



**STATUS UPDATES FOR YELLOWSTONE CUTTHROAT
TROUT, REDBAND TROUT, AND BULL TROUT IN IDAHO**



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CHAPTER 1: TRENDS IN THE DISTRIBUTION AND ABUNDANCE OF YELLOWSTONE CUTTHROAT TROUT AND NONNATIVE TROUT IN THE UPPER SNAKE RIVER BASIN OF IDAHO

ABSTRACT

The distribution and abundance of Yellowstone cutthroat trout *Oncorhynchus clarkii bouvieri* across their native range is relatively well known, but evaluations of trends in distribution and abundance over time are lacking. In 2010-2011, we resurveyed 74 stream reaches in the upper Snake River basin of Idaho that were previously sampled in the 1980s and again in 1999-2000 to evaluate changes in the distribution and abundance of Yellowstone cutthroat trout and nonnative trout over time. Yellowstone cutthroat trout occupied all 74 reaches in the 1980s, 70 reaches in 1999-2000, and 69 reaches in 2010-2011. In comparison, rainbow trout *O. mykiss* and rainbow x cutthroat hybrid occupancy increased from 23 reaches in the 1980s to 36 reaches in 1999-2000, and then declined to 23 reaches in 2010-2011. Brown trout *Salmo trutta* and brook trout *Salvelinus fontinalis* occupancy was largely unchanged across time periods. Yellowstone cutthroat trout abundance declined from a mean of 40.0 fish/100 linear meters of stream in the 1980s to 32.8 fish/100 m in 2010-2011. In contrast, abundance increased over time for all species of nonnative trout, although the change was statistically significant (at $\alpha = 0.10$) only for brown trout. Population growth rate (λ) was below replacement for Yellowstone cutthroat trout (0.98) and above replacement (>1.00) for all nonnative trout, but 90% confidence intervals overlapped unity for all species. However, population growth differed statistically from 1.00 within several individual drainages for each species. More pronounced drought conditions in any given year resulted in lower Yellowstone cutthroat trout abundance one year later. Our results suggest that over a span of up to 32 years, the distribution and abundance of Yellowstone cutthroat trout in the upper Snake River basin appears to be relatively stable, and nonnative trout do not currently appear to be displacing Yellowstone cutthroat trout across the landscape.

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INTRODUCTION

Yellowstone cutthroat trout *Oncorhynchus clarkii bouvieri* are one of the most abundant and broadly distributed cutthroat trout subspecies in western North America (Behnke 2002). Nevertheless, their distribution and abundance has declined substantially over the last century due to anthropogenic activities that have considerably altered the ecological riverscape that they occupy (reviewed in Gresswell 2011). Such declines led to a petition in 1998 to list Yellowstone cutthroat trout under the Endangered Species Act (ESA), and a court-ordered status review was initiated in 2005, but in both instances the species status did not warrant ESA protection (USFWS 2001, 2006). Nevertheless, Yellowstone cutthroat trout are considered a species of concern by the State of Idaho and other entities, and their status in Idaho is closely monitored by the Idaho Department of Fish and Game (IDFG) (e.g., Meyer et al. 2003a, 2006a; IDFG 2007).

Nonnative trout pose the largest threat to the long-term persistence of Yellowstone cutthroat trout by way of two primary vectors. First, hatchery rainbow trout *O. mykiss* of coastal origin have been stocked throughout the range of Yellowstone cutthroat trout for more than 100 years (Gresswell 2011). Because rainbow trout readily hybridize with Yellowstone cutthroat trout, genetic introgression threatens to reduce pure populations of Yellowstone cutthroat trout across much of their range (May et al. 2007). Second, nonnative brook trout *Salvelinus fontinalis*, a species that typically outcompetes and often displaces cutthroat trout populations in western North America (reviewed in Dunham et al. 2002 and Fausch et al. 2009), has also been stocked across the native range of Yellowstone cutthroat trout, has established numerous self-sustaining populations, and continues to invade some unoccupied streams (Dunham et al. 2002; Fausch et al. 2009). Brown trout *Salmo trutta* are a third nonnative salmonid in sympatry with native Yellowstone cutthroat trout in many areas, but the interaction between these two species appears to be relatively benign (Gresswell 2011; but see Quist and Hubert 2005).

Numerous status assessments have been conducted to evaluate the distribution and abundance of Yellowstone cutthroat trout (e.g., Varley and Gresswell 1988; Thurow et al. 1997; Kruse et al. 2000; Meyer et al. 2006a; May et al. 2007; Gresswell 2011). However, most status assessments have lacked information on trends in abundance. A notable exception is the trend monitoring being done by IDFG, which consists of numerous population monitoring surveys scattered across several river drainages in the upper Snake River basin. Initial surveys were conducted in the 1980s, and the same reaches were sampled again in 1999-2000 (Meyer et al. 2003a). Because more than a decade has passed since the last surveys, our first objective was to repeat the same sampling reaches for a third time to evaluate changes in Yellowstone cutthroat trout occupancy, abundance, and population growth in Idaho. Due to the aforementioned concern posed by nonnative salmonids, we evaluated the same characteristics for rainbow trout, brook trout, and brown trout at these sampling reaches to assess whether these species were expanding in distribution or abundance.

