Received: 3 June 2020 | Accepted: 28 May 2021

DOI: 10.1111/cobi.13783

Conservation Biology

CONTRIBUTED PAPER

# Assessing conservation status with extensive but low-resolution data: Application of frequentist and Bayesian models to endangered Athabasca River rainbow trout

**John R. Post**[1] | **Hillary G. M. Ward**[1,2] | **Kyle L. Wilson**[1,3,4] | **George L. Sterling**[5] | **Ariane Cantin**[1] | **Eric B. Taylor**[6]

[1] Department of Biological Sciences, University of Calgary, Calgary, Alberta, Canada

[2] Ministry of Forests, Lands and Natural Resource Operations, Penticton, British Columbia, Canada

[3] Earth to Ocean Research Group, Department of Biological Sciences, Simon Fraser University, Burnaby, British Columbia, Canada

[4] Central Coast Indigenous Resource Alliance, Campbell River, British Columbia, Canada

[5] Fisheries Branch, Operations Division, Alberta Environment and Parks, Edson, Alberta, Canada

[6] Department of Zoology, Biodiversity Research Centre and Beaty Biodiversity Museum, University of British Columbia, Vancouver, British Columbia, Canada

**Correspondence**
John R. Post, Department of Biological Sciences, University of Calgary, 2500 University Drive NW, Calgary, AB T2N 1N4, Canada.
Email: jrpost@ucalgary.ca

**Article impact statement**: Based on definition of Athabasca rainbow trout designatable unit and estimated decline rate, this species should be listed as endangered.

## Abstract

Use of extensive but low-resolution abundance data is common in the assessment of species at-risk status based on quantitative decline criteria under International Union for Conservation of Nature (IUCN) and national endangered species legislation. Such data can be problematic for 3 reasons. First, statistical power to reject the null hypothesis of no change is often low because of small sample size and high sampling uncertainty leading to a high frequency of type II errors. Second, range-wide assessments composed of multiple site-specific observations do not effectively weight site-specific trends into global trends. Third, uncertainty in site-specific temporal trends and relative abundance are not propagated at the appropriate spatial scale. A common result is the propensity to underestimate the magnitude of declines and therefore fail to identify the appropriate at-risk status for a species. We used 3 statistical approaches, from simple to more complex, to estimate temporal decline rates for a designatable unit (DU) of rainbow trout in the Athabasca River watershed in western Canada. This DU is considered a native species for purposes of listing because of its genetic composition characterized as >0.95 indigenous origin in the face of continuing introgressive hybridization with introduced populations in the watershed. Analysis of abundance trends from 57 time series with a fixed-effects model identified 33 sites with negative trends, but only 2 were statistically significant. By contrast, a hierarchical linear mixed model weighted by site-specific abundance provided a DU-wide decline estimate of 16.4% per year and a 3-generation decline of 93.2%. A hierarchical Bayesian mixed model yielded a similar 3-generation decline trend of 91.3% and the posterior distribution showed that the estimate had a >99% probability of exceeding thresholds for an endangered listing. We conclude that the Bayesian approach was the most useful because it provided a probabilistic statement of threshold exceedance in support of an at-risk status recommendation.

KEYWORDS
Athabasca rainbow trout, conservation status thresholds, hierarchical Bayesian analysis, low-resolution data, population trend analysis

## Resumen

El uso de datos extensivos, pero de baja resolución, de la abundancia es una práctica común en la evaluación del estado de riesgo de una especie con base en los criterios cuantitativos de declinación establecidos por la Unión Internacional para la Conservación de la Naturaleza (UICN) y la legislación nacional sobre especies en peligro extinción. Dicha información puede ser problemática por tres razones: primero, el poder estadístico para rechazar la hipótesis nula de ningún cambio es frecuentemente bajo debido a un tamaño pequeño de la muestra y a la elevada incertidumbre del muestreo, lo que resulta en una frecuencia elevada de errores de tipo II; segundo, las evaluaciones de amplia variedad compuestas de varias observaciones específicas de sitio no sopesan efectivamente las tendencias específicas de sitio dentro de las tendencias globales; y tercero, la incertidumbre en las tendencias temporales específicas de sitio y en la abundancia relativa no se propagan a la escala espacial apropiada. Un resultado común del uso de esta información es la propensión a subestimar la magnitud de las declinaciones, y por lo tanto equivocarse en la identificación del estado de riesgo apropiado para la especie. Usamos tres estrategias estadísticas, de simples a más complejas, para estimar las tasas de declinación temporal para una unidad designable (UD) de trucha arcoíris en la cuenca del río Athabasca al oeste de Canadá. Esta UD es considerada una especie nativa por razones de listado debido a su composición genética, caracterizada como >0-95 de origen nativo de frente a la continua hibridación introgresiva con poblaciones introducidas a la cuenca. El análisis de las tendencias de abundancia de 57 series de tiempo con un modelo de efectos fijos identificó 33 sitios con tendencias negativas, pero sólo dos fueron estadísticamente significativas. En contraste, un modelo lineal mixto de jerarquías sopesado por abundancia específica de sitio proporcionó una estimación de declinación en toda la UD de 16.4% año$^{-1}$ y una declinación a tres generaciones de 93.2%. Un modelo bayesiano de jerarquías produjo una tendencia de declinación a tres generaciones de 91.3% y la distribución posterior mostró que el estimado tuvo una probabilidad >99% de exceder los umbrales para la categorización como especie en peligro. Concluimos que la estrategia bayesiana fue la más útil porque proporcionó una afirmación probabilística de la superación del umbral a favor de una recomendación de categorizar el estado como en riesgo.

**Palabras Clave:**
análisis bayesiano de jerarquías, análisis de tendencias poblacionales, datos de baja resolución, trucha arcoíris de Athabasca, umbrales del estado de conservación

# INTRODUCTION

Assessment of the conservation status of native species involves 2 sequential steps. First is the identification of the unit of biodiversity to be assessed, whether a species, subspecies, or a distinct population or group of populations within taxa, such as a distinct population segment under the U.S. Endangered Species Act or a designatable unit (DU) under Canada's Species at Risk Act (SARA). Once a unit of conservation is determined, available data on characteristics of geographical range and population trends are measured against quantitative thresholds to determine at-risk status. Both steps can be challenging when information on taxa is spatially and temporally sparse. These challenges are exacerbated in situations of invasion and introgression of non-native genotypes into native species. Introgression can increase extinction risk through outbreeding depression, introduction of maladaptive genes, wasted reproductive effort, and genetic swamping (Quilodrán et al., 2020). Substantial introgression can result in genomic extinction (Muhlfeld et al., 2014) and mean the species is no longer considered native and, therefore, the species is not eligible for assessment and legal protection (IUCN, 2012; COSEWIC, 2018).

One of the key quantitative criteria used for at-risk assessment of a conservation unit is evidence of observed, estimated, inferred, or suspected decline in the number of mature individuals over 3 generations (IUCN, 2012; COSEWIC, 2018). Rates of decline are presumed to provide measures of relative risk of extinction (Mace et al., 2008). Evaluation of this criterion requires time-series abundance data, derived either by direct observation or based on an index appropriate for the taxon (e.g., catch per unit effort, juvenile abundance). Direct observation is possible for some taxa that can be counted across their range, but more frequently the available data are an index of abundance from random or incidental data collections. These indices are then inferred to be representative of the total abundance of mature individuals. This type of information has been used in assessment of risk of extinction for about one-third of all species included in the IUCN Red List (Collen et al., 2016).

Despite their common use and importance in assigning risk status, estimating decline trends from time series poses challenges to accurate estimation and to making strong inferences. Often abundance time series are too short to reliably estimate trends (White, 2019), which can lead to acceptance of the null hypothesis of no decline when there is a real decline (i.e., type II error). A meta-analysis of abundance trends in marine mammals demonstrated that 43% of time series either fail to reject the null hypothesis of no decline or lead to the conclusion that data were not sufficient to carry out the analysis and that better monitoring efforts are required (Magera et al., 2013). This is not a unique observation; the problem of lack of power to detect decline trends for conservation assessments has been discussed by many (e.g., Rhodes & Jonzén, 2011; Magera et al., 2013; Keith et al., 2015; Collen et al., 2016; White, 2019). The challenge is in differentiating longer-term population trends from interannual variability with time series that are often short, have a small sample size, and often have substantial observation error.

