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### Bull Trout Trends in Abundance and Probabilities of Persistence in Idaho

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## ARTICLE

## Bull Trout Trends in Abundance and Probabilities of Persistence in Idaho

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### Abstract

We estimated the population growth rates of Bull Trout *Salvelinus confluentus* and used population growth models to evaluate observation error and estimate Bull Trout persistence probabilities by using 25 data sets (averaging 19 years of record) that indexed abundance across Idaho. These data sets were derived from a variety of fish sampling techniques, including weirs, screw traps, redd counts, daytime snorkeling, electrofishing, and angler creel. Bull Trout populations in Idaho were relatively stable prior to 1994, but after 1994, substantially more population growth rates trended statistically upward ( $n = 14$ ) than downward ( $n = 3$ ). Average intrinsic rates of population change were 0.01 (SE = 0.03) prior to 1994 and 0.07 (SE = 0.02) after 1994; across all years of data, the rate of change averaged 0.07 (SE = 0.02). Fifty-nine percent of the data sets had zero to minimal observation error according to Gompertz state-space model estimates; observation error was least common in data from screw traps and redd counts and most common in snorkel data. Gompertz-type density-dependent models were most often the best-fitting models for Bull Trout population growth. Moreover, few of the most reliable modeling results (i.e., those from data sets estimated to have zero to minimal observation error) contained a period effect or time (i.e., year) effect, suggesting that carrying capacity generally did not differ between the pre-1994 and post-1994 periods and generally was not trending positively or negatively through time. Parametric bootstraps predicted that the mean probability of falling below the quasi-extinction level of 20 adults in the next 30 years was 9.8% (median = 4.7%) for data sets estimated to have zero to minimal observation error. The weight of evidence from our modeling results suggests that for most Bull Trout populations in Idaho, abundance is stable or increasing and the risk of extirpation in the foreseeable future is low.

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Concerns about the status of Bull Trout *Salvelinus confluentus* in the western United States have been expressed since at least the mid-1980s (USFWS 1985), when the species was first considered for listing under the Endangered Species Act. The species was designated as threatened in the coterminous USA during the late 1990s (USFWS 1998). Since that time, several status assessments have attempted to quantify trends in Bull Trout distribution and abundance (e.g., Ratliff and Howell

1992; Rieman and McIntyre 1993; Rieman et al. 1997; USFWS 1998; Post and Johnston 2001; High et al. 2008), often via qualitative methods of population assessment. For example, Rieman et al. (1997) used a series of workshops to compile professional opinions on the status of Bull Trout across the entire Columbia River basin and the Klamath River basin; those authors concluded that although Bull Trout were more widely distributed in the region than many other native salmonids, Bull Trout

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subpopulations were “strong” in only 6% of their potential range (a strong population was defined as >500 adults, with all life stages present, abundance stable or increasing, and spawning and rearing habitat not limited). Using a similar definition of a strong population, the U.S. Fish and Wildlife Service (USFWS) concluded that Bull Trout in the Columbia River basin were strong in only 13% of their potential range (USFWS 1998). However, within parts of the Columbia River basin, particularly in Idaho, Bull Trout appear to be relatively abundant and stable (High et al. 2008) and exhibit population trends similar to those of other resident native salmonids, such as Westslope Cutthroat Trout *Oncorhynchus clarkii lewisi* and Mountain Whitefish *Prosopium williamsoni* (Copeland and Meyer 2011). The most recent broad-scale summary of Bull Trout abundance trends in Idaho included data through 2003 (High et al. 2008). With several years of additional data now available, our first study objective was to update these data sets and re-evaluate trends in abundance for Idaho Bull Trout populations, including the addition of several previously unused data sets.

Relative to studies of Bull Trout distribution and abundance, little work has focused on population viability analysis (PVA) for Bull Trout. Population viability analysis is a forecasting or modeling exercise that is used to estimate future population sizes and risks of extinction or quasi-extinction over a defined time period (Gilpin and Soulé 1986; Morris and Doak 2002). Although the techniques that are used to conduct PVA vary widely, most often they are based on estimates or indices of abundance or on demographic data (usually population vital rates). In the past few decades, PVA has gained acceptance by conservation biologists as a useful tool for assessing and managing at-risk species (Morris and Doak 2002; Reed et al. 2002).

As the use of PVA has grown in conservation biology, so have concerns that estimates of extinction risk generated from PVAs are error prone (Reed et al. 2002). For instance, Rieman and McIntyre (1993) used a density-independent model of exponential growth with process error (EGPE; Dennis et al. 1991) to conduct the first formal PVA for Bull Trout; they concluded that few subpopulations in the Flathead River and Swan River basins of Montana and the Pend Oreille River and Rapid River basins of Idaho would persist for 100 years with a probability greater than 0.95. However, the EGPE model has subsequently been criticized as being too simplistic for estimating extinction risk (e.g., Holmes 2001, 2004; Staples et al. 2005). Moreover, some of the techniques that are used to monitor Bull Trout abundance, especially redd counts and daytime snorkeling, tend to produce data sets with substantial amounts of observation error (Dunham et al. 2001; Muhlfeld et al. 2006; Thurow et al. 2006). For the purposes of our study, we follow the definition of observation error from Dennis et al. (2006) as the amount of error inherent in the observation or sampling methods by which population abundance is being monitored. Observation error is in addition to real fluctuations in population abundance caused by demographic and environmental noise (i.e., process

noise). Inclusion of data sets with significant observation error in PVAs inflates the estimates of population variability, leading to pessimistic estimates of population viability (Morris and Doak 2002). This problem has led to recent efforts to estimate the amount of observation error within trend data sets (Dennis et al. 2006), thereby allowing stronger inferences to be drawn regarding the viability of animal populations (Garton et al. 2011; Russell et al. 2012). Our second study objective was to compare several population growth models for describing the dynamics of Idaho Bull Trout populations and to use these models to predict long-term probabilities of persistence for Bull Trout populations in Idaho.

## METHODS

*Delineation of population boundaries.*—Throughout Idaho, Bull Trout are found in numerous drainages (Figure 1) totaling about 103,000 km<sup>2</sup>. Within this area, the USFWS has unofficially designated 272 local Bull Trout populations in 30 core areas (USFWS 2002), although these designations continue to be refined. According to the USFWS, a local Bull Trout population is a unit that closely approximates a panmictic group (Whitesel et al. 2004) and as such conforms to what Hanski and Gilpin (1991) and McElhany et al. (2000) describe as a subpopulation or to what population ecologists have long called a deme (Garton 2002; Garton et al. 2012). The draft Bull Trout recovery plan (USFWS 2002) identified a Bull Trout core area as the closest approximation of a biologically functioning unit for Bull Trout. Hence, Bull Trout core areas generally equate to populations that are made up of interacting subpopulations (Whitesel et al. 2004). Numerous studies have demonstrated that Bull Trout in Idaho often move extensively within populations (Flatter 1999; Partridge et al. 2001; Schiff et al. 2005; Whiteley et al. 2006) and often exhibit some gene flow between subpopulations (Whiteley et al. 2006; Ardren et al. 2011). Because population viability is more appropriately linked to populations rather than to subpopulations (McElhany et al. 2000; Theobald and Hobbs 2002), we assessed the status of Idaho Bull Trout at the population level, although we recognize that not all subpopulations within a given population are interconnected.

