3). Estimates of year- and occasion-specific capture probabilities were low for all three models (i.e., $\beta_{j,t}$ typically ≤ 0.10 ; Appendix Tables A1–A3). Additionally, values of ψ_t ranged from 0.03 to 0.39 for all models, which indicated that the abundance estimates were not constrained by our choices for the year-specific data augmentation variables M_t (Converse and Royle 2012; Appendix Tables A1–A3).

Discussion

Despite uncertainty in both abundance and trend estimates, these results indicate that rainbow trout in the LBR likely declined during both assessment periods. The median posterior estimates for a 10-year standardized population trend were -43.0% using Trend_s estimated from the 2003–2008 data and -50.0% using Trend_t estimated from the 2003–2013 data. Since the size criteria for tagged fish (≥ 250 mm FL) corresponds approximately to the sizes of mature rainbow trout (Rhodes 2005), the estimated decline likely represents a large reduction in the number of mature individuals in this population. For example, The Committee on the Status of Endangered Wildlife in Canada (COSEWIC) guidelines state that “in cases where the declines or its causes are unknown”, a decline in the number of mature individuals $\geq 30\%$ or $\geq 50\%$ over a period of 10 years would qualify a population as “threatened” or “endangered”, respectively (COSEWIC 2018). Rainbow trout in the LBR are naturalized (Gilmour 1950) and hence do not qualify for listing as per COSEWIC guidelines; nonetheless, these criteria demonstrate the magnitude of the decline documented here.

The pattern of decline in adult abundance in the LBR appears similar to declines in other high-profile rainbow trout fisheries caused by whirling disease. Whirling disease was first detected in the Bow River in 2016 and subsequent monitoring detected the parasite throughout the Bow River watershed in February 2017 (Canadian Food Inspection Agency 2017). Although timing of its first occurrence in the province is unknown, extensive testing for *Myxobolus cerebralis* from 1997 to 2001 was negative in the province

Fig. 3. Posterior distributions showing the percent change per year in rainbow trout abundance in the Lower Bow River, Alberta, Canada, during 2003–2008 (upper panel) and 2003–2013 (lower panel). Percent change per year was calculated as a derived variable in the trend model analyses.