Additionally, the conservation application is not only in interpreting statistical significance of regression parameters within a hypothesis-testing paradigm but also to assess weight of evidence that an estimated decline meets at-risk thresholds.

A second challenge in determining population trends is that status is not assessed for single sites, but rather for collections of sites encompassing the whole geographic range of the conservation unit, which is often distributed over large landscapes up to scale of whole continents (Taylor et al., 2013). Therefore, quantifying abundance trends for spatially structured conservation units requires monitoring multiple sites over time. In a designed survey, optimal effort decisions over space and time can be determined if a priori knowledge of the degree of spatial and temporal correlation and the magnitude of observation error is available (Rhodes & Jonzén, 2011). In many cases, however, it is more likely that the available information for trend analysis comes from opportunistically collected data rather than from task-specific designed monitoring programs. Because field researchers are typically limited by resources, they are faced with logistical trade-offs between extensive spatial coverage across broad landscapes, but with low resolution at individual sites or more detailed and more precise measures at a single or few sites. Surveys of species of conservation concern often focus on broader spatial coverage at the expense of precise local estimates. The result is often an extensive data set across the species' range that has low resolution at the individual-site scale. So, the analysis problem is in effectively characterizing temporal patterns at the scale of an entire conservation unit from multiple, but low-resolution, site-specific observations.

We were challenged with the situation of extensive, but low-resolution, abundance trend data and introgressive hybridization in an assessment of the status of a DU of rainbow trout (*Oncorhynchus mykiss*) in Canada. Our objectives were to identify the spatial scale of the DU of native rainbow trout based on evidence of genetic composition, spatial discreteness, and evolutionary significance in an area affected by introgressive hybridization; estimate decline trends at the scale of the whole DU from multiple, localized, and low-resolution relative abundance data; and to determine at-risk status of this DU based on a probabilistic estimate of exceeding criteria for legal listing under SARA.

# METHODS

## Geographic setting and defining the DU

Rainbow trout is endemic to northeastern Siberia and North America, but understanding of finer-scale distribution of native rainbow trout is often complicated by extensive and often unrecorded introductions (McPhail, 2007). In North America, they occur as freshwater resident (rainbow trout) and anadromous (steelhead trout) populations. Freshwater resident populations include Pacific drainages in the coastal and interior regions of Alaska, British Columbia, Washington, Oregon, California, and Baja California and east of the continental divide in 3 Arctic drainages of northern British Columbia and Alberta (Behnke, 1992; McPhail, 2007) (Figure 1). The watersheds east of the continental divide comprise 2 in northern British Columbia (Liard and Peace Rivers [Figure 1]) and 1 in northwestern Alberta (Athabasca River [Figure 1]). All 3 watersheds are tributaries of the Mackenzie River, but native rainbow trout occur only in the headwaters of these watersheds. Therefore, the rainbow trout of these watersheds are spatially discrete from each other and from those west of the continental divide, and likely have been since glaciation ~10,000 years ago (e.g., Nelson & Paetz, 1992; McCusker et al., 2000; Taylor et al., 2007).

The long-term viability of rainbow trout of the Athabasca River watershed is threatened by habitat loss and alteration (largely through oil and gas, forestry development, and associated transportation networks) and introgression with non-native genotypes (Taylor et al., 2007; Sinnatamby et al., 2019). As such, their conservation status in the Athabasca River watershed is of concern and has been assessed by the Committee on the Status of Endangered Species in Canada (COSEWIC) (COSEWIC, 2014). Distribution is highly correlated with elevation, and Athabasca River rainbow trout are restricted, fragmented, or absent from most streams lower than 850-m elevation and most common and with continuous distributions in streams with elevations from 900 to 1500 m. The Athabasca River watershed rainbow trout are thought to be uniquely adapted to cold, unproductive, headwater streams, which are characterized by a lack of interspecific competition and predation (Nelson & Paetz, 1992; COSEWIC, 2014). These habitat characteristics have resulted in several significant differences in the morphology, biology, and habitat use of Athabasca River rainbow trout, in contrast to rainbow trout in most of their natural range to the west (Sterling, 1990, 1992; Nelson & Paetz, 1992). They are therefore considered to be an evolutionarily significant component of rainbow trout biodiversity and hence a DU distinct from other rainbow trout in Canada.

Non-native rainbow trout have historically been stocked in the Athabasca River watershed; the first documented introduction occurred in 1926. These hatchery-raised fish originated from a variety of locations west of the continental divide, including California and the central interior of British Columbia (Taylor et al., 2007). There is strong evidence of spatially constrained introgressive hybridization between these non-native strains of rainbow trout and rainbow trout native to the Athabasca River watershed, which has led to genetically admixed populations (Taylor et al., 2007; Taylor & Yau, 2013). Native rainbow trout in Jasper National Park are considered extirpated owing to a high frequency of non-native alleles. Extirpated populations are those admixed populations in which the proportion of the genome that is indigenous ($Q_i$) as inferred using genetic techniques is <0.95 (i.e., such fish have hatchery genetic composition of >0.05) (Figure 1) and reflect extensive introgressive hybridization with hatchery fish (Taylor & Yau, 2013). Therefore, Jasper National Park was excluded from the DU of native Athabasca River rainbow trout (COSEWIC, 2014), and rainbow trout from the park are no longer considered a native wildlife species for purpose of legal listing under Canada's SARA (COSEWIC, 2018). This loss represents approximately 23% of the total watershed area of the upper Athabasca River watershed

