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Quantifying long-term population growth rates of threatened bull trout: challenges, lessons learned, and opportunities.

Phaedra E. Budy^{1, 2,*}

Tracy Bowerman²

Robert Al-Chokhachy³

Mary Conner⁴

Howard Schaller⁵

¹ U.S. Geological Survey – Utah Cooperative Fish and Wildlife Research Unit

² Department of Watershed Sciences and the Ecology Center, 5210 Old Main Hill Utah State University, Logan, Utah 84322

³ U.S. Geological Survey, Northern Rocky Mountain Science Center

⁴ Department of Wildland Resources and the Ecology Center, 5200 Old Main Hill Utah State University, Logan, Utah 84322

⁵ U.S. Fish & Wildlife Service, Pacific Region - Fisheries and Aquatic Conservation Program

*Corresponding Author: P. E. Budy

Abstract (175)

Temporal symmetry models (TSM) represent advances in the analytical application of mark-recapture data to status assessments. For a population of char, we employed 10 years of active and passive mark-recapture data to quantify population growth rates using different data sources and analytical approaches. Estimates of adult population growth rate were 1.01 (95% CI = 0.84-1.20) using a temporal symmetry model (λ_{TSM}), 0.96 (0.68-1.34) based on log-regressions of annual snorkel data (λ_{A}), and 0.92 (0.77-1.11) from redd counts (λ_{R}). Top performing TSMs included an increasing time trend in 'recruitment' (f) and changes in capture probability (p). There was only a 1% chance the population decreased $\geq 50\%$, and a 10% chance it decreased $\geq 30\%$ (L_{MCMC}). Size structure was stable; however, the adult population was dominated by small adults, and over the study period there was a decline in the contribution of large adults to total biomass. Juvenile condition decreased with increasing adult densities. Utilization of these different information sources provided a robust weight-of-evidence approach to identifying population status and potential mechanisms driving changes in population growth rates.

Introduction

Population growth rates, or the rate of change in a population, is an important viability metric describing the cumulative effects of survival and mortality over time. Accordingly, quantifying population growth rates is one of the most important components in the management of freshwater fishes (Morris and Doak 2002; e.g., Grossman et al. 2006). Estimates of population growth rates can be used in combination with measures of abundance and other vital rates to evaluate the likely persistence of populations given environmental change (e.g., Doak and Morris 1999) and the effectiveness of different management strategies (Maxell 1999; Holmes and York 2003). However, reliable estimates of the rate of population change can be extremely difficult to obtain due to logistical constraints and biological realities

(e.g., the long time periods needed; Ham and Pearsons 2000) and inherent uncertainties associated with dynamic populations (e.g., Hilborn and Walters 1992).

Advances in analytical approaches offer promise for providing unbiased estimates of the rate of population change. For example, state-space models have recently been applied to improve the accuracy and precision of population abundance and density estimates by separating observation and process error in fish abundance data (Chasco et al. 2014; Meyer et al. 2014). Similarly, the temporal symmetry model (TSM), developed by Pradel (1996), offers an alternative approach to obtain robust population growth rate estimates via integrated mark-recapture data. For example, Pine et al. (2001) used a TSM to evaluate population status for imperiled sturgeon (*Acipenser oxyrinchus desotoi*) relative to management actions (e.g., harvest moratorium). Despite potential for the TSM to provide critical insights into factors affecting population growth rates and its application in other high profile status assessments (e.g., Franklin et al. 2000; Anthony et al. 2006; Dugger et al. 2016), the use of TSM in fisheries remains extremely limited (but see Pine et al. 2001). Such limited application is surprising given the widespread use of mark-recapture methods and the effectiveness of this approach for estimating rates of population change (e.g., Schorr 2012; Tenan et al. 2014).

Population growth rate, or trend, assessments are an integral component in the effective recovery and management of endangered species such as bull trout (*Salvelinus confluentus*), a species of char native to the Pacific Northwest listed as 'Threatened' in the United States and 'Of Special Concern' or 'Threatened' for three of four geographic populations in Canada (USFWS 2012; COSEWIC 2012). Obtaining reliable estimates of population growth rate can be challenging for many species (Williams et al. 2002), and such challenges are exacerbated for species such as bull trout, a species of limited economic value and for which few resources are spent on monitoring. In addition, bull trout are difficult to capture and generally associated with complex habitat types (Al-Chokhachy et al. 2010), behaviorally cryptic (e.g., Banish et al. 2008), may occur at low densities (e.g., Al-Chokhachy and Budy 2007) and their distributions are patchy across watersheds (e.g., Eby et al. 2014; Isaak et al. 2015). While there have been a number of efforts to quantify general trends in bull trout abundance (e.g., High et al. 2008; Erhardt

and Scarnecchia 2014), there have been few studies that simultaneously estimate population growth rates and explicitly evaluate the vital rates that drive those trends (i.e., the mechanisms behind observed patterns).

Here, we address this need by employing 10 years of mark-recapture data specifically collected to: 1) quantify population growth rates using different data sources and models, 2) evaluate the information provided by each metric from a biological status assessment perspective (e.g., certain metrics may better capture population growth rates in different life stages), and 3) and identify potential mechanisms driving changes in population growth rate, including density dependent effects, changes in size structure, and biomass.

Methods

Study site and sampling design

As recovery planning for threatened bull trout grew in the late 1990's, a significant number of critical uncertainties were identified that could prevent the prioritization and effectiveness of future management actions as well as our ability to determine population viability and status (USFWS 2015). To guide recovery planning, the South Fork Walla Walla River (SFWWR), was identified *a priori* in 2002 as one of several critical index populations targeted for detailed study, monitoring, and analysis (USFWS 2010). Collectively, this study has addressed critical uncertainties of both genetic structure and movement patterns among different life-history expressions (Homel et al. 2008; Homel and Budy 2008), large and small-scale habitat needs and preferences (Al-Chokhachy and Budy 2007; Al-Chokhachy et al. 2010), demographic rates for early life stages, juveniles and adults (Al-Chokhachy and Budy 2008; Bowerman and Budy 2012; Bowerman et al. 2014), sampling limitations, and recommendations for estimating annual abundance (Al-Chokhachy et al. 2005, 2009).