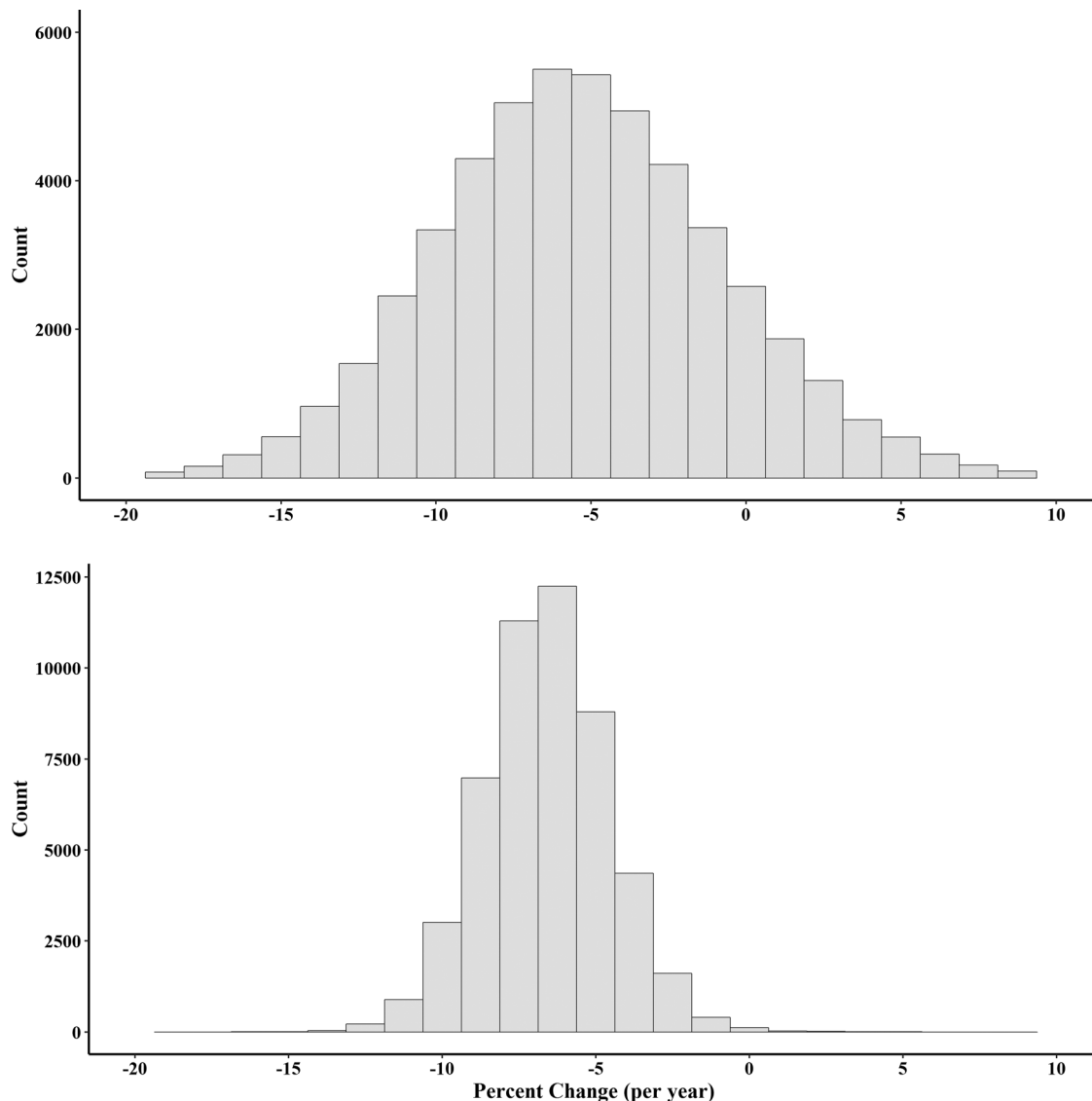
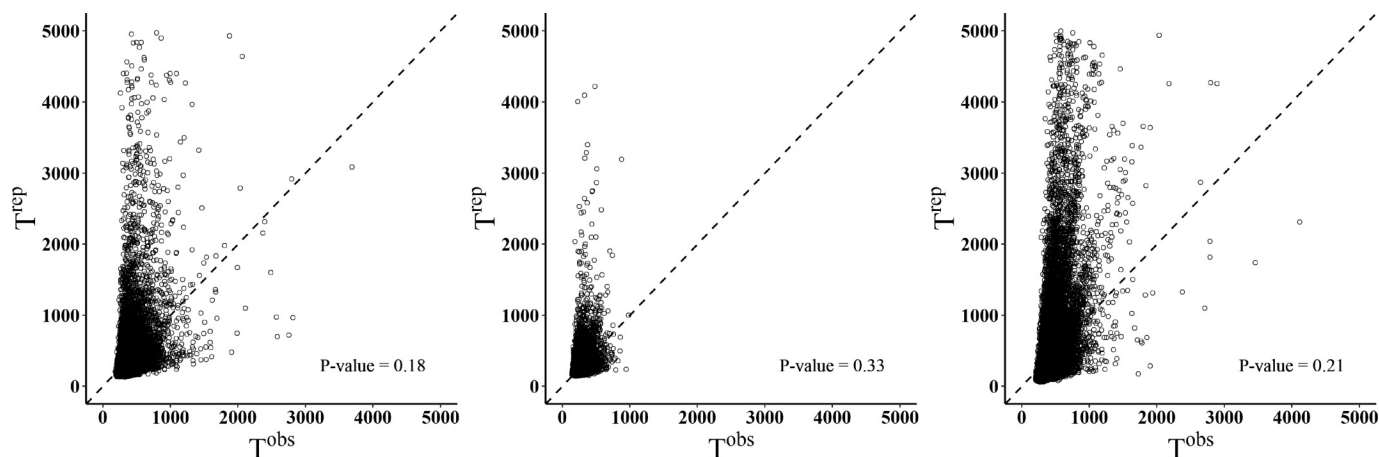