*Available Bull Trout data.*—In total, 25 trend data sets were available from 17 of the 30 Bull Trout populations in Idaho. These data sets were derived from a variety of fish sampling techniques. For example, within two populations, Bull Trout were captured at salmon weirs during their upstream spawning migrations (Schill et al. 1994; Stark et al. 2012), and weirs were generally operated in May–September each year. Within four populations, a 1.52-m rotary screw trap (Kennen et al. 1994) was used to capture Bull Trout during routine monitoring of salmon and steelhead *O. mykiss* out-migration (e.g., Copeland and Venditti 2009). Screw traps were deployed as early as possible in the spring, usually during the last week of February or the first week of March, and were operated until ice-up (usually the first week of December). Bull Trout of all sizes were counted

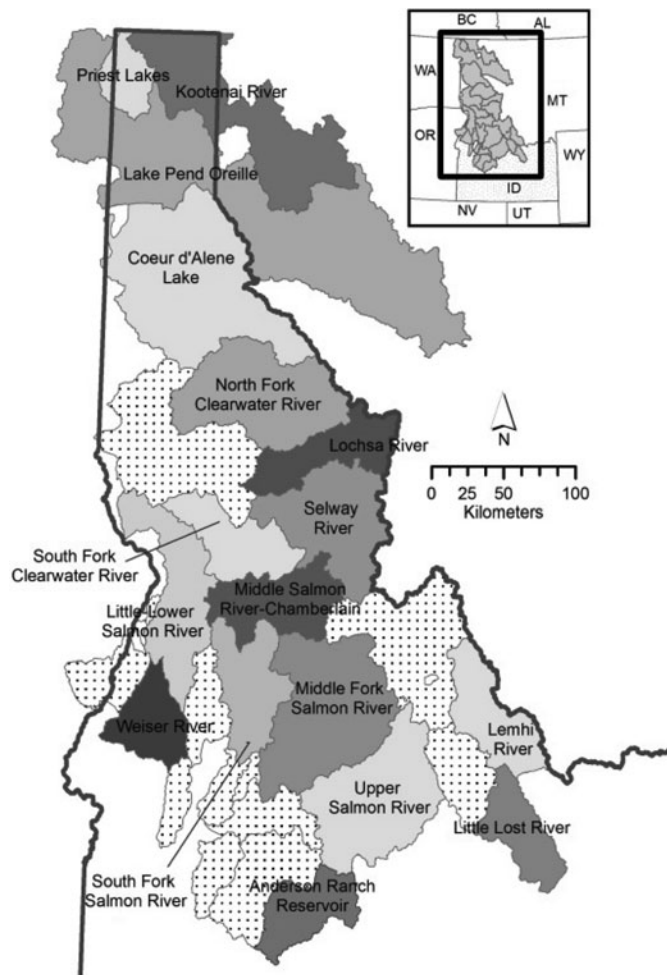


FIGURE 1. Study area depicting the 17 designated Idaho Bull Trout populations for which trend data were available. Unlabeled populations (hatched shading) indicate the 13 designated populations for which trend data were lacking.

at the screw traps, but the average TL was 178 mm and less than 1% of the fish were smaller than 75 mm. Redd counts were used to monitor Bull Trout abundance in six populations, and methods followed those described by Rieman and McIntyre (1996). In general, redd surveys were conducted in September and October by walking a stream and counting Bull Trout redds, with identical sections of river being surveyed each year for each population. Within 10 populations, daytime summer snorkeling was used to index Bull Trout abundance after spring high flows had subsided. Copeland and Meyer (2011) provide more details on snorkeling methods; in general, one to five observers (depending on stream width) snorkeled slowly upstream while counting all salmonids that were 75 mm TL or larger. During snorkeling surveys, visibility (i.e., distance at which patterns on an object the size of an average fish could be distinguished) averaged 4.3 m and water temperature averaged 14.5°C, with fewer than 1% of the surveys occurring at temperatures less than 8°C (the temperature at which Bull Trout typically initiate daytime concealment

behavior; Jakober et al. 2000). For two populations, multiple-pass electrofishing was conducted within the same sections of river by using pulsed-DC electrical output. Finally, angler creel was conducted within one population, with mean annual Bull Trout catch rates (fish/h) used to index abundance.

We recognize that all of these fish sampling techniques can result in abundance index data containing substantial amounts of observation error, but they are generally well correlated with the actual abundance of Bull Trout (e.g., Thurow and Schill 1996; Dunham et al. 2001; Muhlfeld et al. 2006; Thurow et al. 2006) and have been used extensively to assess Bull Trout abundance and trends (e.g., Rieman and McIntyre 1993; Stelfox 1997; Watson and Hillman 1997; Nelson et al. 2002; Seals and Reis 2002; High et al. 2008; Al-Chokhachy et al. 2009).

**Trends in abundance.**—We assessed trends in Bull Trout abundance by using linear regression with sample year as the independent variable and the index of abundance data ( $\log_e$  transformed) as the dependent variable. A benefit of this approach is that the slope of the regression line fitted to the  $\log_e$  transformed abundance data is equivalent to the intrinsic rate of change ( $r_{intrinsic}$ ) for the population (Maxell 1999) and produces unbiased estimates of  $r_{intrinsic}$  despite the potential presence of observation error within the data (Humbert et al. 2009). Values of  $r_{intrinsic}$  less than zero indicate negative population growth, whereas  $r_{intrinsic}$  values greater than zero indicate positive population growth. We used a significance level  $\alpha$  of 0.10 to increase the probability of detecting trends (Peterman 1990; Maxell 1999). Previous work has suggested that an inflection point in Idaho Bull Trout abundance corresponds to about 1994 (High et al. 2008; Copeland and Meyer 2011), so we estimated  $r_{intrinsic}$  for three periods: pre-1994, post-1994, and the entire time period. Data from the year 1994 were included in both the early and late time periods.

**Fitting of population growth models.**—Population viability is inherently based not on total abundance but rather on the number of adults in the population (McElhany et al. 2000; Morris and Doak 2002). Therefore, in addition to the trend data sets, we gathered the most recent estimates of adult Bull Trout abundance in these same populations (Table 1). For the Lake Pend Oreille population, adult abundance was derived from a 2008 mark-recapture estimate of 400-mm TL and larger Bull Trout (M. Hansen, U.S. Geological Survey, unpublished data). For the lower Kootenai River, Coeur d'Alene Lake, and Priest Lakes populations, adult abundance was estimated from the maximum number of redds counted during 2009 in these populations (Idaho Department of Fish and Game, unpublished data). We assumed that all redds were counted in these populations and that there were 3.2 adults for each counted redd (Downs and Jakubowski 2006). For the remaining populations, adult abundance was approximated from the abundance of 70-mm and larger Bull Trout as estimated by High et al. (2005, 2008), who compiled over 2,500 snorkeling and electrofishing surveys to produce abundance estimates for Bull Trout across Idaho. To approximate adult abundance from the High et al. (2005, 2008)

TABLE 1. Description of trend monitoring data sets and estimates of adult abundance for Bull Trout populations in Idaho.