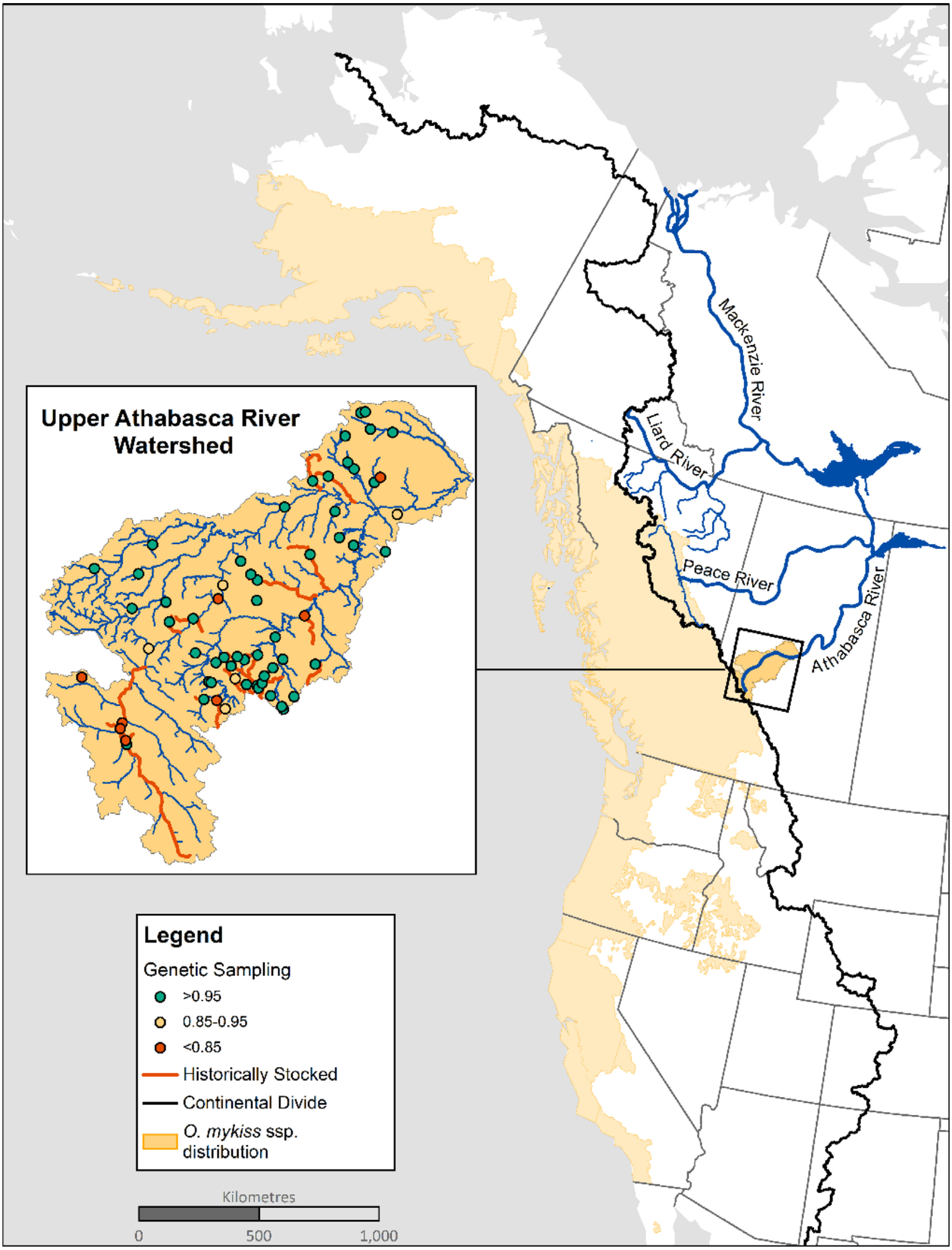

**FIGURE 1** Range map of native rainbow trout in North America (data from Penaluna et al., 2016), the continental divide, and the upper Athabasca River and its flow direction toward the Arctic Ocean. The inset shows genetic sampling in the Athabasca River watershed. Data points identify sites for which genetic analyses were conducted to determine an admixture coefficient ($Q_i$). Genetically pure indigenous samples have a $Q_i > 0.95$, and decreases in $Q_i$ correspond to an increase in the presence of non-native alleles. Data from Taylor and Yau (2013)

that was occupied by native rainbow trout postglacially (current native range 25,489 km$^2$). In addition to this substantial loss of native range, these naturalized non-native populations likely contribute a significant threat to native populations downstream through propagule pressure for introgression.

## Field abundance estimates

Data for this study were acquired from the Government of Alberta's Fisheries and Wildlife Management Information System (FWMIS). Most data on native rainbow trout abundance in the Athabasca River watershed were derived from single-pass electrofishing catch per unit area (CPUA) sampled at the reach scale (sites typically 300–1000 m in length). Single-pass electrofishing in streams, with an upstream blocking net, is more efficient than other methods because it allows greater spatial coverage in equivalent time and is strongly correlated to population estimates derived from mark–recapture studies (COSEWIC, 2014). Sampling was carried out in second- to fourth-order streams in July–August 1997–2011. Although many streams were sampled once throughout the watershed (3052 sites [Figure 2]) and captured native rainbow trout, we compiled data from streams that were sampled at least twice to determine temporal trends in abundance (57 sites) (Figure 2 & Appendix S1).

## Statistical analyses of abundance trends

We estimated temporal trends in abundance for 57 stream sites to assess the status of the Athabasca River rainbow trout (COSEWIC, 2018) (Appendix S1) in 3 stages. The R code for all analyses is provided in Appendix S2. First, we pooled all stream-site data and estimated site-specific trends in CPUA, $A_{i,t}$, for the year at time $t$ and stream $i$ with a log-linear regression:

$$\ln \ln \left(A_{i,t}\right) = \beta_i + \alpha_i \text{year}_{i,t} + \epsilon_{i,t}, \tag{1}$$

where $\alpha_i$ and $\beta_i$ are fixed effects independent for each stream and based on an observation error $\epsilon_{i,t} \sim N(0,\sigma)$, with $\sigma$ shared across all sites. Equation (1) was fit to observed CPUA data via maximum likelihood in R version 4.0.4 (R Core Team, 2020). Site-specific slopes $\alpha_i$ and intercepts $\beta_i$ (log transformed) were used to predict abundance at time $t = 1$. We used exponential models because they are applicable in situations of population growth or decay processes (Gerrodette, 1987) and in conservation applications where the decline criterion is percent decline per generation (IUCN, 2012; COSEWIC, 2018). We derived initial estimates of the DU-wide trend from Equation (1) by summing the site-specific annual percent declines (e.g., $\hat{A}_{i,t=2} - \hat{A}_{i,t=1}$) as a proportion of initial abundances across the set of $I$ sites:

$$\%\,\Delta_1 = \frac{\sum_i^I \hat{A}_{i,t=2} - \sum_i^I \hat{A}_{i,t=1}}{\sum_i^I \hat{A}_{i,t=1}}, \tag{2}$$

where initial abundances are estimated from the log-linear regression in Equation (1):

$$\hat{A}_{i,t_1} = e^{(\beta_i + \alpha_i year_{i,1})}. \tag{3}$$

However, this initial DU-wide estimate derived with log-linear regression fails to account for possible dependencies among sites or propagate uncertainty among parameter estimates, which becomes necessary to derive quantitatively defensible criteria required under IUCN or other national endangered species legislation from the statistical model. In our case, for example, the rate of change for the entire DU (Equation 2) required for COSEWIC assessments was derived from the weighted average of all site-specific trends. However, we needed to allow the DU-wide trends to be weighted more by the population changes in what were originally large populations rather than small populations. This lack of propagation of uncertainty between directly estimated parameters into derived parameters can be problematic when, for example, slopes and intercepts are estimated with varying degrees of uncertainty or when estimates are correlated.

In the second stage of our analysis, we used a frequentist mixed-effects model to jointly estimate both site-specific and DU-wide trends by partially pooling information among sites. This model adds random normally distributed deviates to site-specific trends and intercepts from Equation 1 (i.e., $\ln \ln (A_{i,t}) = \beta_i + \alpha_i \text{year}_{i,t} + \epsilon_{i,t}$) such that

$$\alpha_i = \alpha_{\text{DU}} + \epsilon_{\alpha,i}, \tag{4}$$

$$\epsilon_{\alpha,i} \sim N(0, \sigma_\alpha) \tag{5}$$

and

$$\beta_i \sim N\left(0, \sigma_\beta\right), \tag{6}$$

where $\alpha_{\text{DU}}$ is the average slope across the entire DU and $\epsilon_{\alpha,i}$ and $\beta_i$ are random normal deviates in the trend (or intercept) for site $i$ with mean 0 and variance $\sigma_\alpha$ (or $\sigma_\beta$). Like model 1, estimates for site-specific trends pool information and uncertainty from all sites (by placing constraints on among-site trends as arising from a normal distribution). Unlike model 1, with the mixed model we also estimated a global trend $\alpha_{\text{DU}}$. Furthermore, although model 1 treats each site as independent, the mixed model can account for some dependencies among sites such that sites with weak evidence (i.e., high uncertainty) shrink to the global mean, whereas sites with strong evidence (i.e., low uncertainty) can deviate more widely from the global mean. However, strong evidence can often require large amounts of data, >30 observations per group. Hence, mixed models relying on sparse observation data from a whole watershed may not allow for strong site-specific deviations from the global mean. We estimated our mixed-effects model with lme4 in R and calculated corresponding $p$-values (based on Satterthwaite