The SFWWR is a tributary of the Walla Walla River in Northeastern Oregon (Fig. 1), originating in the Blue Mountains, located at the eastern boundary of the arid steppe of the Columbia River Basin. Despite the relatively low elevation of the SFWWR (610 – 1000 m) and the hot summer climate of this

region, sufficient groundwater influences maintain cool stream temperatures (Schaller et al. 2014) preferred by bull trout (<12 °C; Dunham et al. 2003; Isaak et al. 2010, 2015).

The SFWWR study area is contained primarily in the Umatilla National Forest, where relatively few forest management activities occur, and primary recreational activities include hiking, fishing, and off-road motorcycle use. The study area is approximately 21 km in length, with stream habitat conditions ranging from confined-channel reaches with steep or bedrock hillslopes to relatively unconfined reaches with complex, meandering channels. The fish assemblage within the study area is composed of native fishes: rainbow and steelhead trout (*Oncorhynchus mykiss* spp.), Chinook salmon (*O. tshawytscha*), mountain whitefish (*Prosopium williamsoni*), and sculpin (*Cottus* spp.), in addition to bull trout. Downstream of the SFWWR study area, habitat conditions are more degraded, with higher water temperatures, stream channelization, and dams and diversions that likely act as barriers to migration (Schaller et al. 2014).

Sampling methods

Mark-recapture data

We divided the SFWWR study site into 102 reaches at least 200 m in length (average width = 10 m). From those 102 possible reaches, we used a systematic sampling design (random start) to select sample reaches and achieve spatial balance throughout the study area (Stevens and Olsen 2004). From 2002 to 2011, we sampled the same 21 reaches (>20% of the study area) each year between mid-June and early August (Fig. 1).

We captured bull trout (hereafter active sampling) using multiple techniques, including minnow traps, trap nets with snorkelers, electroshocking fish down to a seine, and angling. We used multiple techniques to avoid potential sampling bias (Al-Chokhachy and Budy 2008) and to effectively sample across all habitat types. When captured, all bull trout ≥ 120 mm total length (TL) were anesthetized and tagged with both a year-specific external anchor tag and a surgically implanted passive integrated

transponder (PIT) tag. Fish were weighed, measured, and released at the point of capture (see Al-Chokhachy and Budy 2008 for additional sampling details). Recaptured individuals were anesthetized, checked for tag loss, weighed, measured, and released.

In this dataset, we also included resights at two separate stationary passive in-stream antennas (PIAs); one was located in approximately the middle of the study area, and the other was located at the bottom of the study area (Fig. 1). All data collected during the discrete summer sampling period were considered capture (initial marking) or recapture (both active and PIA detections) data in the analyses.

Analyses

Population growth rate-temporal symmetry model

We used a temporal symmetry model (TSM; Pradel 1996; Hines and Nichols 2002) implemented in Program MARK (White and Burnham 1999) to estimate annual population growth rate ($\lambda_{\text{TSM}t}$) as well as a central estimate (mean) during the study period ($\lambda_{\text{TSM}m}$) for adult bull trout (>300 mm TL). We constrained our analyses to this size class as it corresponds to the predominantly reproductive (> age 4), population within the SFWWR (Al-Chokhachy and Budy 2008), as well as suggested bull trout recovery goals (Rieman and Allendorf 2001). The TSM has the typical assumptions of open (demographic) capture-recapture models, such as those for the Cormack-Jolly model (e.g., Seber 1982; Hines and Nichols 2002). However, there are two important additional assumptions particular to the TSM; first, the study area size and boundary must remain unchanged through time, and second, effort should remain relatively constant (Hines and Nichols 2002; Franklin et al. 2004). These assumptions ensure that recruitment and, concomitantly, λ , are not falsely biased high or low due to changes in study areas size or sampling intensity.

The TSM uses capture histories for each animal in the population collectively to simultaneously estimate survival (ϕ) through a forward procedure in time, and entry into the population through a reverse procedure in time. The innovative parameter in this model is seniority probability (γ), the probability that if an animal is present in the population at time t , it was also alive and in the population at time $t-1$. This

parameter effectively describes the relative contribution of survivors from the previous period to $\lambda_{\text{TSM}t}$ (Nichols and Hines 2002). When γ is combined with apparent survival (ϕ), it can be used to estimate recruitment (f) or λ (Pradel 1996; Hines and Nichols 2002; and see Cooch and White 2014 for a detailed explanation). This approach was particularly relevant in our analyses, as it enabled us to determine the proportional influence that f had on λ .

We first estimated λ using the $(\phi f p)$ structure of the temporal symmetry model, where ϕ is apparent survival, the probability that a bull trout alive in year t survived to the next year ($t + 1$) and remained within the study area (i.e., available for recapture/resight), f is recruitment, defined in the model as the number of adult bull trout entering the tagged population between year t and $t + 1$ per adult bull trout already in the population at time t , and p is the probability of capturing an unmarked individual, or physically recapturing or resighting (via PIAs) a previously marked individual. For this model structure, λ is a derived estimate, calculated as $\lambda = \phi + f$. Given that we restricted our population of interest to bull trout >300 mm TL, the recruitment parameter here refers to recruitment into the marked adult population.