Bull Trout population	Description	Data type	Period of record	Years of data	Reaches studied	Estimate of adult abundance		
						Estimate	Year of estimate	Source or method of estimation
Lower Kootenai River	Kootenai River tributaries	Redd count	1995–2010	16	3	333	2009	Redd count extrapolation
Coeur d' Alene Lake	St. Joe River tributaries	Redd count	1992–2010	19	3	182	2009	Redd count extrapolation
Lake Pend Oreille	Lake Pend Oreille tributaries	Redd count	1983–2010	26	6	12,513	2008	Mark–recapture estimate
Priest Lakes	Upper Priest Lake tributaries	Redd count	1996–2010	15	18	109	2009	Redd count extrapolation
North Fork Clearwater River	Little North Fork Clearwater River	Redd count	1994–2010	17	2	2,474	2003	High et al. 2005
Lochsa River	Squaw Creek	Redd count	1994–2010	17	2	884	2003	High et al. 2005
	Lochsa River and tributaries	Snorkeling	1988–2009	22	34			
	Crooked Fork Creek	Screw trap	1992–2010	19	1			
Selway River	Selway River and tributaries	Snorkeling	1989–2009	21	26	371	2003	High et al. 2005
South Fork Clearwater River	South Fork Clearwater River	Screw trap	1994–2010	14	2	235	2003	High et al. 2005
	South Fork Clearwater River and tributaries	Snorkeling	1985–2009	25	59			
Little Salmon–Lower Salmon River	Lower Salmon River tributaries	Snorkeling	1985–2009	25	35	777	2003	High et al. 2005
South Fork Salmon River	Rapid River	Weir	1973–2010	38	1			
	South Fork Salmon River	Screw trap	1992–2010	19	1	2,311	2003	High et al. 2005
	South Fork Salmon River and tributaries	Snorkeling	1986–2006	21	27			
Middle Fork Salmon River	Middle Fork Salmon River and tributaries	Snorkeling	1985–2009	25	77	10,728	2003	High et al. 2005
Mid-Salmon River (Chamberlain)	Mid-Salmon River tributaries	Snorkeling	1985–2009	25	11	293	2003	High et al. 2005
Lemhi River	Lemhi River and tributaries	Snorkeling	1985–2006	22	7	5,802	2003	High et al. 2005
Upper Salmon River	Upper Salmon River and tributaries	Snorkeling	1986–2006	21	20	3,146	2003	High et al. 2005
	East Fork Salmon River	Weir	1984–2010	14	1			
	Redfish Lake	Creel	1996–2010	15	1			
	Marsh Creek	Screw trap	1993–2010	18	1			
Anderson Ranch Reservoir	South Fork Boise River	Electrofishing	1998–2010	7	1	1,041	2003	High et al. 2005
Weiser River	Weiser River tributaries	Snorkeling	1999–2010	12	7	310	2003	High et al. 2005
Little Lost River	Little Lost River tributaries	Electrofishing	1995–2010	7	2	4,553	2003	High et al. 2008

estimates, we assumed that 10% of all 70-mm and larger Bull Trout were adults.

These estimates of adult Bull Trout abundance were used to establish abundance ( $\hat{N}_t$ ) for the year in which the estimate was made. From that year, the trend data were used to project adult abundance forward and backward in time (see Garton et al. 2011 for details) based on the finite rate of change ( $\hat{\lambda}_t$ ) estimated for that population from sequential, paired annual indices of abundance:

$$\hat{\lambda}_t = \frac{\sum_{i=1}^n M_i(t+1)}{\sum_{i=1}^n M_i(t)},$$

where  $M_i(t+1)$  and  $M_i(t)$  are indices of abundance for year  $t+1$  and year  $t$ , respectively (e.g., the total number of Bull Trout captured in two consecutive years at a particular screw trap). An index of the relative size of the previous year's population ( $\hat{\theta}_t$ ) was calculated as the reciprocal of  $\hat{\lambda}_t$ . In this way, adult abundance was projected forward from the year in which the estimates of adult abundance were made:

$$\hat{N}_{t+1} = \hat{N}_t \times \hat{\lambda}_t.$$

Likewise, projections backward were made using the formula

$$\hat{N}_{t-1} = \hat{N}_t \times \hat{\theta}_t.$$

An additional step was needed to reconstruct adult Bull Trout abundance for the 10 trend data sets based on snorkeling; although there were typically hundreds of snorkel reaches within each Bull Trout population, reaches were not consistently snorkeled from year to year. To help ensure that the snorkel data represented Bull Trout population trends rather than spatiotemporal variability in sampling effort, we considered only those snorkel reaches that had been sampled at least twice in each decade (1980s, 1990s, and 2000s) and where data had been collected since the trend analyses conducted by High et al. (2008). Furthermore, we only included reaches that were surveyed in consecutive years in order to obtain unbiased estimates of the rate of population change for the interval (following Connelly et al. 2004). For example, if snorkel surveys within a population were conducted at 20 reaches in 2002 and 30 reaches in 2003 but only 10 reaches were surveyed in both years, then the rate of change for that population from 2002 to 2003 was based only on data from the 10 shared reaches. Based on these criteria,

data from 304 snorkeled reaches were used to estimate trends in adult Bull Trout abundance for the snorkel data sets.

We fitted a suite of stochastic population growth models to the time series population reconstructions for each Bull Trout population by using maximum likelihood methods. Thorough descriptions of these models are provided by Dennis et al. (2006) and Garton et al. (2011), but here we highlight a few important points. First, we tested the fit of the Gompertz state-space model (Dennis et al. 2006); this model is a stochastic version of the Gompertz model and estimates the amount of observation or sampling error ( $\hat{\tau}^2$ ) in abundance monitoring data that otherwise would be ascribed to process noise ( $\hat{\sigma}^2$ ). The formula for the Gompertz state-space model is

$$\hat{r}_t = \hat{a} - \hat{b} \cdot \log_e N_t + \hat{\tau}^2 + \hat{\sigma}^2,$$

where  $\hat{r}_t$  is the estimated instantaneous rate of change in year  $t$  ( $\log_e N_{t+1} - \log_e N_t$ ),  $\hat{a}$  is the estimated intercept,  $\hat{b}$  is the estimated slope (a measure of the strength of density dependence),  $\hat{\tau}^2$  is the estimated observation error, and  $\hat{\sigma}^2$  is the estimated process noise (a measure of environmental and demographic variation).

The fit of the data sets to this model was important because data sets with significant observation error produce spuriously inflated estimates of variability in population growth, resulting in pessimistic estimates of population viability (Morris and Doak 2002). The Gompertz state-space model was therefore used to identify data sets that were estimated to have no observation error and thus theoretically produced uninflated estimates of extinction risk. Secondarily, we identified data sets that were estimated to have minimal observation error, which we arbitrarily set at  $\hat{\tau}^2 < 0.10$ ; we assumed that minimal observation error would only slightly inflate the estimates of extinction risk. We assumed that estimates of extinction risk from data sets with  $\hat{\tau}^2$  of 0.10 or greater had the potential to be substantially inflated; such data sets were retained in further analyses to evaluate this assumption.

All data sets were then evaluated with the remaining suite of stochastic population growth models, including (1) the EGPE model (Dennis et al. 1991); (2) the Ricker-type model of density dependence in population growth (Dennis and Taper 1994); and (3) the Gompertz-type model of density dependence in population growth (Dennis et al. 2006). A “period effect” or a “time effect” in population carrying capacity was tested for all models (see below and Garton et al. 2011). One- and two-year time lags (Garton et al. 2011) were also tested in preliminary analyses but were not supported and therefore are not presented here.