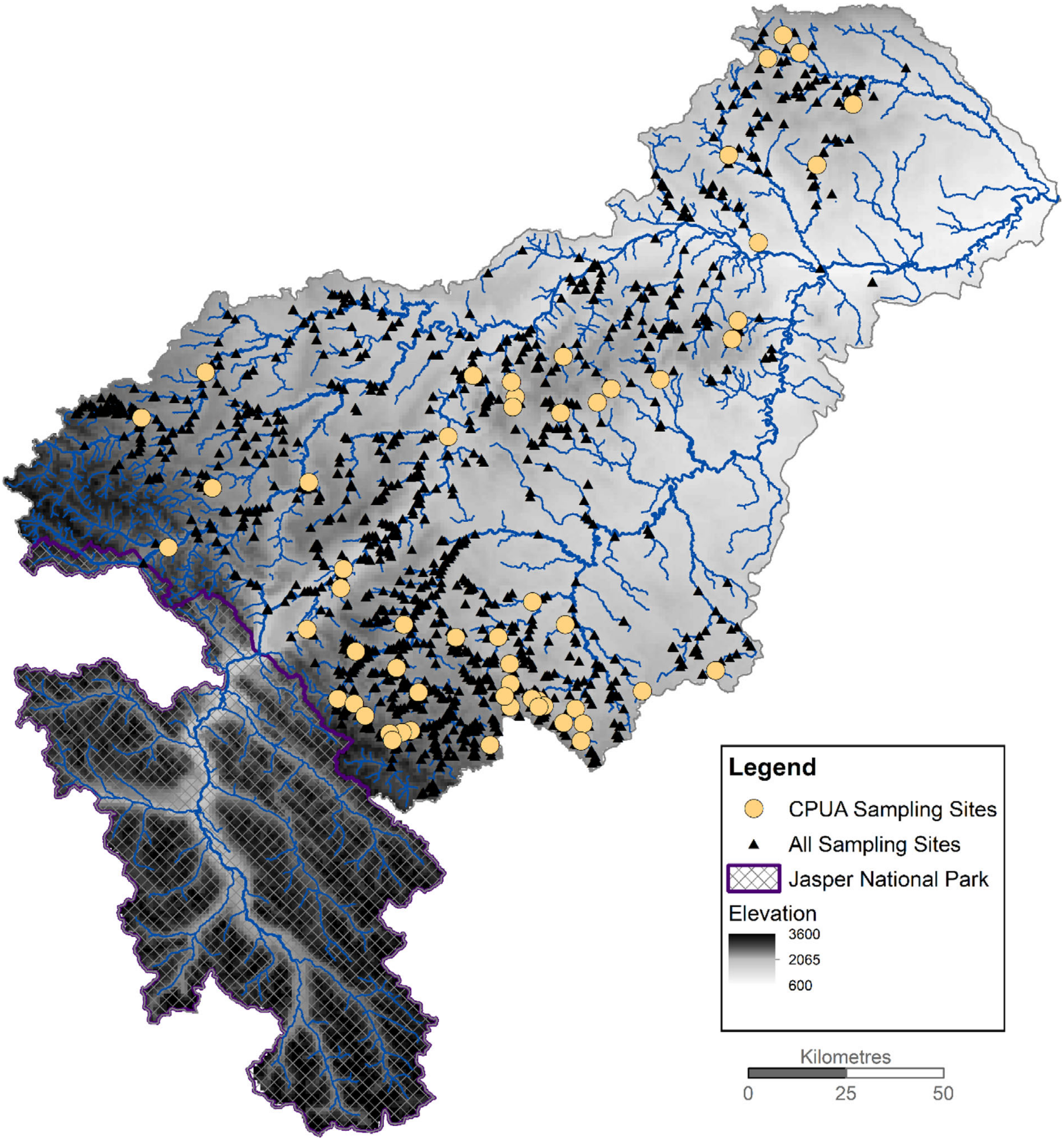

**FIGURE 2** Distribution of sampling points for Athabasca rainbow trout in the Upper Athabasca River watershed, where native rainbow trout were present, and the 57 sites for which time series of catch-per-unit-area are available. The uppermost area of the upper Athabasca River watershed in Jasper National Park is indicated because it is no longer considered to contain native rainbow trout due to substantial introgression with non-native stocked fish and therefore not part of the designatable unit for at-risk assessment

denominator degrees of freedom) and bootstrapped confidence intervals for site-specific trends with lmerTest and sim, respectively (Bates et al., 2015; Gelman & Su, 2020; Kuznetsova et al., 2017). We inferred significance for stream-specific random slopes if their bootstrapped 95% confidence intervals did not cross 0.

In the third stage of our analysis, we built a hierarchical Bayesian mixed-effects model to jointly estimate site-specific and DU-wide trends on a joint posterior distribution. Because limited temporal replication existed for CPUA observations in each stream, we incorporated uncertainty in estimates of the expected CPUA based on an average coefficient of variation across all sites assuming lognormal and multiplicative error. Based on this uncertainty, Markov chain Monte Carlo (MCMC) methods were used to sample the posterior distribution for the slope ($\alpha_i$) and intercept ($\beta_i$) in Equation (1) for each stream and to obtain probabilistic estimates of parameters and corresponding quantitative criteria. In other words, by using Bayesian techniques, we propagated the uncertainty in trends over time at each site with observation error to estimate uncertainty in trends over time for the whole DU. We solved Equation (1) in the hierarchical Bayesian model such that the slope $\alpha_i$ was hierarchical across all sites (i.e., assuming common environmental factors might jointly shape trends across the entire DU) and intercepts were independent fixed effects (i.e., that initial population sizes were independent among sites). The hierarchical slopes $\alpha_i$ were estimated probabilistically from a hyperprior such that

$$\alpha_i \sim N\left(\alpha_{\mathrm{DU}}, \frac{1}{\sqrt{\tau_\alpha}}\right), \tag{7}$$

where $\alpha_{\mathrm{DU}}$ is the slope across the entire DU and $\tau_\alpha$ is the inverse of the variance of site-specific slopes across the entire DU. The global slope $\alpha_{\mathrm{DU}}$ was given a vague normal prior centered on 0, and $\tau_\alpha$ was given a vague gamma distribution prior. Bayesian estimates of site-specific intercepts were estimated from independent vague priors such that

$$\beta_i \sim N\,(0, 10)\,, \tag{8}$$

where 10 is the presumed variance describing the width of their respective normal priors. Preliminary estimates of $\alpha_i$ and $\beta_i$ were consistent across less informative priors. Estimated abundances $\hat{\mathrm{A}}_{i,t}$ were then fitted to observed abundance $A_{i,t}$ based on the assumption of a lognormal likelihood such that

$$A_{i,t} \sim LN\left[\ln \ln\left(\hat{\mathrm{A}}_{i,t}\right), \sigma\right], \tag{9}$$

where $\sigma$ is the SD in observation error and

$$\sigma = \sqrt{\ln \ln\,(cv^2 + 1)}\,, \tag{10}$$

where $cv$ is the coefficient of variation of the untransformed abundance data. We modeled $cv$ with vague gamma prior under the assumption that uncertainty in observed abundances had multiplicative error. Maximum likelihood estimates from our first model provided the starting values and a basis for comparison with the Bayesian hierarchical model.

We derived estimates of the relative change in abundance per year ($\%\Delta_1$) for the entire DU with the relative uncertainty in local trends weighted by their site-specific initial abundances in Equation (2). We then projected the probability of a change in CPUA forward in years $N_{\mathrm{years}}$, with the posterior samples of $\beta_i$ and $\alpha_i$ to get status metrics relevant for COSEWIC assessments such that

$$\%\,\Delta_{N_{\mathrm{years}}} = (1 + \%\Delta_1)^{N_{\mathrm{years}}} - 1. \tag{11}$$

Thus, we propagated uncertainty from site-specific trends into probabilistic estimates of decline for the entire DU to align with policy-relevant assessment criteria.

We estimated our hierarchical model in openBUGS (Bayesian Inference Using Gibbs Sampling) 3.2.1 (available from http://www.openbugs.info/w/). This software implements an MCMC based on the Gibbs sampler to obtain a representation of the posterior probability density function (Thomas et al., 1992). To estimate model parameters, the MCMC was run for 100,000 iterations, and the first 10,000 iterations were removed to eliminate burn-in effects. Chains were initialized from 2 different starting points. Convergence of the chains was visually assessed by monitoring trace plots of the Markov chains as well as examining the Gelman–Rubin diagnostics (provided in the BRugs package for the R programming environment) so that the potential scale reduction factor for each parameter was <1.1 indicating convergence to a common posterior mode (Gelman et al., 2013).