We modeled p while maintaining a general structure of ϕ and f (i.e., $\phi_t f_t$), as we used a Bayesian MCMC approach to estimate $\lambda_{\text{TSM}t}$ (described below). We considered several *a priori* hypotheses when modeling p to test for potential changes in recapture probability throughout the study period. That is, we modeled p based on annual detection efficiency of two passive instream antennas (PIA) in place in the study area during sampling period (H1), as a binary dummy variable used to describe a change in area available to sample starting in 2008 due to both an increase in Chinook salmon redds and a change in channel morphology (H2), and as an ordinal variable used to describe a combination of conditions in H1 and H2 (H3). In addition, we constructed models in which p varied from year to year (t), had a linear time (T), log-linear ($\ln T$), quadratic (TT), and constant ($\cdot$) trend through time.

To compare among competing models, we used Akaike's Information Criterion corrected for small sample size (AICc) and compared models using both ΔAICc (Lebreton et al. 1992; Burnham and Anderson 2002) and normalized AICc weights (w_i ; Burnham and Anderson 2002). To evaluate model goodness-of-fit, we estimated overdispersion from extrabinomial variation (median $\hat{c}$) using a simulation

procedure in Program MARK with a Cormack-Jolly-Seber model framework for the global model (i.e., ϕ_t , p_t). Our results indicated extremely little evidence of overdispersion (median $\hat{c} = 0.96$), and therefore, we proceeded with our TSM analyses without adjusting for $\hat{c}$ (Lebreton et al. 1992; Cooch and White 2014). Using the model with the best structure on p [i.e., $\phi_t f_t p(\text{best structure})$], we used the $\phi_t \gamma_t$ form of the TSM model to determine whether survival or recruitment had greater influence on λ (Nichols and Hines 2002). This model structure allows determination of the proportional influence of recruitment on λ , because $\gamma_{t+1} = \phi_t / (\phi_t + f_t)$ and $1 - \gamma_{t+1} = f_t / (\phi_t + f_t)$. We quantified this proportional influence accordingly, with values of $\gamma < 0.5$ indicating a greater influence of adult survival, while values > 0.5 indicate that recruitment has a greater influence on λ_{TSM} . We used a Bayesian MCMC procedure implemented in Program MARK to generate posterior distributions of $\phi_t \gamma_t$. For the model $\phi_t \gamma_t p$ (best structure), we specified a hyper-distribution for all years of γ [the best structure for p was modeled with an ordinal dummy variable and was not time varying (see H3 above), hence p was not confounded with first and last estimates of ϕ_t or f_t]. We used the $\phi_t \lambda_t$ form of the Pradel model to estimate λ_{TSMm} and its process variance (σ^2) during the study period. See Conner et al. (2013) for details of the MCMC analysis, including information on prior distributions for all model parameters.

Population growth rate based on abundance and redd counts

For comparison with the temporal symmetry model, we also estimated population growth rate (λ) and its associated process variance for the study period based on abundance (λ_A) and redd count data (λ_R). We used count data collected during snorkel surveys as a non-invasive sampling method to measure of abundance of bull trout within sampled reaches (e.g., Meyer et al. 2014). We used the size bin of fish >220 mm, because this was the size cut-off used during snorkel surveys (fish size was visually estimated) and was the adult size bin closest to the size category used in the TSM (for additional field method details, see Al-Chokhachy and Budy 2008; Al-Chokhachy et al. 2009). Bull trout >220 mm are in the same small, adult life stage as the >300 mm size bin used in the TSM.

Redd count data are one of the most widely available metrics used to monitor bull trout population abundance and trends of spawning adults (Rieman and Myers 1997; Meyer et al. 2014;

Kovach et al. 2016). Redd counts were conducted annually by an experienced group of state, federal, and tribal biologists in index reaches within the SFWWR study area (see Al-Chokhachy et al. 2005), and used here as an index of annual adult population size. Redd counts have their own well-established sources of error and bias that are discussed at length elsewhere (Dunham et al. 2001; Muhlfeld et al. 2006; Howell and Sankovich 2012). Biases in redd counts can arise from several different issues (e.g., habitat, conditions, observer) but generally result in an underestimate of the annual abundance of reproductive fish; however, precision can also vary greatly across years. Although redd counts and abundance estimates were conducted in index reaches, we summed both metrics annually to represent single counts for the entire study area.

For both abundance and redd data, we began with density dependent and density independent state space models that use a mixed model framework to estimate both sampling (observation) and process variance (Staples et al. 2004; Dennis et al. 2006; Humbert et al. 2009). The density independent model is a special case of the Dennis et al. (2006) state space model, which is density dependent in its general form. Dennis et al. (2006) note that the density independent version serves as the null hypothesis for statistical tests for density dependence. Both density independent and dependent state-space models use logarithms of the count data and a first order autoregressive structure to model the temporal autocorrelation between counts. Both models assume that temporal process variation is distributed normally with a mean of 0 and variance σ^2 and that process errors are independent, and observation errors are multiplicative lognormal on the original scale (Staples et al 2004; Dennis et al. 2006). Density dependence is assumed to have a Gompertz-form population growth function, which was found to be the most common general shape in a comprehensive study of a large number of time series of count data sets for mammals, birds, fish, and insects (Sibly et al. 2005). Based on the lowest AICc, the best model for both snorkel abundance and redd count datasets was density independent. Consequently, we reverted back to the more parsimonious density independent model to estimate λ and σ^2 (Dennis et al. 1991). We then compared mean λ and σ^2 from the TSM to estimates from the density independent log-regression models based on both abundance (λ_A) and redd (λ_R) count data to: 1) assess model performance, and 2)

evaluate additional biological insights that can be gained from each approach, or the combination of approaches (i.e., what does each metric tell us about the population status and rate of change?).