The difference between the Ricker and Gompertz models is that the Ricker model assumes a linear (negative) relationship between population growth rates and population size, whereas the Gompertz model assumes a log (negative) relationship and thus larger density-dependent effects at smaller population sizes. Both models provide an estimate of carrying capacity, defined as the quasi-equilibrium abundance (i.e., the population size at

which the growth rate is zero; Garton et al. 2011). Models that included a period effect in our study implied that carrying capacity differed between the pre-1994 and post-1994 periods; “period” was consistently nonsignificant in the models, and this variable was eventually discarded. Models that included a time effect implied that carrying capacity was changing linearly through time, either increasing or decreasing depending on the sign of the estimated coefficient.

We fitted models to each data set by using PROC MIXED and PROC REG in the Statistical Analysis System (SAS Institute 2009), treating time and period as fixed effects and reconstructed population size as a random effect. Akaike’s information criterion corrected for small sample size was used to compare the relative performance of the models, and Akaike weights ( $w_i$ ) were calculated to describe the weight of evidence for the models (Burnham and Anderson 2002)—that is, the probability that a particular model was the most correct model among all of the models tested. Additionally, the adjusted coefficient of determination ( $r^2$ ) was used to describe the approximate amount of variation in annual rates of change that was explained by the models.

*Projections of population persistence.*—We performed parametric bootstraps (Efron and Tibshirani 1998) on minimum population size by projecting 100,000 replicate abundance trajectories for 10 years and 30 years into the future for each population:

$$\hat{N}(t+1) = \hat{N}(t) \times e^{\hat{r}(t)},$$

where  $\hat{N}(t+1)$  is the estimated population abundance at time  $t+1$ ;  $\hat{N}(t)$  is the estimated population abundance at time  $t$ ; and  $\hat{r}(t)$  is the estimated stochastic growth rate using maximum likelihood parameter estimates for the given model.

These bootstrapped trajectories were used to calculate the probability that a population would decline below a quasi-extinction threshold of 20 adult Bull Trout. Probability of quasi-extinction was calculated as the proportion of replications in which population abundance declined below the quasi-extinction threshold at some point during the time horizons of 10 years and 30 years. The quasi-extinction threshold of 20 adults was chosen because demographic stochasticity can create substantial variability in population growth rates only at low population sizes, and it has been argued that a good rule of thumb is to consider demographic stochasticity a critical factor in population viability only if a population is smaller than about 20 adults (Goodman 1987; Lande 1993; Morris and Doak 2002). The maximum time horizon of 30 years was chosen to limit future predictions to a short time period (Beissinger and Westphal 1998).

We considered each model within the sum of  $w_i \geq 0.95$  to be a competing “best” model. Although here we report only the best model for each population, we estimated the probability of quasi-extinction based on parameter estimates from all of the competing best models for each data set by using model averaging to incorporate model uncertainty into the estimates (Burnham and Anderson 2002). In other words, the probability

of extinction for an individual Bull Trout population was estimated as the model-averaged bootstrapped probability of extinction across all competing best models for that data set (Garton et al. 2011).

We assumed that Bull Trout population viability was independent between populations. We deemed this a reasonable assumption because correlations in abundance between Bull Trout populations were generally low: Pearson's product-moment correlation coefficients (Pearson's  $r$ ) for the rates of change between all pairs of populations averaged 0.10 (SE = 0.02; median = 0.10).

## RESULTS

The data sets that indexed Bull Trout abundance contained, on average, 19 years of record (Table 1). Approximations of starting Bull Trout population size averaged 2,485 adults (median = 884 adults) and ranged from a low of 109 adults (Priest Lakes population) to a high of 12,513 adults (Lake Pend Oreille population; Table 1). Most (57%) of the populations included in our analyses were estimated to possess fewer than 1,000 adults.

### Trends in Abundance

Bull Trout populations tended to be relatively stable prior to 1994, but most of the populations increased in abundance

after 1994 (Table 2). Prior to 1994,  $r_{intrinsic}$  was zero for three data sets, positive for four data sets, and negative for five data sets (one of which was significant at  $\alpha = 0.10$ ). After 1994,  $r_{intrinsic}$  was zero for 2 data sets, positive for 18 data sets (14 significant), and negative for 5 data sets (3 significant). Average rates of change were 0.01 (SE = 0.03) prior to 1994 compared with 0.07 (SE = 0.02) after 1994. Across all populations and all years of data, the average rate of change was 0.07 (SE = 0.02).

### Observation Error

For 3 of the 25 Bull Trout trend data sets, monitoring was not conducted annually; thus, density-dependent population growth models could only be fitted to the remaining 22 data sets. Of those 22 data sets, 10 data sets had no measurable observation error and 3 data sets were estimated to have minimal observation error (i.e.,  $0 < \hat{\tau}^2 < 0.10$ ; Table 3). Snorkeling data were most prone to high observation error, as 70% of the snorkeling data sets had  $\hat{\tau}^2$  values of 0.10 or higher. In contrast, only 17% of the redd count data sets and 25% of the screw trap data sets had  $\hat{\tau}^2$  values of 0.10 or greater.

### Population Growth Models

The suite of population growth models generally provided a good fit to Idaho Bull Trout trend data sets, with the best models explaining on average about half of the variation in

TABLE 2. Intrinsic rates of change ( $r_{intrinsic}$ ) for Bull Trout populations in Idaho. Shaded estimates of  $r_{intrinsic}$  indicate statistically significant trends (i.e., those that do not overlap zero). Missing estimates indicate cases where data were insufficient for that period of record (CL = 90% confidence limit).

Bull Trout population	Data type	Pre-1994			Post-1994			All years		
		Estimate	Lower CL	Upper CL	Estimate	Lower CL	Upper CL	Estimate	Lower CL	Upper CL
Lower Kootenai River	Redd count				0.00	-0.03	0.02	0.01	-0.01	0.03
Coeur d'Alene Lake	Redd count				0.05	0.02	0.09	0.05	0.02	0.09
Lake Pend Oreille	Redd count	-0.03	-0.05	0.00	0.00	-0.02	0.02	0.00	-0.01	0.01
Priest Lakes	Redd count				-0.06	-0.11	-0.02	— <sup>a</sup>		
North Fork Clearwater River	Redd count				0.18	0.13	0.23	— <sup>a</sup>		
Lochsa River	Redd count				0.10	0.05	0.15	— <sup>a</sup>		
	Snorkeling	0.25	-0.15	0.65	0.18	0.11	0.25	0.17	0.12	0.22
	Screw trap				0.01	-0.04	0.07	0.01	-0.04	0.07
Selway River	Snorkeling	0.00	-0.37	0.36	0.04	-0.02	0.10	-0.02	-0.07	0.02
South Fork Clearwater River	Screw trap				0.16	0.08	0.24	— <sup>a</sup>		
	Snorkeling	-0.25	-0.35	-0.15	-0.07	-0.12	-0.01	-0.11	-0.14	-0.08
Little Salmon-Lower Salmon River	Snorkeling	0.05	-0.06	0.16	-0.04	-0.09	0.00	-0.01	-0.03	0.02
	Weir	-0.01	-0.04	0.01	0.06	0.03	0.09	0.01	0.00	0.02
South Fork Salmon River	Screw trap				0.17	0.11	0.22	0.14	0.09	0.20
	Snorkeling	-0.02	-0.20	0.16	0.20	0.10	0.30	0.16	0.11	0.21
Middle Fork Salmon River	Snorkeling	0.00	-0.11	0.12	-0.15	-0.23	-0.08	-0.15	-0.19	-0.12
Mid-Salmon River (Chamberlain)	Snorkeling	0.05	-0.11	0.22	0.20	0.16	0.24	0.16	0.13	0.20
Lemhi River	Snorkeling	-0.09	-0.28	0.10	0.05	-0.04	0.14	0.08	0.03	0.13
Upper Salmon River	Snorkeling	0.11	-0.17	0.39	0.04	-0.11	0.19	0.15	0.08	0.22
	Weir	0.00	-0.09	0.10	0.05	0.02	0.09	0.06	0.04	0.08
	Creel				0.09	0.02	0.16	— <sup>a</sup>		
	Screw trap				0.10	0.01	0.19	— <sup>a</sup>		
Anderson Ranch Reservoir	Electrofishing				0.18	0.04	0.31	— <sup>a</sup>		
Weiser River	Snorkeling				0.35	0.01	0.69	— <sup>a</sup>		
Little Lost River	Electrofishing				-0.04	-0.09	0.02	— <sup>a</sup>		