Fig. 4. Predictive replicate discrepancy statistics versus observed test statistics for three multisession models fit using the no-U-turn sampling algorithm in Stan. Posterior predictive p values were calculated as the proportion of points above the dashed 1:1 line. Left panel: independent intercepts model. Middle panel: 2003–2008 trend model. Right panel: 2003–2013 trend model.



(Fish and Wildlife Policy, Alberta Environment and Parks, Edmonton, Alberta, unpublished data). Therefore, the best available evidence suggested that whirling disease arrived in the LBR sometime during 2002–2016. Young-of-year and juvenile rainbow trout are particularly susceptible to whirling disease, which can cause recruitment failures (Markiw 1992; Walker and Nehring 1995; Vincent 1996). However, the impact of whirling disease on wild rainbow trout populations is highly variable (Bartholomew and Reno 2002). Management responses to whirling disease varied, but have included actions such as stopping or limiting stocking of infected fish into natural waters, emergency bag limit reductions for recreational anglers, and educational campaigns for the public (Modin 1998; Nickum 1999; Nehring 2006).

Floods in 2005 and 2013 represent another potential contributing factor to the LBR decline. Although both floods caused extensive damage, peak flows in the LBR during the 2013 flood were more than two times those observed during the 2005 flood (Veiga et al. 2015). These flows in 2013 substantially restructured fish habitat throughout the LBR (City of Calgary 2018). Previous studies that have assessed the impact of severe flood events on trout abundances have found responses ranging from dramatic decreases in trout density (Jowett and Richardson 1989; Kitanishi and Yamamoto 2015) to no change between pre- and postflood measurement periods (George et al. 2015). High flow events leading to food supply limitations and subsequent population collapse were responsible for boom-and-bust population cycles in a tailwater rainbow trout fishery below the Glen Canyon Dam in Arizona (Korman et al. 2017). However, this mechanism seems unlikely in the LBR, as substantial wastewater inputs have increased biological productivity (Sosiak 2002; Askey et al. 2007), and these inputs have remained relatively constant throughout the study period (see Taube et al. 2016). Intriguingly, abundance declined in both 2005 and 2013 according to postflood surveys (Fig. 3), perhaps because adult fish were displaced downstream. However, the mechanism of downstream displacement was unlikely to have been responsible for the entire decline observed, since declines also occurred in non-flood years.

High angling effort on the LBR may also have contributed to the observed decline via postrelease mortality. At present, no estimates of catch-and-release mortality exist in the LBR during the high effort summer fly-fishery. However, meta-analyses showed that catch-and-release mortality of rainbow trout ranged from 3% to 9% when fish were captured once via fly-fishing at water temperatures similar to those observed in the LBR during July–September (i.e., 10–22 °C; Bartholomew and Bohnsack 2005; Hühn and Arlinghaus 2011; however see Boyd et al. 2010). The best available creel survey on the LBR estimated that 49 700 rainbow trout were captured and released by anglers during July–September 2006 in a 50 km section of the LBR (Council and Ripley 2006), and our highest estimate of abundance in this section of the river is 20 700 catchable-size trout (Fig. 3; 414 fish·km⁻¹ × 50 km). Given these numbers, the exploitation rate for this fishery was potentially 0.07–0.22 for the summer fishery in 2006 (calculated as dead fish/abundance; Ricker 1975). These values may be high and could result in a constant mortality policy that does not scale with decreases in population size (see also Roughgarden and Smith 1996). This approximation ignores the potential for sublethal effects, such as interactions between the number of times a fish is captured and released and mortality rate (Bartholomew and Bohnsack 2005; Pope et al. 2007) and increased susceptibility to disease (Pickering and Pottinger 1989).