Population Structure and Density Dependence

In order to investigate additional population changes and underlying factors potentially explaining the observed estimates of population growth rate, we evaluated whether the size structure or total biomass of bull trout changed during the study period and tested for the effects of density dependence. We tested for annual differences in proportions of three common size classes sampled routinely over the study period: subadult (150-300 mm TL), small adult (300-420 mm TL), and large adult (>420 mm TL) as well as the total biomass ($\text{g} \cdot 10^5$). Because the proportion data were not normally distributed, we used a Kruskal-Wallis test (Zar 1999) to evaluate whether the proportions in three size classes varied from year to year. We estimated the total annual biomass of fish >150 mm in year i , as:

$$\text{Biomass}_i = p_{ij} \cdot \tilde{N}_i \cdot W_{ij}$$

where p is the proportion of bull trout captured in size class j , $\tilde{N}$ is the population abundance based on snorkel data described above, and W is the median fish weight. We then tested for a trend in total biomass over time using linear regression. We used a repeated measures model to account for autocorrelation among biomass measurements from year to year. We considered variance components, compound symmetry, and autoregressive [ar(1)] covariance structures (Littell *et al.* 1996). Variance components, which specifies the same covariance through time, was the most appropriate covariance structure (the ar(1) model did not converge properly).

To test hypotheses of potential density dependent effects on population regulation independently from the TSM, we first considered the effects of total annual adult density on early life stages. Abundance for fish >220 mm in each reach was estimated based on mark-recapture data (Otis *et al.* 1978; Williams *et al.* 2002) collected during two closed-capture sessions within each year (for detailed methods, see Al-Chokhachy and Budy 2008; Al-Chokhachy *et al.* 2009). We calculated density for each reach as the reach abundance estimate divided by reach length multiplied by average width (m), and annual

density as the mean density of all 21 sampled reaches. We then regressed total adult density on density estimates of juveniles (<120mm) and total adult density on the number of redds, both with a time lag of 1 year (to test the hypothesis that adult abundance affected age-0 and age-1+), and with a time lag of 2 years (similar to a standard stock-recruit relationship). Notably, depending on where this population lies relative to carrying capacity, these potential density affects could be positive (more adults equates to more offspring) or negative (e.g., redd superimposition at high densities of spawning adults) (e.g., McNeil 1964; Paul et al. 2000).

Second, to test for intra-annual density effects on the performance of different cohorts, we regressed annual estimates of total population density on a mean body condition index based on fish actively captured each year, for four size classes (<150 mm, 150-300 mm, 300-420 mm, >420 mm TL). We used relative weight (Wr) as an index of body condition calculated as:

$$Wr = \frac{mass}{Ws} * 100$$

where $Ws = 10^{(-5.327 + 3.115 * \log_{10}(TL))}$; Hyatt and Hubert 2000). We considered inter-annual effects of density, as density- dependent effects are often delayed and can be manifested at many different stages of the life cycle (McNeil 1964; Paul et al. 2000; Johnston and Post 2009).

Results

Population growth rate-temporal symmetry model

There were 390 adult bull trout included in the temporal symmetry analysis, with a range of 12 to 78 bull trout per year captured and marked on the study area. A hypothesis with the strongest support from the data described effects of capture probability (p) of combined PIA detection efficiency and the area available to sample ($H3$). Thus we maintained this model structure for capture efficiency in all subsequent modeling of parameters ϕ and f . Four of the six top models (within 2 $\Delta AICc$ units of top model) had an increasing trend in f . Model weights indicated that top models with time trends were 2.4

times more likely than those without. Full model selection results are available in Supplemental Information (Table S1).

Estimated capture probability (p) was 0.52 (95% CI = 0.37-0.66) from 2002-2006, but then dropped in 2007, and was 0.26 (95% CI = 0.12-0.48) from 2008-2011. Although survival and recruitment of adult bull trout varied from year to year (not shown), the proportional contribution of recruitment ($1 - \gamma_i$) was > 0.50 for six of nine years (Fig. 2a). This pattern indicates recruitment (f), and not survival (ϕ), explained more of the variation in population growth rates during most years of the study period (also supported by the increasing trend in f in top models; Nichols and Hines 2002).

Point estimates of λ_{TSMt} for adult bull trout were < 1 (i.e., declining population) for 6 of the 9 years of this study and > 1 (i.e., increasing population) for only three years (Fig. 2b); however, the confidence intervals overlapped 1 for all years in the time series. The estimated median λ_{MCMC} for the time series was 1.01 (95% CI = 0.84 - 1.20), indicative of a stable population growth rate. Overall realized population change (Δ_t) is the proportion of the initial population size remaining at the end of the monitoring time period. Based on (Δ_t), there was a 50% probability the confidence interval was below 1 in six out of the nine years (Fig. 3). However, the probability of a decline of 30% or greater was very low (0.10), suggesting it was unlikely that a large population decline had occurred (Supplemental Information - Table S2).

Population growth rates based on abundance- and redd counts

Population growth rate was 0.96 (95% CI = 0.68-1.34) and 0.92 (95% CI = 0.77-1.11) based on log-regressions of annual snorkel and redd counts, respectively (Table 1; Fig. 4; bottom panel). Estimated λ_s from the state-space models applied to abundance and redd count data was 4-8% lower than for the TSM (Table 1; Fig. 4). The annual λ_t point estimates were the most variable for the abundance data and redd data (Fig. 4; top panel), which were described by high process variance over the entire time period (Table 1). There was particularly large variability in λ_A , with a low estimate of 0.4 in 2007 and a high of 2.5 (Fig. 4; top panel). These estimates were well outside the bounds of expected annual population growth rates for a bull trout population. Although λ_t estimates from the regression-based models differed

considerably from the TSM in most years, the correlation between the two approaches that used data from marked individuals, λ_{TSMt} and λ_{A} , was relatively high ($r = 0.77$), while the correlation between λ_{TSMt} and λ_{R} was considerably lower ($r = 0.39$).