## RESULTS

Based on the most commonly applied frequentist approach, the log-linear regression showed that 33 of 57 sites had negative trends in CPUA, but only 2 showed statistically significant declines ($p < 0.05$) (Figure 4). With the site-by-site weighting in Equation (2), the estimated trends from all sites resulted in a DU-wide trend of −17.7% per year. Frequentist inference from the fixed-effects model tended toward rejecting the statistical significance of the best trend estimate (−17.7% per year) in favor of failing to reject the null of no significant change in the abundance of Athabasca River rainbow trout.

The frequentist hierarchical mixed-effect model supported the observation that Athabasca River rainbow trout are in widespread decline (Figure 4). The hierarchical model estimated a significant unweighted global trend of −33.2% per year ($p < 2 \times 10^{-16}$, Satterthwaite df = 54.1) that, when weighted by site-specific abundances as in Equation (2), translated to a DU-wide trend of −16.4% per year. In contrast to the first model, site-specific trends tended to shrink to the global mean (estimated SD among site trends $\sigma_\alpha = 0.114$), leaving site-specific intercepts (corresponding to estimated initial abundances) to account for much of the remaining variation among streams (estimated SD among site intercepts $\sigma_B = 25.04$). Overall, we estimated 26 of 57 sites had significant trends in CPUA; 20 of these sites had significant declines. Hence, compared with the fixed-effects model, the hierarchical mixed-effect model suggests that most sites shared a similar decline and most of the variability was in their initial abundances. Extrapolating to 3 generations (15 years), as per criterion A4 of COSEWIC, 2018, the mixed model estimated a DU-wide trend of −93.2%, exceeding criteria thresholds for endangered status, but this extrapolation lacked appropriate estimates of uncertainty for application in a risk assessment.

The hierarchical Bayesian model showed substantial variability in the temporal trends among the 57 sites (Figure 3). The variance among the individual trends collapsed to some degree toward the mean unweighted trend of −13.2% per year, and 15 of the individual trend estimates were negative at the 80% credible interval (Figure 4). Weighting of the site-by-site analysis by relative abundance in a Bayesian framework resulted in a DU-wide trend of −16.1% per year (80% credible intervals of −11.6

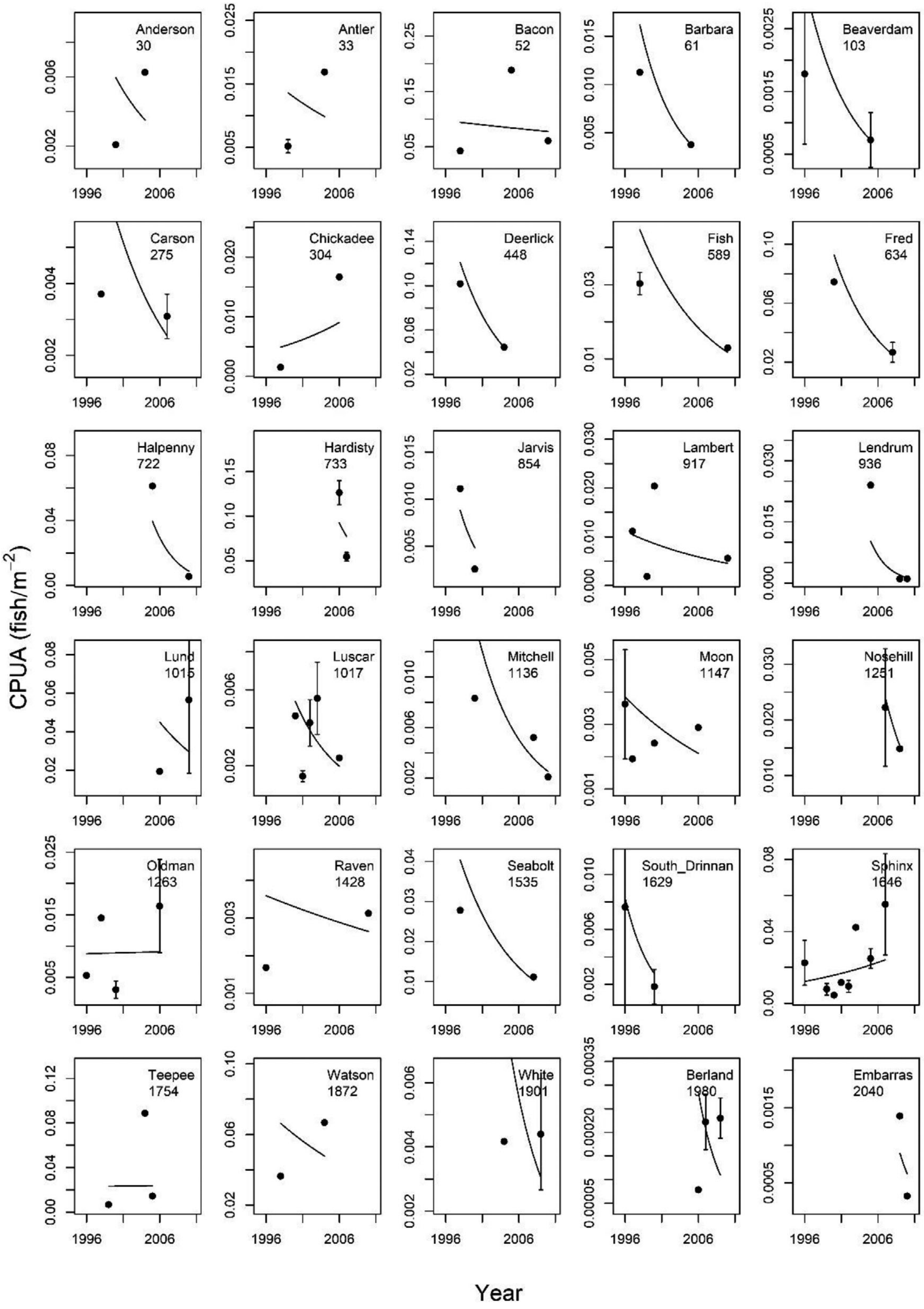

**FIGURE 3** Time series of catch-per-unit-area (CPUA) (error bars, 1 SE) for 57 tributaries in the Athabasca River drainage sampled for Athabasca rainbow trout and posterior mean trend estimates from the Bayesian model (black lines). Numbers below tributary names are stream identity numbers in the Government of Alberta's Fisheries and Wildlife Management Information System database