A number of potential concerns exist regarding these data and associated analyses, but we suggest that the trend documented was unlikely to be caused by these issues. For instance, a key study limitation was that no block nets were used during data collection, which was precluded by the large size of the LBR. Consequently, the estimated population sizes may be biased, as these were generated using closed population models. Furthermore,

the direction and magnitude of this bias depends on the behavior of animals along the periphery of the study area (Van Katwyk 2014). However, it is unclear how changes in fish behavior along the periphery of these relatively large study sites could result in the consistent population decline observed across the entire study period. Similarly, the decision to use a multisession modeling framework ignored the possibility that an individual fish occurred in more than 1 year (Royle et al. 2014), and we acknowledge that these models feature less ecological resolution than the outputs that would be generated via open population capture–recapture models (see Korman et al. 2017). The approach used here, however, was warranted because rainbow trout are short-lived (i.e., maximum age of 7 years; Rhodes 2005) and have high instantaneous total mortality (van Poorten and Post 2005), which indicated that there was likely high population turnover among years. Additionally, these data did not support the use of an open population model, as only nine total recaptures occurred across years. Similarly, no estimates of instantaneous tag loss exist, even though it may have been important (McFarlane et al. 1990; Walsh and Winkelman 2004; Vandergoot et al. 2012). However, tagging crews used the same protocols throughout the study period, and hence differences in instantaneous tag loss among years are unlikely to explain the consistent decline observed. While we acknowledge some weaknesses in the available data, it is unlikely that there was a consistent resultant “year” effect (i.e., consistent changes in animal behavior along the periphery of our study area or with tag loss differences among years). Lastly, the modeling approach we used incorporated both process and observation variability in its assessment of trout abundance, and while we did not explicitly model population resilience, we postulate the magnitude of decline over two to three generations should not be ignored in the hope that natural variability returns the population to a previous state.

The issues facing the LBR fishery and documented here are germane to many inland recreational fisheries, which are typified by poor or infrequent surveillance-style monitoring (Lester et al. 2003; Nate et al. 2003). For example, fundamental data limitations precluded the ability to determine the cause(s) of the estimated decline, despite compelling evidence that a decline occurred (Figs. 2 and 3). A paucity of reliable age and length data, along with inconsistent mark–recapture surveys, led to an inability to attribute the trend observed to reductions in juvenile or adult survival and hence to causal variables acting specifically on these life stages. As a result, the available data did not support the construction of explicit models to test among hypotheses responsible for the decline. Although additional information can reduce the number of alternative explanations for a decline (see Venturelli et al. 2014), calls to collect more data often fail to recognize key funding and personnel constraints limiting biologists (Canessa et al. 2015). Approaches that explicitly account for the marginal costs of data collection pursuant to management objectives and constraints could provide a strategic framework for triaging monitoring resources (e.g., value of information analysis; Hansen and Jones 2008). Similarly, targeted monitoring that views data collection as a component of a broader structured decision-making process, rather than as a lone activity, would maximize the utility of the data for distinguishing among competing hypotheses and help guide management actions in the face of uncertainty (Nichols and Williams 2006). Thus, improving the scientific defensibility of inland fisheries management via strategic monitoring and experimental management is necessary (McAllister and Peterman 1992; Post 2013; Hansen et al. 2015).

The threats facing the LBR fishery include stressors that are both within and beyond the control of local managers, which is similar to the SOS concept forwarded by S.R. Carpenter et al. (2017). Specifically, whirling disease and large flood events are uncontrollable from a management standpoint, with high fishing effort remaining as the lone stressor that managers can address.