Size (age) structure and biomass

Results of the Kruskal-Wallis test indicated the proportion of marked fish in each size category (150-300 mm, 300-350 mm, and >420 mm) was stable, with no significant difference across time ($P = 0.880$; Fig. 5a). The sample was dominated by small fish: on average, 80% of fish were in the 150-300 mm size class, 12% were in the 300-420 mm size class, and only 7% were in the largest size class (>420 mm). Total biomass averaged $11.1 \text{ g} \cdot 10^5$ across all years in the time series, with the highest biomass measured in 2002 (20.2) and the lowest in 2008 (5.6) (Fig. 5b). Although variable across years, the biggest change in the total biomass was the result of a decrease in the number of large fish >300 mm after 2002. Across the time series, total biomass demonstrated a slightly declining trend, but that trend was largely driven by the change from 2002-2003 and the slope was not significant ($P=0.209$).

Density dependent effects

We observed an apparent negative relationship between total fish density and the number or redds, as well as density of the smaller fish (<150 mm) at all time lags; however, none of the relationships tested were significant. We observed a negative and significant relationship between total adult density and condition of the smallest fish (< 150 mm) at the 0 and 1-year lag ($P \leq 0.064$). There was also a negative relationship between total fish density and the condition of 150-300 mm size class, but only the 1-year time lag was significant ($P = 0.049$). There was no relationship between total fish density and condition of the larger fish (Table 2).

Discussion

Estimating population growth rate over time periods relevant to recovery implementation remains one of the greatest challenges in conservation and management of almost all imperiled species (e.g., Morris and Doak 2002). We investigated options for overcoming these challenges by quantifying the rate

of population change for a population of threatened bull trout in northeastern Oregon using three different types of data and supporting analytical methods. The temporal symmetry model (TSM) was our primary analysis of interest, a relatively underutilized mark-recapture model, which we applied to ten years of consistently collected mark-recapture data. Relative to the two other estimates of population growth rate, the most precise estimates were provided by the TSM and were close to $\lambda = 1$; however, each of the status metrics also suggested some potential for declining trends during the period of this study. The λ_{TSM_t} confidence intervals were below 1 for all years of the time series, and λ_{TSM_t} was < 1 for most years. To better understand what this uncertainty in population growth rate point estimates could mean from a demographic standpoint, we evaluated the probability of the population declining by $\geq 50\%$, considered the endangered threshold by IUCN standards (IUCN 2001), and by $\geq 30\%$, the threatened threshold. Based on these criteria, there was only a 0.01 probability the population declined by $\geq 50\%$ and a 0.10 probability it declined by $\geq 30\%$ during the study period (see Supplemental Information). Collectively, these results indicate two important findings. First, our weight-of-evidence approach demonstrated that the overall population is relatively stable, a critical aspect in fishery management. However, this finding should be taken with the caveat that there is some probability, albeit low, the population may be gradually declining. Second, the abundance of large fish has decreased substantially such that the observed population stability may be predominantly driven by an increase in the relative abundance of smaller individuals (discussed further below).

Early evaluations of temporal symmetry models suggested that maintaining study area size and effort would likely be some of the most important factors to control, because any increase or decrease in initial capture effort (including study area size) could be interpreted as change in recruitment and thus affect estimates of λ (Pradel 1996; Hines and Nichols 2002). In contrast, however, the ability to incorporate changes in effort or sampling effectiveness with testable hypotheses on recapture probability ('p') highlights an additional strength of the TSM approach. Because we were aware of this potential 'effort' issue *a priori*, we were extremely careful to keep our study area and field methods exactly the same across all the years of the time series. However, there were unsurprisingly some unavoidable

changes within the study system that likely contributed to a decline in recapture rates: 1) antenna detection efficiency varied in 2008 and subsequent years as a result of high spring discharge events, 2) the number of endangered Chinook salmon spawning in the study area increased throughout the time series, which decreased the total area available for sampling (i.e., salmon and redds had to be avoided), and 3) throughout the lower half of the study area, the channel (and habitat) was altered by a large flood in 2008. Using the TSM approach, we were able to account for these changes explicitly as a change in recapture probability (p). Recapture probability was included in all top TSM models that emerged and thus was unlikely to have influenced our estimates of λ_{TSM} .

The majority of our top performing models from the TSM included an increasing trend in recruitment (f) over time, which represents per-capita additions into the adult population (here > 300 mm; Pradel 1996). Based on the average annual growth rate of bull trout in this system, recruitment of offspring into this size class occurs four to six years post-spawning (Al-Chokhachy and Budy 2008; Bowerman 2013; USFWS 2010). Most (67%) estimates of the annual proportional contribution of recruitment ($1-\gamma_i$) were $>50\%$, which indicates that recruitment (f) contributed more to population growth than apparent survival (ϕ), in most years (Nichols and Hines 2002). This pattern confirms that adult survival is moderately low (Al-Chokhachy and Budy 2008) and has not changed appreciably over the course of the study. Low survival rates of large adult bull trout may be the result of high post-spawning mortality (up to 50%; Reiman and Allendorf 2001), as well as poor conditions in the lower river where many migratory fish overwinter (*sensu* Al-Chokhachy et al. 2016). Low survival may also be a factor contributing to the high interannual variability observed in fluvial bull trout populations (Kovach et al. 2016). In contrast to our results, when Pine et al. (2001) applied the TSM to a population of recovering sturgeon, a long-lived fish with very late maturation, they demonstrated that survival contributed more to λ than recruitment and concluded that even though the population growth rate was increasing, adult harvest should be tightly restricted. These two studies demonstrate one of the unique strengths of the TSM, in that it enables users to identify the vital rates that drive overall population growth rates and allows researchers to link the population response to conservation actions. For this (herein) population of

bull trout, management actions that increase the survival of large, mostly migratory adults, and recruitment into this life stage, may provide the greatest increase in population growth rates. Large fish contribute considerably more to recruitment though greater fecundity than do small adults (Bowerman 2013), such that survival of these large individuals may be integral to maintaining populations. In this system and elsewhere, potential actions that increase recruitment of juveniles and survival of larger size classes are almost all associated with water regulation and passage issues in the lower river.