<sup>a</sup>Estimates are equivalent to post-1994 estimates due to a lack of pre-1994 data.

TABLE 3. Parameter estimates fitting data sets that describe Idaho Bull Trout adult abundance to the Gompertz state-space model (which estimates observation error as  $\hat{\tau}^2$  and process noise as  $\hat{\sigma}^2$ ;  $a$  = intercept;  $b$  = slope), and the best-fitting population growth models with resulting model statistics (EGPE = exponential growth with process error;  $AIC_c$  = Akaike's information criterion corrected for small sample size;  $w_i$  = Akaike weight). Data sets were separated into those that were estimated to have no observation error, minimal observation error (i.e.,  $\hat{\tau}^2 < 0.10$ ), or high observation error (i.e.,  $\hat{\tau}^2 \geq 0.10$ ).

		Gompertz state-space model parameter estimates				Population growth model results				
Bull Trout population	Data type	$\hat{\tau}^2$	$\hat{\sigma}^2$	$a$	$b$	Best model	$r^2$	AIC <sub>c</sub> $w_i$	Estimated adult carrying capacity (SE)	Ending adult population size
Data sets with no observation error										
Lower Kootenai River	Redd count	0.00	0.49	2.71	−0.43	Gompertz	0.28	0.43	480 (8)	341
Coeur d' Alene Lake	Redd count	0.00	0.18	3.45	−0.50	Gompertz	0.31	0.43	232 (24)	197
Lake Pend Oreille	Redd count	0.00	0.04	7.20	−0.87	Gompertz	0.41	0.45	17,239 (120)	14,937
Priest Lakes	Redd count	0.00	0.31	4.74	−0.66	Gompertz + Year	0.62	0.45	93 (42)	95
South Fork Clearwater River	Screw trap	0.00	0.70	2.60	−0.41	EGPE	0.00	0.67	— <sup>a</sup>	1,998
Lochsa River	Screw trap	0.00	0.31	4.40	−0.66	Gompertz	0.32	0.38	1,511 (118)	2,170
Selway River	Snorkeling	0.00	0.49	2.22	−0.76	Gompertz	0.45	0.71	181 (6)	153
Little Salmon–Lower Salmon River	Snorkeling	0.00	0.22	4.98	−0.76	Gompertz	0.40	0.52	682 (19)	316
	Weir	0.00	0.14	2.56	−0.47	Gompertz	0.28	0.48	1,345 (53)	1,677
Upper Salmon River	Creel	0.00	0.51	9.71	−1.24	Gompertz + Year	0.59	0.44	4,074 (1,440)	9,569
Data sets with minimal observation error										
Lochsa River	Redd count	0.08	0.13	1.80	−0.29	Gompertz	0.45	0.64	703 (102)	675
South Fork Salmon	Screw trap	0.08	0.13	1.80	−0.29	Gompertz + Year	0.49	0.61	6,117 (3,564)	2,953
	Snorkeling	0.07	0.28	0.15	−0.09	EGPE	0.00	0.43	— <sup>a</sup>	722
Data sets with high observation error										
North Fork Clearwater River	Redd count	0.12	0.28	1.15	−0.17	Gompertz + Year	0.49	0.56	5,075 (3,596)	1,856
South Fork Clearwater River	Snorkeling	0.16	0.99	0.49	−0.08	Gompertz + Year	0.39	0.69	62 (154)	77
Lochsa River	Snorkeling	0.47	0.21	0.67	−0.13	Gompertz + Year	0.63	0.99	1,659(1,525)	543
Middle Fork Salmon River	Snorkeling	0.36	0.17	0.16	−0.04	Gompertz + Year	0.53	0.99	1,503 (17,329)	10,728
Mid-Salmon River (Chamberlain)	Snorkeling	0.36	0.08	0.19	−0.03	Gompertz + Year	0.55	0.99	715 (655)	554
Lemhi River	Snorkeling	0.33	0.25	1.67	−0.22	Ricker + Year	0.54	0.89	7,979 (326)	1,431
Upper Salmon River	Screw trap	0.35	0.68	4.11	−0.61	Gompertz	0.37	0.47	1,815 (707)	2,218
Weiser River	Snorkeling	1.22	0.26	3.89	−0.62	Gompertz + Year	0.86	0.97	121,885 (118,891)	2,399
Upper Salmon River	Snorkeling	0.32	1.08	3.11	−0.45	Gompertz + Year	0.40	0.48	6,776 (3,839)	548

<sup>a</sup>The EGPE model does not produce an estimate of carrying capacity.

annual rates of change (excluding the EGPE models, which inherently explain none of the variation; Table 3). The Gompertz model was nearly always (19 of 22 instances) the best-fitting model (Table 3). Essentially none of the best models contained a period effect, suggesting that carrying capacity generally did not differ between the pre-1994 and post-1994 time periods. In addition, only a few of the best models with zero or minimal observation error contained a time (i.e., year) effect, indicating that carrying capacity generally was not trending positively or negatively through time. For the trend data sets that were estimated to have high observation error, all but one model contained a year effect; thus, a positive or negative trend in carrying capacity through time was indicated for these data sets, although the presence of high observation error reduces the reliability of this result. For the data sets that were estimated to have zero or minimal observation error, there was a strong positive correlation between ending adult population size (in the last year of run reconstruction) and carrying capacity (Pearson's  $r = 0.91$ ), whereas for data sets with high observation error there was no correlation between ending adult population size and carrying capacity (Pearson's  $r = 0.00$ ).