For instance, managers can attempt to reduce catch-and-release mortality through indirect means such as gear restrictions or warm-weather closures (Cooke and Schramm 2007; Boyd et al. 2010), and indeed, the latter have occurred in the LBR in recent years when mean water temperatures exceeded 20 °C (i.e., full river closures in 2015 and voluntary restrictions 2017 where anglers were advised rather than required to not fish). Similarly, programs seeking to educate anglers on proper catch-and-release techniques may be helpful (Adams 2017). However, we suggest these may be patchwork solutions to managing release mortality, given that the LBR is a popular open-access fishery that flows through a densely populated urban center.

Angler effort restrictions may represent an important management option for maintaining rainbow trout in the LBR. Active management policies that seek to reduce fishing effort are often socially unacceptable (Schueller et al. 2012) and hence have rarely been implemented in inland recreational fisheries (Pereira and Hansen 2003). An approach that has been implemented with success, albeit in big-game wildlife management systems, is access limitation via lottery systems (Boxall 1995; Scrogin et al. 2000). Similar limited-entry management systems have been recommended and implemented in coastal sport fisheries (Cox et al. 2002; Abbott and Wilen 2009), and a harvest-tag program (but not effort limitation) is currently used to manage Alberta's high-effort walleye (*Sander vitreus*) fisheries (Sullivan 2003). Empirical evaluations of case studies such as these represent an important area for future work.

The LBR fishery demonstrates the complexities of maintaining inland recreational fisheries in the presence of multiple stressors. A key take-away from this study was that a combination of these stressors might have pushed rainbow trout in the LBR on an unsustainable trajectory during 2003–2013. We identified the most plausible causes of the rainbow trout decline and suggest these probably acted in concert to affect the patterns observed, similar to sustainability issues caused by multiple stressors in other inland recreational fisheries (Hansen et al. 2015). All three hypotheses warrant further investigation. Despite ambiguity in the causal factors responsible for the decline, we posit that managers of the LBR are left with few options short of active effort restrictions to maintain the fishery.

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Appendix A. Methods used to evaluate goodness-of-fit via posterior predictive p values for the multisession models used in our analyses

We evaluated our models using posterior predictive p values (Gelman et al. 2014). Seber (1982) provided an asymptotic discrepancy statistic based on the χ^2 distribution for a single closed capture–recapture model assuming multinomial sampling:

$$(A.1) \quad T = \sum_{\omega \in \Omega} \frac{(x_{\omega} - \hat{e}_{\omega})^2}{\hat{e}_{\omega}}$$

where x_{ω} is the number of individual fish with capture history ω , \hat{e}_{ω} is the expected number of animals with that capture history calculated at the parameter estimates, and Ω represents the set of capture histories excluding the all-zero history of “0000”. Link and Barker (2009) extended this statistic to a Bayesian posterior predictive check, such that e_{ω} is calculated for each draw (h) of the posterior. We added an additional summation symbol to the statistic described by Link and Barker (2009) to evaluate the global fit of the multisession models for all years considered in our analyses. We calculated our observed test statistics as

$$(A.2) \quad T_h^{\text{obs}} = \sum_{t=1}^7 \sum_{\omega \in \Omega} \frac{(x_{\omega} - e_{\omega}^h)^2}{e_{\omega}^h}$$

where e_{ω}^h corresponds to the expected number of animals with capture history parameter ω based on the parameter estimates for posterior draw h . We then compared T_h^{obs} with a replicate test statistic calculated as

$$(A.3) \quad T_h^{\text{rep}} = \sum_{t=1}^7 \sum_{\omega \in \Omega} \frac{(x_{h\omega}^{\text{rep}} - e_{\omega}^h)^2}{e_{\omega}^h}$$

where $x_{h\omega}^{\text{rep}}$ is drawn from the posterior predictive distribution for x_{ω} (Link and Barker 2009). The posterior predictive p value for each model was then calculated as the proportion of $T_h^{\text{rep}} > T_h^{\text{obs}}$ (Gelman et al. 2014), and we judged p values > 0.05 and < 0.95 as indications of sufficient fit (see also Royle et al. 2014).