Comparisons of population growth rate based on different components of the population and using different approaches can be biologically informative and can provide greater confidence in conclusions when results are consistent (e.g., Marmorek and Peters 2002). To complement the mark-recapture-based TSM approach, we also estimated population growth rate based on annual abundance estimates and redd counts, analyzed in a regression-based trend model (Dennis et al. 1991). The TSM and the redd count-based regression provided the most precise estimates, with 95% confidence intervals that were approximately half that of abundance-based regression model. Inter-annual variability in λ_{TSM} estimates was less than that of the other two estimates, perhaps reflecting a superior capacity to separate process and sampling variance, since changes in capture probability (sampling variance) were explicitly incorporated into the modeling process. Nonetheless, estimates of population growth rate based on abundance data were consistent with results from the purportedly less biased TSM. Here, these two approaches yielded estimates that were relatively close, with overlapping confidence intervals and estimates of λ that were strongly correlated (0.77). This weight-of-evidence approach provided greater confidence in our conclusions, and demonstrated that trend estimates based on abundance data were informative, despite the considerable variance and potential biases discussed at length elsewhere (Dennis et al. 1991; Thompson et al. 1998; Morris and Doak 2002).

In contrast, λ_{R} estimates from the regression-based model of redd counts (Dennis et al. 1991) described a somewhat different component of the population and its' associated population growth rate. Rather than the total number of adults used in the TSM and population estimates, redd counts only represent spawning females, and as a result, these estimates represent population growth rates for slightly

different portions of the population. The estimate of λ_R was substantially lower (4-8%) than λ_{TSM} with similar variance, and the correlation between λ_R and λ_{TSM} was quite low (0.39). Redd counts in this basin most closely represent only the very largest-sized spawning fish (Al-Chokhachy et al. 2005), and the lower value of λ_R compared with λ_{TSM} suggests that the portion of the population composed of large individuals may be declining, while the population as a whole is relatively stable. Large adults are likely more susceptible to environmental stressors (e.g., high water temperatures and low flows) during migration into the lower reaches of this system and thus experience higher mortality (Bowerman 2013; Al-Chokhachy et al. 2016; Howell et al. 2016). In addition, although size cut-offs used in TSM and abundance analyses were meant to represent adult bull trout, smaller individuals in those size classes may not all be reproductive (i.e., probability of spawning increases with size), and once individuals have spawned, they most likely spawn annually, although a small percentage could spawn biannually (Downs et al. 2006; Bowerman 2013; Howell et al. 2016). Collectively, our observations suggest that while the λ_{TSM} is the more robust estimate of population growth rate for the overall, adult population of bull trout in the SFWWR, the λ_R estimate represents a direct measure for the large, highly-fecund migrating fish. A declining trend in the population growth rate of large, migratory fish has been observed in other bull trout populations (e.g., Nelson et al. 2002). Because it could have both population and metapopulation-level implications, this pattern is reason for significant conservation concern (e.g., Morita and Yokota 2002).

Corresponding with the declining λ_R the contemporary size distribution is strongly biased toward small adults and the contribution of large fish to total biomass has declined. Elsewhere, dramatic increases in size, age, and abundance of bull trout have been documented following changes in harvest and management regulations as a result of listing under the Endangered Species Act (ESA) (e.g., Johnston and Post 2009; Erhardt and Scarnecchia 2014). In the SFWWR, it appears that management activities have been insufficient to increase the proportion of large adults. Given there was not historically a substantial sport fishery on bull trout, changes in harvest after ESA listing are unlikely to have substantially affected the bull trout in our study area. In addition, the habitat is relatively intact in the headwater spawning and rearing areas, so there is little opportunity for management changes in those

areas. Instead, factors outside of the study area may be particularly important in determining the size structure of this population. In-stream flows in migratory habitat throughout the lower Walla Walla River have increased to some degree in recent years, but these changes do not appear to have resulted in a response by the large, migratory portion of the SFWWR population (Doak and Morris 1999; Holmes and York 2003). Further, Schaller et al. (2014) observed that the migratory life-history strategy for SFWWR bull trout has been impacted by poor habitat conditions, stressful thermal conditions, and lack of seasonal connectivity in the lower mainstem Walla Walla River. Such bottlenecks in migratory habitat are likely to continue to have detrimental effects on large, adult bull trout (Al-Chokhachy et al. 2016).

Factors that impact habitat in migratory corridors affect this and other fluvial fish populations in two primary ways: 1) they reduce the reproductive contribution of the highly-fecund, migratory component of the population, and 2) they limit dispersal among local populations. Because these large fish have a disproportionate effect on population viability due their very high fecundity (Morita and Yamamoto 2002), management actions that affect large, adult survival would need to be a priority to help maintain or increase population growth rates (Bowerman 2013). At a metapopulation level, reducing the number of potential dispersers eliminates the potential for rescue effects elsewhere and reduces genetic exchange (Kovach et al. 2015). This matter provides further reason for conservation concern, as the SFWWR is the largest and healthiest sub-population remaining in the Walla Walla metapopulation (USFWS 2010).