### Projections of Population Persistence

Parametric bootstraps based on model-averaged parameter estimates predicted that for the abundance data sets estimated to have zero or minimal observation error, the mean probability of falling below the quasi-extinction threshold of 20 adults in 10 years was 3.5% (median = 1.7%) and the mean probability of falling below this threshold in 30 years was 9.8% (median = 4.7%; Figure 2). In comparison, for data sets estimated to have high observation error, the mean probability of falling below 20 adults was 16.2% (median = 4.4%) for the 10-year period and 34.3% (median = 11.0%) for the 30-year period. Thus, a decline below the quasi-extinction level in 10 years was 3.7 times more likely—and in 30 years was 3.1 times more likely—for data sets with high observation error than for data sets with zero or minimal observation error.

Data sets with zero or minimal observation error were characterized by a negative exponential relationship between the ending adult population size (after  $\log_e$  transformation) and the probability that the population would decline below 20 adults in 30 years ( $r^2 = 0.32$ ,  $F = 5.06$ ,  $P = 0.05$ ; Figure 3). For the data sets with high observation error, no such relationship existed ( $r^2 = 0.02$ ,  $F = 0.11$ ,  $P = 0.75$ ; Figure 3).



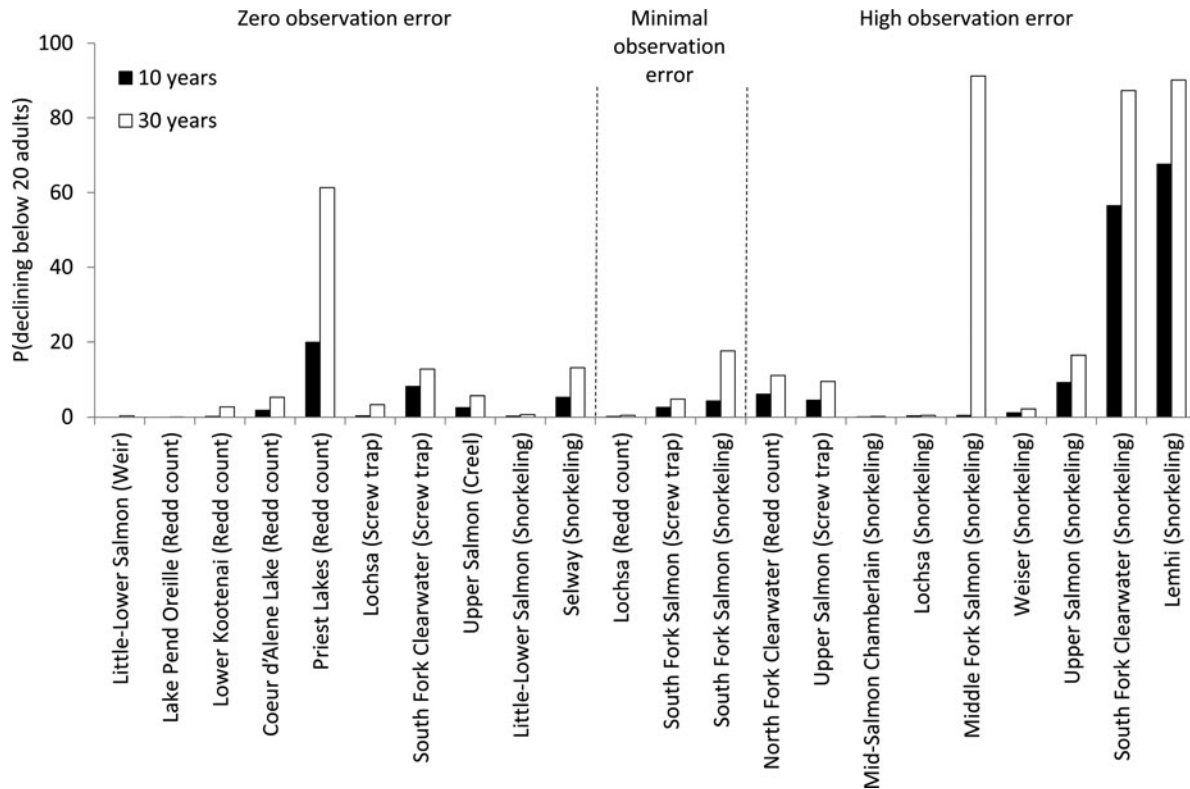


FIGURE 2. Estimated probability of Bull Trout populations in Idaho declining below the quasi-extinction threshold of 20 adults in 10 years or 30 years.

## DISCUSSION

### Data Limitations

Over half of the available long-term Bull Trout trend data sets were estimated to contain a statistically significant amount of observation error. This finding supports repeated assertions that Bull Trout trend monitoring data, which are frequently obtained from redd counts or snorkeling surveys, are often rife with sampling error (Dunham et al. 2001; Muhlfeld et al. 2006; Thurow et al. 2006) and are therefore inappropriate for use in PVA modeling (Columbia River Fisheries Program Office, 2005 memorandum to R. White, Project Manager, on Bull Trout 5-year review). The development of the Gompertz state-space model (Dennis et al. 2006) allows biologists to separate abundance trend data sets with high observation error from other data sets that are likely to produce more accurate estimates of persistence. Realistically, though, even for data sets with high observation error, PVA modeling results should still be considered useful for instances in which extinction probabilities are predicted to be low, since observation error can only inflate the estimated risk of extinction.

Our results suggest that for monitoring the trends in adult Bull Trout abundance in stream settings, data that are collected from snorkeling short index reaches (typically 100 m long in our study) will likely contain more sampling error than data that are generated by other traditional fish sampling techniques. This is

not surprising, as most of the fish that are counted during snorkel surveys are juveniles and subadults, which are subject to higher variability because of interannual fluctuations in recruitment. However, for the data included in our study, 11% of the Bull Trout observed during snorkel surveys were 400 mm TL or larger. Since Bull Trout of this length are usually considered mature (Downs et al. 2006; Muhlfeld et al. 2012) and since previous population modeling exercises have assumed that about 10% of all Bull Trout in a population are adults (Rieman and McIntyre 1993; Rieman and Allendorf 2001), the proportion of spawning adults among the fish observed during snorkeling was probably similar to the proportion of spawning adults within the actual populations. For this reason, we believe that the use of snorkel data sets in PVAs is appropriate if (1) observation error is not high or (2) observation error is high but the projected extinction risk is low (since, as mentioned above, observation error can only bias the extinction risk upward).

High et al. (2008) previously overlooked screw traps as a data source, and these data generally appeared to have minimal observation error despite the fact that screw traps captured spawning adults even less frequently than snorkeling (only 1% of the fish captured in screw traps in our study were  $\geq 400$  mm TL). The two types of data set that represented the most direct monitoring of adult Bull Trout abundance (i.e., weirs and redd counts) were usually reliable insofar as they infrequently had high observation error. Regardless of the population monitoring method, we