Appendix Tables A1–A3 appear on the following pages.

Table A1. Marginal posterior summaries of parameters (2.5%, 50%, and 97.5% percentiles, posterior standard deviation (SD)) and diagnostic values (Neff = number of effective samples, \hat{R} = Gelman–Rubin statistic) from the independent intercepts multisession model 1 fitted to Lower Bow River rainbow trout data during 2003–2013.

Parameter	2.5%	50%	97.5%	SD	Neff	\hat{R}
ψ_{2003}	0.16	0.20	0.39	0.06	2998	1
ψ_{2005}	0.15	0.19	0.29	0.04	5342	1
ψ_{2007}	0.15	0.21	0.34	0.05	4176	1
ψ_{2008}	0.12	0.15	0.23	0.03	3810	1
ψ_{2011}	0.15	0.18	0.25	0.03	3823	1
ψ_{2012}	0.07	0.09	0.16	0.02	7360	1
ψ_{2013}	0.03	0.04	0.06	0.01	5750	1
$\beta_{0_{2003}}$	7.13	7.49	8.04	0.23	4348	1
$\beta_{0_{2005}}$	7.07	7.34	7.74	0.17	6097	1
$\beta_{0_{2007}}$	7.08	7.42	7.92	0.21	4725	1
$\beta_{0_{2008}}$	6.85	7.11	7.51	0.17	4171	1
$\beta_{0_{2011}}$	7.08	7.28	7.60	0.13	4205	1
$\beta_{0_{2012}}$	6.27	6.63	7.14	0.22	8221	1
$\beta_{0_{2013}}$	5.52	5.79	6.23	0.18	6248	1
N_{2003}	1256	1789	3083	479.62	3520	1
N_{2005}	1181	1542	2287	283.01	5264	1
N_{2007}	1199	1672	2749	407.29	4134	1
N_{2008}	950	1217	1827	226.03	3733	1
N_{2011}	1200	1458	1995	203.47	3723	1
N_{2012}	532	759	1259	188.93	7262	1
N_{2013}	257	326	501	0.86	5289	1
σ_{2003}	0.02	0.29	0.82	0.22	2945	1
σ_{2005}	0.01	0.23	0.70	0.19	3634	1
σ_{2007}	0.01	0.29	0.81	0.22	2892	1
σ_{2008}	0.01	0.28	0.80	0.21	2992	1
σ_{2011}	0.01	0.24	0.70	0.19	2179	1
σ_{2012}	0.01	0.28	0.80	0.21	5045	1
σ_{2013}	0.02	0.39	0.99	0.26	4676	1
$p_{2003,1}$	0.02	0.05	0.07	0.01	4690	1
$p_{2003,2}$	0.02	0.04	0.07	0.01	4684	1
$p_{2003,3}$	0.03	0.06	0.09	0.02	4586	1
$p_{2003,4}$	0.02	0.04	0.06	0.01	4799	1
$p_{2005,1}$	0.04	0.07	0.10	0.01	6204	1
$p_{2005,2}$	0.04	0.07	0.10	0.01	6084	1
$p_{2005,3}$	0.03	0.06	0.08	0.01	6285	1
$p_{2005,4}$	0.04	0.07	0.10	0.02	5971	1
$p_{2007,1}$	0.03	0.06	0.10	0.02	4670	1
$p_{2007,2}$	0.03	0.06	0.09	0.02	4655	1
$p_{2007,3}$	0.04	0.06	0.09	0.02	4558	1
$p_{2007,4}$	0.02	0.05	0.07	0.01	7573	1
$p_{2008,1}$	0.06	0.11	0.15	0.02	4121	1
$p_{2008,2}$	0.07	0.12	0.16	0.02	4128	1
$p_{2008,3}$	0.05	0.09	0.13	0.02	4360	1
$p_{2008,4}$	0.01	0.05	0.07	0.01	6092	1
$p_{2011,1}$	0.05	0.09	0.11	0.02	4414	1
$p_{2011,2}$	0.06	0.09	0.12	0.02	4430	1
$p_{2011,3}$	0.09	0.14	0.17	0.02	4268	1
$p_{2011,4}$	0.05	0.08	0.10	0.01	4624	1
$p_{2012,1}$	0.01	0.04	0.07	0.01	6534	1
$p_{2012,2}$	0.04	0.08	0.12	0.02	8591	1
$p_{2012,3}$	0.04	0.08	0.13	0.02	8489	1
$p_{2012,4}$	0.05	0.10	0.15	0.03	8261	1
$p_{2013,1}$	0.06	0.13	0.19	0.03	7038	1
$p_{2013,2}$	0.07	0.15	0.21	0.04	6911	1
$p_{2013,3}$	0.10	0.20	0.28	0.05	6515	1
$p_{2013,4}$	0.06	0.12	0.19	0.03	7039	1