Many populations of fish, including some populations of bull trout, exhibit strong evidence of density dependent population regulation (e.g., decreased vital rates and population growth rates with increased density; Johnston et al. 2007). While we did not find evidence of density-related effects on population demographic rates based on our necessarily coarser analysis and shorter time series, we did observe that the condition of small fish was negatively associated with the total adult fish density at time lags of 0 and 1 years. However, we found no other evidence of density dependent population regulation. The differences between our results and Johnston et al. (2007) likely stem from the magnitude of change observed. The strong density-dependent effects observed by Johnston et al. (2007) occurred during a 28-

fold increase in bull trout abundance, whereas the population in our study was stable. Our results suggest the SFWWR bull trout population is currently in a density independent state. Even though this is considered to be a relatively large population in contemporary terms, many current populations are likely much smaller than their historical carrying capacity (e.g., Reiman and McIntyre 1993; *but see* Erhardt and Scarnecchia 2014). Further, lower reaches of the SFWWR have been degraded (Schaller et al. 2014), such that successful rearing may now occur in a much smaller and colder portion of the watershed than what was once used historically. Given the importance of recruitment in maintaining this population, even modest expansions of the area of successful recruitment could have considerable positive impacts.

Challenges, lessons learned, and opportunities

Our study was carefully designed, covering a > 20 km of spawning and rearing habitat, with a high degree of effort expended over a relatively long time period (10 years). Nonetheless, our study design in combination with a complex mark-recapture modeling approach demonstrated some frustrating limitations. In particular, we could not estimate independent population growth rates for different components of the population; we had originally hoped to estimate separate population growth rates for known migratory versus resident life history expressions. However, through our efforts we found survival and thus λ were extremely positively biased for known migrants, largely because fish that both migrated and survived had a much higher probability of recapture (i.e., detection at any one of several PIA), relative to a resident fish or a fish whose migratory status remained unknown (i.e., a fish that was never re-detected after tagging). In addition, when analyzed separately, the sample size of migratory fish (25% of total sample) decreased dramatically, resulting in estimates with large variance in addition to bias, even with several PIAs in place to collect data continuously. Hence, specific life-history expressions may need targeted sampling programs if the goal is to estimate life-history specific vital rates and population growth rate. In this system, this limitation could be overcome with the additional use of a weir that sampled known migrants as they returned to headwaters to spawn (e.g., Howell et al. 2016); however, this would have required significant additional infrastructure and operational costs, and may have resulted in ecological drawbacks.

The management questions of greatest importance should be carefully considered when designing an extensive and expensive, multi-year mark-recapture study such as this (Al-Chokhachy et al. 2009). For the TSM to achieve optimum performance, the ability to maintain a relatively high capture probability ($\geq 20\%$) and a near-constant, and well-documented sampling efficiency is imperative (Pradel 1992). Further, assessing the effectiveness of a management action for a long-lived animal will always require long time series of data, because if the population is stabilizing, the time period to gauge response may have to parallel the life span of the organism, at a minimum (; Pine et al. 2001; Naslund et al. 2005; Erhardt and Scarnecchia 2014). Similarly, the response to a conservation action could be quite delayed for a long-lived animal (e.g., Bjorndal et al. 1999; Holmes and York 2003). Given these types of considerations, Chasco et al. (2014) make a compelling argument that for some populations (e.g., salmon), it may make more sense to allocate funds to a mitigation action that provides a large perturbation and possible positive change, rather than an intensive monitoring program.

From a management perspective, the trade-off among different sampling approaches is between precision and cost, with respect to meeting management goals. Mark-recapture programs such as those described here are quite costly and require considerable effort; however, they are valuable in that they allow managers to assess progress (or lack thereof) towards recovery, and to quantify critical vital rates and identify limiting factors. Count data (abundance and/or redds) are cheaper to collect but may not provide adequate precision for estimating population growth rates, and are subject to limitations imposed by the count method used. In addition, count data do not provide information on the underlying process that drive population change (Ludwig 1999; White et al. 2002). Redd data are commonly used by fisheries managers to monitor population status and when used here to estimate population growth rate, provided precision similar to that of the more labor-intensive TSM. As such, redd counts appear to be adequate for evaluating long-term population growth rates in many populations (e.g., High et al. 2008; Meyer et al. 2014), provided that managers consider known biases and limitations (Dunham et al. 2001; Howell et al. 2012), and are aware that only a portion of population may be represented in data (in this case, large, reproductive females; Al-Chokhachy et al. 2005). Additionally, application of specific

analytical tools, such as the state-space model used herein, will likely yield greater precision than simply using raw count data (Dennis et al. 2006; Humbert et al. 2009). Royle (2004) similarly developed the use of N -mixture models to estimate population size from spatially-replicated count data, a method that is another potential avenue of future research. Although typically more costly than count data, the TSM may be a uniquely useful approach where mark-recapture data are already being collected (e.g., many fish, small mammal, and bird populations). In these situations, implementation may simply require small changes to upfront study design or careful consideration during post-hoc analysis, and could yield important insights into factors driving population abundance over time.

Despite some limitations, which are present in all population monitoring programs, the temporal symmetry approach has many strengths and has been under-utilized for stream fishes. First, the TSM provides information about population vital rates, which allows the modeler to investigate mechanistic hypotheses (Pine et al. 2001) and can help inform management actions. For example, we observed that currently, recruitment into the adult component of the SFWWR bull trout population is contributing more to maintaining the population than survival; this type of information allows managers to focus on factors that may be most limiting. Second, as demonstrated here, estimates of λ from the TSM model are typically more precise than estimates of λ based on counts data (Thompson et al. 1998). Third, the TSM has some advantages over an asymptotic λ from a projection matrix, because it does not rely on assumptions about mean vital rates, stable age distributions, and stationary conditions (Nichols and Hines 2002; Franklin et al. 2004).