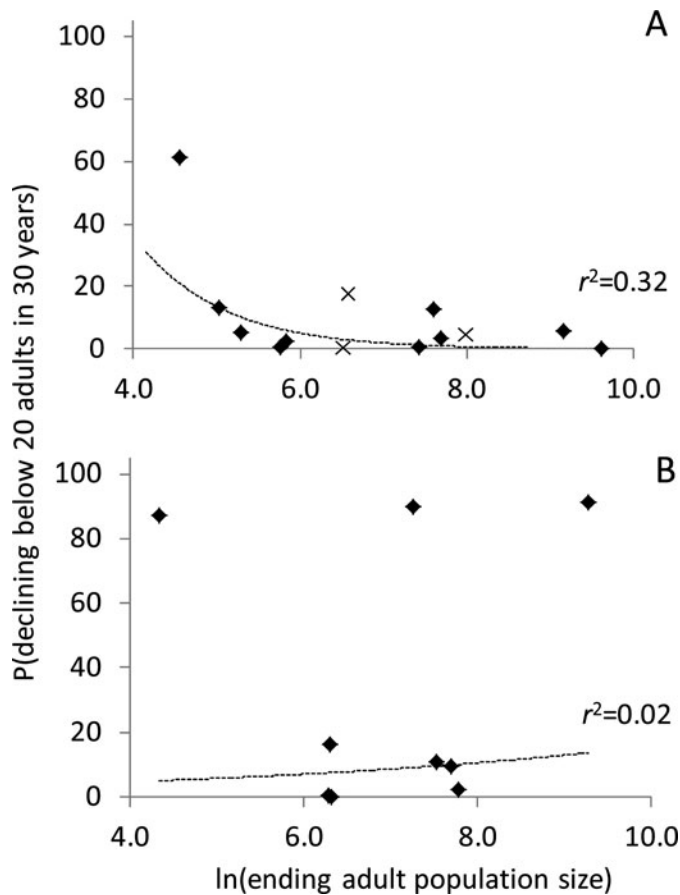


FIGURE 3. Relationships between ending adult population size and the risk of extirpation (i.e., the probability of declining below 20 adults in 30 years) for Bull Trout populations in Idaho: (A) results from trend monitoring data sets with zero (black diamonds) or minimal (x symbols) observation error; and (B) results from data sets with high observation error. Dashed lines and coefficient of determination ( $r^2$ ) values represent negative exponential regression results.

considered all data sets with no measurable observation error to have produced the most reliable estimates of persistence.

Overestimation of adult population sizes would likely have resulted in overestimation of the probabilities of persistence; however, we believe that if anything, our adult abundance approximations were likely underestimates for most of the populations we evaluated. For instance, when redds were extrapolated to estimate adult population size, we assumed that all of the redds produced by the population were actually counted and that all of the adults spawned each year, but neither assumption is likely to be true. In the Lake Pend Oreille population, for example, 1,869 redds were counted in 2008. Based on previous spawning run investigations for this population, 3.2 adults exist for each redd constructed and 93% of adults are repeat spawners (Downs and Jakubowski 2006; Downs et al. 2006). Assuming that these findings are applicable throughout the Lake Pend Oreille population, adult abundance in this population during 2008 would be estimated at 6,430 fish. However, an unrelated mark-recapture study conducted in Lake Pend Oreille during 2008 produced an

estimate of 12,513 Bull Trout ( $\geq 400$  mm TL; Hansen, unpublished data). Since 400-mm and larger fish are mostly mature in this population (Downs et al. 2006; also see Muhlfeld et al. 2012), we used the latter estimate for adult abundance in the present study. Even the mark-recapture estimate assumes that there is no resident or fluvial component to the population. The difference between the mark-recapture estimate and the redd count extrapolation suggests that some Bull Trout redds were missed in the Lake Pend Oreille population during sampling efforts in 2008. Similarly, redds were undoubtedly missed in the other three populations for which approximations of adult population size were based entirely on redd count extrapolations (i.e., lower Kootenai River, Coeur d'Alene Lake, and Priest Lakes populations), suggesting that those abundance approximations may have been similarly underestimated.

The remaining approximations of adult population size in Table 1 were derived from abundance estimates for 70-mm TL and larger Bull Trout as reported by High et al. (2005, 2008), and for a number of reasons those authors considered their estimates to underrepresent actual abundance. This was largely because the density estimates were obtained with snorkeling and electrofishing removal methods, and both techniques are known to underestimate actual abundance (Thurrow and Schill 1996; Thurrow et al. 2006; Meyer and High 2011). To approximate adult population size from the abundance estimates of High et al. (2005, 2008), we assumed that 10% of all 70-mm and larger Bull Trout were adults. This assumption was deemed reasonable and possibly conservative because, as mentioned above, previous studies that have used population modeling exercises to simulate Bull Trout population structure, effective population size, and similar metrics have assumed that 17% of all Bull Trout were adults (Rieman and McIntyre 1993) or that 6–13% of Bull Trout larger than 50 mm were adults (Rieman and Allendorf 2001).

We assumed that the trend data sets available for a population were unbiased representations of the true trend within that population. For most populations, this assumption is tenuous because the trend data were obtained from only a portion of the population. Nonetheless, for the five Bull Trout populations with multiple trend data sets available, there was agreement between trend directions within the same population in 20 of 24 direct comparisons (Table 2). Furthermore, many of the trend data sets were initiated to monitor species other than Bull Trout, such as the screw trap and snorkel data sets for the Salmon River and Clearwater River basins. Although these data sets contained data on all salmonids encountered, they were established to monitor trends in salmon and steelhead, and it therefore seems unlikely that their use would have resulted in Bull Trout data that were consistently more optimistic than the mean growth rate for the population would have been.

### Trends in Abundance

Humbert et al. (2009) found that trend estimation based on regressions of log-linear abundance against time produced unbiased estimates of the rate of change, but CIs were correct only

when process noise was absent or small in relation to observation error. Since few of our data sets fit this condition, some of the statistically significant trends in Table 2 (both positive and negative) may not have been significant if the 90% CIs were correct or vice versa for the trends that were not statistically significant. However, since the estimated rates of change were unbiased, the statewide mean trends and the trends for different time periods should be accurate. Moreover, the sheer number of positive post-1994 estimates (19) compared with negative post-1994 estimates (5) suggests that regardless of statistical significance, many Bull Trout populations in Idaho have been at least stable, if not increasing, since 1994. We considered the inclusion of a more comprehensive random coefficients regression model (using PROC MIXED in the Statistical Analysis System and following the modeling recommendations of Piepho and Ogutu 2002) to produce statewide trend estimates by time period. However, the resulting estimates of trends were 0.01 (SE = 0.03) for the pre-1994 period, 0.08 (SE = 0.02) for the post-1994 period, and 0.07 (SE = 0.02) across all years—essentially identical to the estimates already reported herein from use of the more simplistic approach of Maxell (1999).

Although the post-1994 upward trend in Bull Trout abundance in Idaho corresponds with the 1994 implementation of no-harvest regulations for Bull Trout in the state, we suspect that this correspondence is largely coincidental. Indeed, other sympatric native salmonids (Chinook Salmon *O. tshawytscha*, steelhead, Mountain Whitefish, and Westslope Cutthroat Trout) and nonnative salmonids (Brook Trout *Salvelinus fontinalis*) have also been increasing in a strikingly similar manner over much of the study area since 1994 (High et al. 2008; Copeland and Meyer 2011). Copeland and Meyer (2011) suggested that salmonids (including Bull Trout) in central Idaho have been responding coherently to large-scale bioclimatic indices over the past several decades, with Bull Trout abundance being especially associated (positively) with mean annual streamflow.