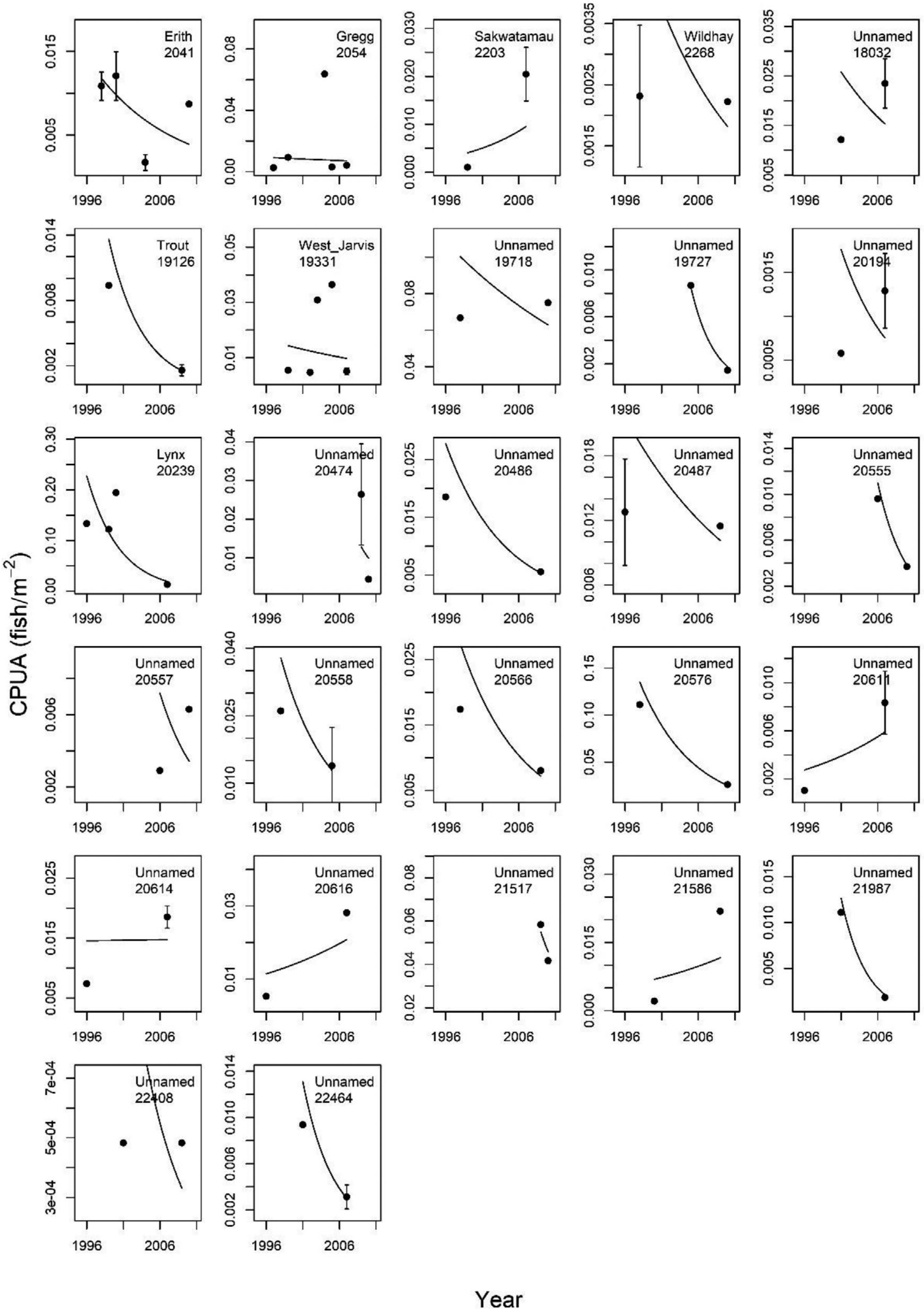

**FIGURE 3** Continued

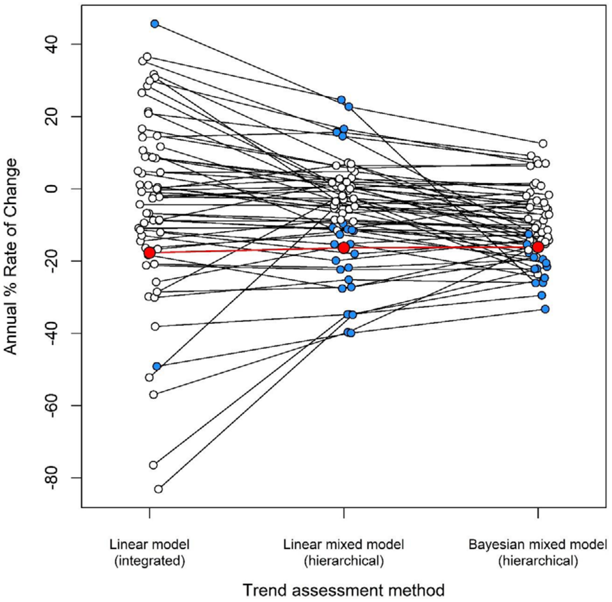

**FIGURE 4** Estimated trends in catch-per-unit-area of Athabasca rainbow trout for 57 sites in the Upper Athabasca River watershed analyzed with 3 statistical models. The frequentist linear model shows statistically significant (filled circles) and nonsignificant (open circles) trends. The frequentist linear mixed model shows estimated site-specific trends (blue circles, 95% bootstrapped confidence intervals for random slopes that do not cross 0; open circles include 0). For the Bayesian mixed model analysis, blue circles indicate the 80% credible intervals for site-specific trends do not cross 0, whereas open circles do. Red circles indicate abundance weighted estimates for designatable-unit-wide declines from each approach. Estimates are joined by lines for each of the 57 stream sites

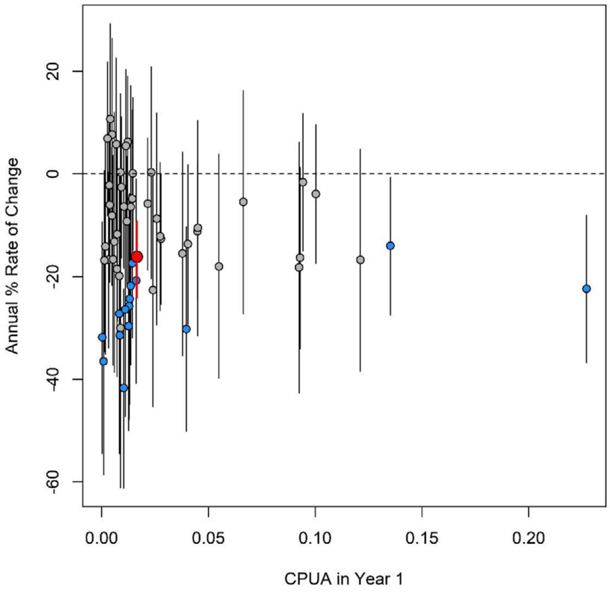

**FIGURE 5** Relationship between the Bayesian hierarchical posterior estimates of annual percent rate of change and catch-per-unit-area (CPUA) (fish per m$^2$) of Athabasca rainbow trout in the first year of data collection at each site (blue circles, declining population trends at 80% credible interval; red point and vertical bars, mean and 80% credible intervals for the abundance weighted annual decline rate at the scale of the whole designatable unit, respectively)

to −20.9% per year) (Figure 5)—similar to the DU-wide point estimate from the frequentist hierarchical mixed-effect model analysis. Despite less certain individual site trends, there was high certainty of a decline in the Athabasca River rainbow trout at the scale of the whole DU over 3 generations (15 years), as applicable to criterion A4 of COSEWIC (2018); posterior mean trend was −91.3% (80% credible interval: −84.3 to −97.0%) (Figure 6). We used the posterior distribution in the DU-wide trend to make probabilistic inferences on our confidence of various numerical decline thresholds. There was >99% probability that declines across the whole DU exceeded the threshold for endangered status (>−50% or −70%; threshold depending on whether the cause or causes of the change are understood and reversible [see COSEWIC, 2018 for complete status definitions]).

## DISCUSSION

Extensive low-resolution abundance data are common in the assessment of at-risk status based on quantitative criteria (Magera et al., 2013; White, 2019). These data can be problematic in the application of criteria to assessments for 3 reasons. First, statistical power to measure declines is often low because of few site-specific observations with high sampling uncertainty, leading to a high frequency of type II errors. Second, a DU-wide decline estimate requires weighting of individual site estimates by their relative abundance. Third, range-wide assessments based on mean and variance of multiple site-specific decline rates do not effectively incorporate uncertainty across multiple individual estimates. We characterized these statistical inadequacies for a risk assessment of the Athabasca River rainbow trout in Canada through an alternate approach that appropriately propagated local and global uncertainty. This resulted in a DU-wide assessment of risk status based on IUCN and COSEWIC population decline (criterion A).