Conclusion

We show that an important index population of threatened bull trout (SFWWR) is likely stable overall, and that the probability that the overall population declined is also low (Conner et al. 2015). However, we also show a declining trend in the abundance of large fish, resulting in a population now dominated by small adults. In this area, few of the threats that originally led to the threatened status of bull trout have been removed, and in the future, the threat of climate change may provide an additional threat to bull trout (Isaak et al. 2015; Kovach et al. 2015; Al-Chokhachy et al. 2016). Consequently, the

current 'stable' status should be viewed with caution, as any change in the incidence or distribution of anthropogenic stressors could change that status rapidly and significantly. In addition, the evidence suggesting the number of large migratory bull trout in the SFWWR is decreasing has critical population and meta-population level implications, providing reason for conservation concern. Finally, we believe the true value of the type of approach we used is not only the unbiased estimates of population growth rate and recruitment, but also in the value of the additional and complimentary information that can be collected at the same time for no additional effort. This additional information includes estimates of other critical vital rates such as survival, growth, and fecundity (e.g., Al-Chokhachy et al 2009, Bowerman and Budy 2012; Schaller et al. 2014), and in this case, where there is a network of PIAs, the extensive information on movement patterns and life-history expression (e.g., Homel and Budy 2008; Schaller et al. 2014). Finally, it is the utilization of all these different information sources together that provides for a robust weight-of-evidence type approach to address and evaluate important conservation challenges (Hilborn and Walters 1992; Marmorek and Peters 2002; Grossman et al. 2006).

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Tables

Table 1. Parameter estimates of rate of change (λ) and its temporal process variance (σ^2) for temporal symmetry model (Pradel 1996) and Dennis et al. (1991) based methods. Data for mark-resight and abundance counts are from adult fish ≥ 300 mm, from a bull trout population in the South Fork Walla Walla River, Oregon, 2002-2011.

Data type	Method	λ	<u>95% CI</u>		σ^2
			Lower	Upper	
Mark-resight	Temporal symmetry	1.01 ^a	0.84	1.20	0.05
Abundance counts	Regression-based	0.96	0.68	1.34	0.24
Redd counts	Regression-based	0.92	0.77	1.11	0.08

^a MCMC

Table 2. Slope parameter (β) estimated from a linear regression of juvenile density, redds and condition indices versus total density of >120 mm bull trout. Data are from a bull trout population in the South Fork Walla Wall River, Oregon, 2002-2011, of size classes (1) < 150 mm, (2) 150-300 mm, (3) 300-420 mm, and (4) >420 mm TL.

Parameter	Lag	β	<i>P-value</i> ^a
Juvenile density	0	-1.64E-05	0.370
	1	-1.51E-07	0.506
	2	-3.35E-07	0.124
Number redds	0	-5.36E-03	0.343
	1	-7.79E-03	0.243
	2	-1.10E-02	0.126
Body cond size 1	0	-4.71E-04	0.064
	1	-5.63E-04	0.063
	2	-8.51E-04	0.822
Body cond size 2	0	-1.13E-04	0.557
	1	-4.07E-04	0.049
	2	-2.08E-04	0.425
Body cond size 3	0	3.76E-04	0.186
	1	-2.99E-04	0.371
	2	9.26E-05	0.731
Body cond size 4	0	8.24E-04	0.222
	1	-7.99E-05	0.928
	2	-4.51E-04	0.634

^a Bold p-values are significant at $\alpha = 0.10$.

Figure captions

Fig. 1. Map of the South Fork Walla Walla River illustrating the study location in northeast Oregon, U.S.A and the study reaches (grey circles) where mark-recapture and resight occur. The location of the two passive in-stream antennas (PIA) for detecting PIT-tagged fish are shown with black squares; the Harris Park Bridge (WW1) denotes the lower boundary of the study area and the uppermost study reach indicates the upper boundary.

Fig. 2. Estimates of annual (a) contribution of recruitment ($1 - \text{seniority}_t$), and (b) annual population growth rate (λ_t) from the temporal symmetry model $\phi(t) f(t) p(H3)$. Estimates are based on a Bayesian Markov chain Monte Carlo (MCMC) procedure; the median and 2.5 and 97.5 percentiles are shown. Data are for adult fish ≥ 300 mm ($n=390$), from a bull trout population in the South Fork Walla Walla River, Oregon, 2002-2011.

Fig. 3. Estimated posterior distribution of overall realized population change (Δ_t) based on the posterior distribution of λ_t from 20,000 Markov chain Monte Carlo (MCMC) simulations, from the top TSM model (modeled as a random effect) for all adult bull trout >300 mm TL in the South Fork Walla Walla River, Oregon, 2002-2011. Overall realized population change is the proportion of the initial population size remaining at the end of the monitoring time period.

Fig. 4. Estimates of annual rate of population change (λ_t) from the temporal symmetry model $\phi(t) f(t) p(H3)$ based on mark-resight data for adult fish ≥ 300 mm TL, ($n=390$), and the regression-based model (Dennis et al. 1991) using snorkel counts of fish >220 mm TL and redd counts. Data are for a bull trout population in the South Fork Walla Walla River, Oregon, 2002-2011.

825 Fig. 5. The annual (top panel) proportion of fish in each size class, and (bottom panel) total biomass
826 ($\text{g} \cdot 10^5$) for fishes (150-300 mm, 300-420 mm, >420 mm) of bull trout in the South Fork Walla Walla
827 River, Oregon, 2002-2011.

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Figure 1.

165x127mm (300 x 300 DPI)

Figure 2.

266x368mm (300 x 300 DPI)

Figure 3.

154x116mm (300 x 300 DPI)

Figure 4.

271x381mm (300 x 300 DPI)

Figure 5.

251x352mm (300 x 300 DPI)