It may be surprising that Bull Trout abundance has been stable or increasing across much of Idaho for the last several decades, considering that (1) climate change has been warming stream temperatures in portions of the Bull Trout's range in Idaho since at least 1980 (Isaak et al. 2010, 2011) and (2) Bull Trout are expected to be among the fish species with the greatest sensitivity to climate change in western North America (Rieman et al. 2007; Isaak et al. 2010, 2012) due to their need for cold water temperatures and large patches of connected habitat (Rieman and McIntyre 1995; Dunham and Rieman 1999; Wenger et al. 2011). While it is likely that continued stream warming will at some point become measurably detrimental to Bull Trout, the disconnect between more than three decades of climate-induced stream warming and the positive trend in abundance for many Idaho Bull Trout populations over the same period is paradoxical. This apparent inconsistency suggests that other abiotic or biotic stream conditions may currently be mitigating some of the negative impacts of climate change on Bull Trout, at least within the range of climate alteration observed to date. For ex-

ample, winter is often a stressful period of high mortality for stream-dwelling salmonids in temperate climates (reviewed by Cunjak 1996). Although predicted changes in winter ice and flow dynamics due to climate change are complex (reviewed by Linnansaari and Cunjak 2012), milder winter conditions in the future (and presumably over the last several decades already) may result in increased fall-to-spring growth, improved egg survival, accelerated alevin development, and reduced exposure to severe mechanical ice break-up, all of which may reduce winter mortality for Bull Trout populations.

### Population Growth Models

State-space models have become the standard approach for estimating the magnitude of observation error relative to process noise in time series models of population abundance and rates of change. Determining the relative magnitude of observation error and process noise in population abundance data is an important step in validating PVAs (Dennis et al. 2006), as is determining which population growth models yield the best fit to the data sets at hand. We believe that applying the Gompertz state-space model to test for density dependence while simultaneously evaluating the magnitude of observation error is the most reasonable modeling approach for use with long-term Bull Trout monitoring data sets. The finding of zero or minimal observation error for most of the data sets helps substantiate the estimates of future persistence that were projected under model bootstrapping, which assumed that all or nearly all of the error was due to process noise. If this assumption was incorrect, then the projections were conservative in that the probabilities of quasi-extinction were overestimated. Moreover, if a density-independent model (such as the EGPE) was used when density dependence was operating in the population (and in the data), then the estimates of quasi-extinction would again be overestimated. The power of using the information-theoretic approach is that it combines the predictions of all alternative models of stochastic population dynamics correctly on the basis of each model's probability of being the correct model for that particular time series of abundances. In all cases, the projections of persistence were conservative because they ascribed all of the error to process noise even though in certain cases some or most of the error might be due to observation error.

For the data sets that were estimated to have zero or minimal observation error, the lack of a period effect or a time effect in our modeling results suggests that carrying capacity has not changed for Bull Trout populations over the last several decades. The strong coherence between carrying capacity and ending adult population size (in the last year of run reconstruction) suggests that most Bull Trout populations in Idaho are now at or near their carrying capacity. Thus, the increasing abundance of Bull Trout since 1994 may have filled available habitat that was previously underseeded with Bull Trout. Because Bull Trout have a long developmental period (Pratt 1992), filling the available habitat would presumably be a protracted process. The lack of a similar coherence between carrying capacity and

ending adult population size for data sets with high observation error suggests that model estimates of carrying capacity were unreliable when observation error was high.

### Projections of Population Persistence

We assumed that the population level (rather than the subpopulation level) was the appropriate scale at which to apply PVA models for Bull Trout in Idaho because population viability is more appropriately linked to populations than to subpopulations (Ruggiero et al. 1994; McElhany et al. 2000; Theobald and Hobbs 2002). However, PVA modeling has been applied at nearly every scale imaginable, including subpopulations, populations, states, evolutionarily significant units, subspecies, and species. The scale at which population growth model projections are applied affects viability because adult population size is obviously smaller at more condensed scales, and smaller populations are inherently at greater risk of falling below quasi-extinction thresholds. We conducted Bull Trout PVA modeling at the same scale and by using the same population growth models as in a previous study that assessed the viability of Bull Trout populations in Montana (Staples et al. 2005). An order-of-magnitude larger scale (relative to the spatial size of an average population) was used to assess the viability of greater sage-grouse *Centrocercus urophasianus* populations in western North America (Garton et al. 2011). Although dispersal, habitat fragmentation, and population characteristics of Bull Trout are not the same as those for greater sage-grouse, the spatial scales used in these previous studies suggest that at a minimum, the scale at which we applied our analyses for Bull Trout was not too large.

Our estimated probabilities of persistence would have been lower had we used a higher threshold for quasi-extinction. The term quasi-extinction was first defined by Ginzburg et al. (1982) as the minimum number of individuals below which a population is likely to be critically and immediately imperiled. Although quasi-extinction levels should ideally be specific to the environmental and life history characteristics of a particular species (Reed et al. 2003), selection of a quasi-extinction level is essentially a subjective decision (Morris and Doak 2002) that involves determining how much extinction risk is considered acceptable or tolerable (Shaffer et al. 2002; Wilhere 2008). Higher values than we used (e.g., 100 adults) would likely translate to an effective population size of 50 for Bull Trout (Rieman and Allendorf 2001); above this level, populations are generally considered to be resistant to the immediate effects of inbreeding depression (Franklin 1980). However, demographic stochasticity is considered more important than genetic concerns in determining persistence for small populations (Lande 1988), and demographic stochasticity is generally considered to be a critical factor in population viability only if the population is smaller than about 20 adults (Goodman 1987; Lande 1993; Morris and Doak 2002). Regardless of the quasi-extinction threshold used, since relative estimates of persistence or extinction between populations are more useful than absolute values generated by the models (Beissinger and Westphal 1998), our results may best serve to

highlight which Bull Trout populations in Idaho are more secure or more vulnerable to extirpation over the next several decades.

The probability of populations declining below the quasi-extinction level of 20 adults was over three times higher for data sets with high observation error than for those with zero or minimal observation error, thereby supporting our premise that observation error would artificially inflate extinction risk. Nevertheless, extinction risk was relatively low for most Bull Trout populations, regardless of whether or not the data sets had measurably high observation error. Our results indicate the need for better trend monitoring data sets from some Bull Trout populations, such as the Lemhi River and Middle Fork Salmon River populations, for which the only existing data sets have high observation error. Moreover, 13 Bull Trout populations in Idaho have no long-term abundance monitoring data of which we are aware. Description of trends and persistence probabilities for Bull Trout in Idaho cannot be completed until additional abundance time series become available for populations that currently lack such data.

We recognize that (1) some of the assumptions we made are arguable, (2) some of the sampling methods had shortcomings, and (3) accurate characterization of trends and abundance for every Bull Trout population presents challenges considering the sparse abundance of Bull Trout and the vast and remote landscape they occupy. We also recognize that our PVA modeling results assume that stream habitat conditions in the foreseeable future (which we define as roughly the next three decades; also see Shepard et al. 2003) will not be radically and expeditiously altered by overwhelming wildfire, severe stream warming, or some other overarching ecosystem change that could sweep across the riverscape. Despite these assumptions, the weight of evidence from the present study suggests that most of the Bull Trout populations in Idaho are generally at low risk of extirpation in the foreseeable future. Assuming that our results pragmatically reflect the persistence probabilities for Idaho Bull Trout populations with available trend data, we hope that our results will help to focus management efforts on long-term maintenance of strong populations and on those at-risk populations with the best prospects of persistence or with the greatest need for management intervention.

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