In our hierarchical Bayesian analysis, data were pooled from multiple low-resolution time series from sites sampled across a widely distributed rainbow trout DU and thus provided an aggregate probabilistic estimate of rate of population decline. This estimate was interpreted in the context of decline criteria to assign a risk status of Endangered (COSEWIC, 2014). Hierarchical modeling, including frequentist and Bayesian paradigms, is a well-known approach to tackle the challenges and biases resulting from multiscale sampling (Royle & Dorazio, 2008; Bolker et al., 2009), and both hierarchical models provided similar estimates of declines in Athabasca River rainbow trout. However, applications of these statistical approaches in listings have been slow to be adopted in conservation applications despite their obvious appeal in addressing these estimation challenges. In particular, the Bayesian approach provides a continuous probability distribution, rather than a discrete inference of exceedance, or not, of risk thresholds. The more traditional approach is to assess independent site-specific analyses of temporal trends with discrete inference from null hypothesis testing that, in our case, failed to identify significant declines and would

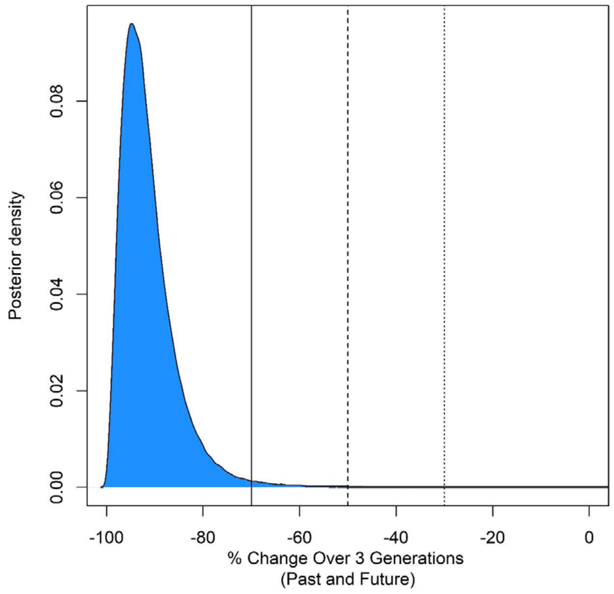

**FIGURE 6** Posterior probability distribution for estimated rate of change in Athabasca River rainbow trout, weighted by estimates of their catch-per-unit-area (CPUA) in the first year of data collection, over 3 generations, and over 15 years (dotted, dashed, and solid lines, decline thresholds of 30%, 50%, and 70%, respectively). These include current observations and any extrapolations necessary for a 15-year estimate

certainly have led to a not-at-risk designation for this DU. Based on this more commonly used approach of site-specific data, an analysis of marine mammals showed that better monitoring data were necessary for robust at-risk status assessments (Magera et al., 2013). It is likely in this marine-mammal application that a hierarchical Bayesian mixed-effects approach would have more accurately characterized decline rates, rejected the hypothesis of no decline, and lead to a more appropriate assignment of risk status.

The theory embedded in the hierarchical Bayesian approach is that the small-scale site-specific observations of trend and relative abundance are parameters associated with the joint probability model at the spatial scale of the whole DU (Berliner 1996 et al., 1996; Gelman et al., 2013). The conceptual interpretation is that even though individual site-specific observations, and their temporal trends, have substantial uncertainty on their own, the posterior distribution across sites best represents trends at the global scale. So, consistency in decline pattern among site-scale observations, despite their individual uncertainty, increases certainty in global trends. The results of the frequentist fixed-effects and hierarchical mixed-effects approaches and the hierarchical Bayesian mixed model are not contradictory, but rather imply divergent assumptions about the structure of the information. Bayesians would argue that the conclusions from site-by-site observations should be updated with additional observations if the goal is to best represent conclusions at the larger scale (Berliner, 1996; Gelman et al., 2013)—in this case, at the scale of the DU. Statistically, by pooling the information from site-specific observations, the hierarchical models, whether frequentist or Bayesian, shrink individual estimates of local population trends toward the aggregate mean (here the scale of the DU) thus reducing uncertainty in estimates of the trend across the DU. The Bayesian approach has the advantage of providing a posterior probability distribution against which the at-risk threshold criteria can be assessed. In addition, this approach allows imputing a trend estimate with a posterior probability distribution at the required time scale of 3 generations, or in fact any other time scale, despite many of the empirical time series being of shorter duration.

The IUCN quantitative criteria involve decline thresholds (e.g., >30%, 50%, or 70%) over 3 generations. The hierarchical Bayesian analysis provides a posterior distribution on which the decline thresholds can be placed. This allows inferences to be drawn about probability of the threshold being exceeded, rather than just a simple conclusion of exceedance or not. In our analysis, we simply accepted that the threshold would be exceeded if the threshold had a >50% probability of being exceeded. The corollary is that we accepted a probability of mistakenly rejecting a threshold when it was met with the probability of up to 50%. It can be argued, in a precautionary sense, that this probability of failing to recognize an appropriate risk status is much too high. The key advantage of this approach is that practitioners can provide an explicit statement of the degree of risk aversion and weight of evidence used in their listing recommendation.

An additional strength of this approach is in propagating uncertainty across the hierarchy of observations to allow weighting of trend observations based on local and global uncertainty and local relative abundance. Because the conservation assessment task was to develop a trend analysis of the scale of the DU, the contribution of site-specific trends in abundance and inherent uncertainty is summarized at the appropriate spatial scale. In our example, it was the largest subpopulations that tended to have larger declines and therefore dominated the posterior probability distribution of decline for the DU.

The quantitative criterion used to assess status from decline rate refers to declines in population abundance over 3 generations. An analytical issue in this assessment was in estimating a 3-generation trend given variable and typically shorter time series. Our analyses incorporated data from sites for which there were 2 or more estimates of CPUA, yet these time series did not necessarily align with the required 3-generation time scale. The model estimate was in units of annual percent decline rate yet needed to be extrapolated to 3 generations (15 years in this case). The hierarchical analysis, which appropriately incorporates uncertainty in these estimates, provided posteriori estimates for extrapolation of the data to the required 3-generation criteria despite inclusion of many time series not meeting this requirement. We then contrasted these estimated trends for the whole DU to the at-risk thresholds for criterion A4 (COSEWIC, 2018), which includes data from the past plus a sufficient number of additional years to represent the full 3 generations.

In addition to the substantial decline in the abundance of Athabasca River rainbow trout across the DU, the native genome is being eroded by introgressive hybridization with hatchery fish. Unfortunately, there are not sufficient spatial data to determine the rate of decline of the native genome at the scale of the DU. Temporal genetic data on the degree of introgression are available for only 3 paired sites located in the main stem of the Athabasca River. Between 2000 and 2011, $Q_i$ values (admixture coefficient, representing the proportion of the genome that is of indigenous origin) decreased from 0.5% to 4.3% per year, and the average decrease was 29.2% over 3 generations (15 years) at these sites (Taylor et al., 2007; Taylor & Yau, 2013). The rate at which introgression will proceed across this large fractal watershed, with hundreds of tributaries, is uncertain, but it is clearly advancing due to the movement of nonnative genotypes and their progeny in the DU.

In summary, multiple spatially distributed observations of abundance, despite low individual resolution, can be used within a hierarchical Bayesian framework to estimate rangewide decline rates of organisms. These analyses are therefore more appropriate than more broadly utilized frequentist fixed-effects statistical approaches for application to situations with multiple hierarchically structured abundance estimates and should be employed to provide a more robust and defensible assessment of risk status at these larger scales. With robust probabilistic assessments of exceedance of decline thresholds, evidence-based decisions of risk status can be made within a precautionary policy framework, such as those developed by IUCN globally and by COSEWIC in Canada.

In our experience in assigning at-risk status for Canadian species assessment carried out by COSEWIC over more than a decade, the committee is most comfortable with dichotomous assignment of status based on the statistical significance of trends estimated through simple regression techniques, where the mean trend exceeds thresholds. But this approach, although simple, is ineffective in incorporating weight of evidence accumulated across space with uncertainty. This weight of evidence is more effectively characterized by the continuous description of trend uncertainty provided by the approach we advocate. But the final assessment still needs to be dichotomous, at risk (i.e., threatened or endangered) or not at risk, which forces proponents to be explicit about their willingness to underestimate risk status given the precautionary principle. In our Athabasca rainbow trout example, the mean decline trend is much greater than the threshold for endangered and the portion of the posterior distribution that is below the threshold is very small, so the dichotomous decision is clear. But in the case where the posterior distribution straddles the threshold, practitioners will have to be explicit about their risk aversion to failing to assign risk when there is risk. As far as we can tell, the literature does not provide guidelines on this. If, for example, the threshold splits the posterior distribution by approximately half, an assessment of not at risk is associated with a probability of being wrong about one-half of the time, arguably inappropriate given the precautionary principle as applied to the consequences of extinction. The precise threshold for exceeding quantitative decline criteria represents management's tolerance to the risk of not protecting a threatened or endangered species. Although it can be reasonably argued that a 50% chance of making such an error is too high, is 20% or 5% more appropriate? Conservation agencies should develop guidelines for use of the IUCN status-assessment approach based on population decline criteria coupled with explicit measures of uncertainty.