Table A2. Marginal posterior summaries of parameters (2.5%, 50%, and 97.5% percentiles, posterior SD) and diagnostic values (Neff = number of effective samples, \hat{R} = Gelman–Rubin statistic) from the multisession trend model 2 fitted to Lower Bow River rainbow trout data during 2003–2008.

Parameter	2.5%	50%	97.5%	SD	Neff	\hat{R}
ψ_{2003}	0.16	0.22	0.32	0.04	5311	1
ψ_{2005}	0.17	0.20	0.24	0.02	4650	1
ψ_{2007}	0.15	0.18	0.22	0.02	4183	1
ψ_{2008}	0.13	0.17	0.23	0.02	4009	1
β_0	6.96	7.19	7.50	0.14	4172	1
β_1	−0.68	−0.25	0.19	0.22	4745	1
N_{2003}	1311	1760	2532	312.61	5300	1
N_{2005}	1320	1579	1958	162.66	4688	1
N_{2007}	1182	1414	1787	155.09	4289	1
N_{2008}	1054	1325	1815	155.09	3976	1
σ_{2003}	0.01	0.27	0.71	0.19	3897	1
σ_{2005}	0.01	0.24	0.61	0.16	4370	1
σ_{2007}	0.01	0.20	0.56	0.15	5676	1
σ_{2008}	0.01	0.36	0.81	0.21	3074	1
$p_{2003,1}$	0.03	0.05	0.07	0.01	5945	1
$p_{2003,2}$	0.03	0.04	0.06	0.01	5974	1
$p_{2003,3}$	0.04	0.06	0.09	0.01	5515	1
$p_{2003,4}$	0.02	0.04	0.06	0.01	5949	1
$p_{2005,1}$	0.05	0.07	0.09	0.01	6954	1
$p_{2005,2}$	0.05	0.07	0.09	0.01	6913	1
$p_{2005,3}$	0.04	0.05	0.07	0.01	7410	1
$p_{2005,4}$	0.05	0.07	0.09	0.01	6902	1
$p_{2007,1}$	0.06	0.08	0.10	0.01	6513	1
$p_{2007,2}$	0.05	0.08	0.10	0.01	6437	1
$p_{2007,3}$	0.07	0.10	0.13	0.01	5944	1
$p_{2007,4}$	0.02	0.05	0.07	0.01	7540	1
$p_{2008,1}$	0.06	0.10	0.13	0.02	4077	1
$p_{2008,2}$	0.07	0.10	0.15	0.02	4017	1
$p_{2008,3}$	0.05	0.08	0.11	0.02	4147	1
$p_{2008,4}$	0.01	0.05	0.07	0.02	5993	1

Table A3. Marginal posterior summaries of parameters (2.5%, 50%, and 97.5% percentiles, posterior SD) and diagnostic values (Neff = number of effective samples, \hat{R} = Gelman–Rubin statistic) from the multisession trend model 3 fitted to Lower Bow River rainbow trout data during 2003–2013.