## ACKNOWLEDGMENTS

We acknowledge staff from Alberta Environment and Parks, Jasper National Park, and the Foothills Model Forest Hinton who collected the extensive field data over several decades that we used to assess the conservation status of the Athabasca River rainbow trout. Support for this research was provided by Natural Sciences and Engineering Research Council of Canada (NSERC) Discovery Grants (to J.R.P. and E.B.T.), Environment and Climate Change Canada (to H.G.M.W.), and Banting Postdoctoral Fellowship Program (to K.L.W.).

## ORCID

*John R. Post* https://orcid.org/0000-0002-2963-2824

## LITERATURE CITED

Bates, D., Maechler, M., Bolker, B., & Walker, S. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, *67*, 1–48.

Behnke, R. J. (1992). *Native trout of western North America. Monograph 6*. American Fisheries Society.

Berliner, L. M. (1996). Hierarchical Bayesian time series models. Pages 15–22 in K. M. Hanson, & R. N. Silver, editors. *Maximum entropy and Bayesian methods*. Springer.

Bolker, B. M., Brooks, M. E., Clark, C. J., Geange, S. W., Poulsen, J. R., Stevens, M. H. H., & White, J. S. S. (2009). Generalized linear mixed models: a practical guide for ecology and evolution. *Trends in Ecology & Evolution*, *24*, 127–135.

Collen, B., Dulvy, N. K., Gaston, K. J., Gärdenfors, U., Keith, D. A., Punt, A. E., Regan, H. M., Böhm, M., Hedges, S., Seddon, M., Butchart Stuart, H. M., Hilton-Taylor, C., Hoffmann, M., Bachman, S. P., & Akçakaya, H. R. (2016). Clarifying misconceptions of extinction risk assessment with the IUCN Red List. *Biology Letters*, *12*, 20150843.

COSEWIC. (2014). Assessment and status report on the Rainbow Trout *Oncorhynchus mykiss* in Canada. Author.

COSEWIC. (2018). *Operations and procedures manual*. Author.

Gelman, A., Carlin, J. B., Stern, H. S., Dunson, D. B., Vehtari, A., & Rubin, D. B. (2013). *Bayesian data analysis* (3rd ed.). Chapman and Hall/CRC Press.

Gelman, A., & Sung Su, Y.-S. (2020). *arm: data analysis using regression and multilevel/hierarchical models*. R package version 1.11-2. https://CRAN.R-project.org/package=arm.

Gerrodette, T. (1987). A power analysis for detecting trends. *Ecology*, *68*, 1364–1372.

International Union for Conservation of Nature (IUCN). (2012). *IUCN red list categories and criteria: Version 3.1* (2nd ed.). Author.

Keith, D. et al. (2015). Temporal correlations in population trends: Conservation implications from time-series analysis of diverse animal taxa. *Biological Conservation*, *192*, 247–257.

Kuznetsova, A., Brockhoff, P. B., & Christensen, R. H. B. (2017). lmerTest package: Tests in linear mixed effects models. *Journal of Statistical Software*, *82*, 1–26.

Mace, G. M., Collar, N. J., Gaston, K. J., Hilton-Taylor, C., Akçakaya, H. R., Leader-Williams, N., Milner-Gulland, E. J., & Stuart, S. N. (2008). Quantification of extinction risk: IUCN's system for classifying threatened species. *Conservation Biology*, *22*, 1424–1442.

Magera, A. M., Flemming, M., Kaschner, J. E., Christensen, K. B., & Lotze, L. B. (2013). Recovery trends in marine mammal populations. *PLoS ONE*, *8*, 77908.

McCusker, M. R., Parkinson, E., & Taylor, E. B. (2000). Mitochondrial DNA variation in rainbow trout (*Oncorhynchus mykiss*) across its native range: Testing biogeographical hypotheses and their relevance to conservation. *Molecular Ecology*, *9*, 2089–2108.

McPhail, J. D. (2007). *The freshwater fishes of British Columbia*. The University of Alberta Press.

Muhlfeld, C. C., Kovach, R. P., Jones, L. A., Al-Chokhachy, R., Boyer, M. C., Leary, R. F., Lowe, W. H., Luikart, G., & Allendorf, F. W. (2014). Invasive hybridization in a threatened species is accelerated by climate change. *Nature Climate Change*, *4*, 620–624.

Nelson, J. S., & Paetz, M. J. (1992). *The fishes of Alberta*. University of Alberta.

Penaluna, B. E., Abadía-Cardoso, A., Dunham, J. B., García-Dé León, F. J., Gresswell, R. E., Luna, A. R., Taylor, E. B., Shepard, B. B., Al-Chokhachy, R., Muhlfeld, C. C., Bestgen, K. R., Rogers, K., Escalante, M. A., Keeley, E. R., Temple, G. M., Williams, J. E., Matthews, K. R., Pierce, R., Mayden, R. L., … Fausch, K. D. (2016). Conservation of native pacific trout diversity in western North America. *Fisheries*, *41*(6), 286–300.

Quilodrán, C. S., Tsoupas, A., & Currat, M. (2020). The spatial signature of introgression after biological invasion with hybridization. *Frontiers in Ecology and Evolution*, *8*, 1–15.

Rhodes, J. R., & Jonzén, N. (2011). Monitoring temporal trends in spatially structured populations: how should sampling effort be allocated between space and time? *Ecography*, *34*, 1040–1048.

Royle, J. A., & Dorazio, R. M. (2008). *Hierarchical modeling and inference in ecology: The analysis of data from populations, metapopulations and communities*. Elsevier.

R. Core Team. (2020). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing. https://www.R-project.org/

Sinnatamby, N., Cantin, A., & Post, J. R. (2019). Threats to at-risk salmonids of the Canadian Rocky Mountain region. *Ecology of Freshwater Fish*, *29*, 477–494.

Sterling, G. L. (1990). Population dynamics of rainbow trout (*Oncorhynchus mykiss*) in the tri-creeks experimental watershed of west-central Alberta; a post-logging evaluation. Alberta Forestry, Lands and Wildlife.

Sterling, G. L. (1992). Fry emergence survival of rainbow trout, *Oncorhynchus mykiss* (Walbaum), following timber harvest in two foothill streams of west-central Alberta. University of Alberta.

Taylor, E. B., Darveau, C. A., & Schulte, P. M. (2013). Setting conservation priorities in a widespread species: Phylogeographic and physiological variation in the lake chub, *Couesius plumbeus* (Pisces: Cyprinidae). *Diversity*, *5*, 149–165.

Taylor, E. B., Tamkee, P., Sterling, G., & Hughson, W. (2007). Microsatellite DNA analysis of rainbow trout (*Oncorhynchus mykiss*) from western Alberta, Canada: Native status and evolutionary distinctiveness of “Athabasca” rainbow trout. *Conservation Genetics*, *8*, 1–15.

Taylor, E. B., & Yau, M. M. (2013). *Analysis of introgression between indigenous and introduced rainbow trout (Oncorhynchus mykiss) in western Alberta*. Alberta Environment and Sustainable Resource Development, Operations Division, Fisheries Branch.

Thomas, A., Spiegelhalter, D. J., & Gilks, W. (1992). BUGS: A program to perform Bayesian inference using Gibbs sampling. Pages 837–842 in J. Bernardo, J. Berger, A. Dawid, & A. F. M. Smith, editors. *Bayesian statistics 4*. Oxford University Press.

White, E. R. (2019). Minimum time required to detect population trends: The need for long-term monitoring programs. *Bioscience*, *69*, 40–46.

## SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

**How to cite this article:** Post JR, Ward HGM, Wilson KL, Sterling GL, Cantin A, Taylor EB. Assessing conservation status with extensive but low-resolution data: Application of frequentist and Bayesian models to endangered Athabasca River rainbow trout. *Conservation Biology*. 2021;1–13. https://doi.org/10.1111/cobi.13783