Parameter	2.5%	50%	97.5%	SD	Neff	\hat{R}
ψ_{2003}	0.18	0.23	0.30	0.03	4158	1
ψ_{2005}	0.17	0.20	0.24	0.02	4105	1
ψ_{2007}	0.15	0.17	0.20	0.01	3767	1
ψ_{2008}	0.14	0.16	0.19	0.01	3458	1
ψ_{2011}	0.15	0.18	0.25	0.02	2950	1
ψ_{2012}	0.06	0.07	0.10	0.01	4145	1
ψ_{2013}	0.04	0.06	0.09	0.01	4194	1
β_0	6.91	7.04	7.19	0.07	3871	1
β_1	−0.83	−0.51	−0.20	0.16	4031	1
β_2	−1.00	−0.69	−0.39	0.16	3831	1
N_{2003}	1423	1810	2413	252.17	4181	1
N_{2005}	1324	1579	1954	160.73	4158	1
N_{2007}	1209	1385	1621	104.82	4061	1
N_{2008}	1133	1285	1492	91.45	3695	1
N_{2011}	1211	1464	1971	197.43	2457	1
N_{2012}	462	589	793	85.53	4320	1
N_{2013}	338	466	683	89.02	4108	1
σ_{2003}	0.02	0.28	0.70	0.19	3485	1
σ_{2005}	0.01	0.24	0.61	0.17	3770	1
σ_{2007}	0.01	0.19	0.52	0.14	6504	1
σ_{2008}	0.02	0.32	0.67	0.18	3608	1
σ_{2011}	0.01	0.25	0.69	0.19	2351	1
σ_{2012}	0.01	0.18	0.55	0.15	8843	1
σ_{2013}	0.24	0.82	1.29	0.26	3407	1
$p_{2003,1}$	0.03	0.05	0.07	0.01	4860	1
$p_{2003,2}$	0.03	0.04	0.06	0.01	5087	1
$p_{2003,3}$	0.04	0.06	0.08	0.01	4718	1
$p_{2003,4}$	0.03	0.04	0.06	0.01	5115	1
$p_{2005,1}$	0.05	0.07	0.09	0.01	5615	1
$p_{2005,2}$	0.05	0.07	0.09	0.01	5552	1
$p_{2005,3}$	0.04	0.05	0.07	0.01	5960	1
$p_{2005,4}$	0.04	0.07	0.09	0.01	5305	1
$p_{2007,1}$	0.06	0.07	0.10	0.01	8200	1
$p_{2007,2}$	0.06	0.08	0.10	0.01	7995	1
$p_{2007,3}$	0.08	0.10	0.13	0.01	7205	1
$p_{2007,4}$	0.02	0.05	0.07	0.01	7540	1
$p_{2008,1}$	0.08	0.10	0.13	0.01	5119	1
$p_{2008,2}$	0.09	0.11	0.14	0.01	5082	1
$p_{2008,3}$	0.06	0.09	0.1	0.01	5371	1
$p_{2008,4}$	0.01	0.05	0.07	0.02	6012	1
$p_{2011,1}$	0.05	0.08	0.11	0.01	3032	1
$p_{2011,2}$	0.06	0.09	0.12	0.02	2870	1
$p_{2011,3}$	0.09	0.14	0.17	0.02	2717	1
$p_{2011,4}$	0.05	0.08	0.10	0.01	3513	1
$p_{2012,1}$	0.01	0.04	0.07	0.01	3701	1
$p_{2012,2}$	0.07	0.10	0.14	0.02	6675	1
$p_{2012,3}$	0.07	0.11	0.15	0.02	6653	1
$p_{2012,4}$	0.09	0.13	0.18	0.02	6140	1
$p_{2013,1}$	0.04	0.08	0.14	0.03	4172	1
$p_{2013,2}$	0.04	0.09	0.15	0.03	4148	1
$p_{2013,3}$	0.06	0.12	0.21	0.04	4025	1
$p_{2013,4}$	0.03	0.07	0.13	0.03	4137	1