Drought has an almost universal negative effect on stream-dwelling fish populations (Matthews and Marsh-Matthews 2003). Impacts can be (1) immediate, such as with short-term changes in fish populations due to loss of habitat quantity or quality (Magoulick and Kobza 2003) or physiological stress on individuals, or (2) delayed, such as reduced reproductive success (Elliott et al. 1997). Resident salmonids have been shown to be negatively affected by drought conditions (e.g., Elliott 2000; Hakala and Hartman 2004; White and Rahel 2008), and drought has often been implicated as a primary factor affecting cutthroat trout populations (Dunham et al. 1999; Haak et al. 2010; Gresswell 2011). Consequently, as a second objective

we evaluated whether drought conditions were related to Yellowstone cutthroat trout abundance in the upper Snake River basin.

METHODS

The upper Snake River basin in eastern Idaho is a high desert region of the Intermountain West with streams that range in elevation from 1,020 m at Shoshone Falls to headwater tributaries near 2,400 m. Shoshone Falls is a 65-m waterfall on the Snake River that forms a natural barrier to upstream invasion by redband trout *O. mykiss gairdneri*, which are native below the waterfall. Snowmelt drives discharge in most tributaries of the upper Snake River and stream flows normally peak in May and June. However, dams control flows in the larger tributaries for downstream irrigation use, resulting in peak flows being delayed to summer months in these reaches.

Over a hundred stream reaches across the upper Snake River basin were originally surveyed by IDFG biologists in the 1980s to monitor Yellowstone cutthroat trout populations. To control for spatial variation in trout abundance (Milner et al. 1993), Meyer et al. (2003a) only resurveyed reaches that could be precisely located using maps, photos, field notes, or other distinguishing characteristics. Of the 77 reaches resurveyed by Meyer et al. (2003a), we were able to resample 74 reaches in 2010-2011 (private property access was denied at 3 of the originally sampled locations). To control for temporal variation in trout abundance (Hicks and Watson 1985; Petty et al. 2005), sampling was repeated close to the original calendar date, with more than one-half of repeat surveys occurring within 14 days of the original sampling date (mean = 17 days). Stream reaches that we surveyed in this study ranged from 49 to 7,300 m long, from 2 to 79 m wide, and from 1,457 to 2,097 m in elevation, and included first- to seventh-order streams (at a 1:100,000 hydrography layer).

Trout were collected by electrofishing, anesthetized, identified to species, measured for total length (TL) to the nearest mm, and released. In small, shallow streams ($n = 57$), two- or three-pass electrofishing removals were made using backpack electrofishing units and pulsed DC at settings of 50-60 Hz, 0.5-2.0 ms pulse width, and 300-800 volts. Trout abundance and associated variance were estimated using the maximum likelihood model in the MicroFish software package (Van Deventer and Platts 1989). If no trout were captured on the second pass, we considered the catch on the first pass to be the estimated abundance. Use of block nets during fish sampling (to meet the assumption of a closed population) was not standardized between reaches or time periods, although in general they were used infrequently (<20% of the time); we assumed this had minimal influence on our study because previous studies have demonstrated that block nets have little effect on salmonid movement or population estimates in streams (Young and Schmetterling 2004, 2012).

At reaches too large to perform removal electrofishing ($n = 17$), mark-recapture electrofishing was conducted with a canoe- or boat-mounted unit using a pulsed DC waveform operated at 60 Hz, 400-500 volts, and a duty cycle of 20-40%. All trout were marked with a caudal fin clip during the marking run, and marked and unmarked trout were captured during a single recapture run 1 to 7 days after the marking run. We assumed there was no movement of marked or unmarked fish into or out of the study reach between the mark and recapture runs, and attempted to reduce the likelihood of movement by lengthening the study reaches to 327 - 7,300 m in length (mean = 3,175 m) and avoiding the release of fish near the top or bottom of the reach during the marking run. We used the Fisheries Analysis Plus program (Montana Fish, Wildlife, and Parks 2004) to calculate abundance estimates and associated variance using the

Lincoln-Petersen M-R model as modified by Chapman (1951). To control for size selectivity bias (Reynolds 1996), estimates were separated into the smallest size-groups possible (usually 100 mm) which met the criteria that (1) the number of fish marked in the marking run multiplied by the catch in the recapture run was at least four times the estimated population size and (2) at least three recaptures occurred per size group; meeting these criteria creates modified Petersen estimates that are less than 2% biased (Robson and Regier 1964).

As a result of low capture efficiencies for small fish in larger rivers, we could not estimate abundance of fish <100 mm in the mark-recapture reaches. Also, the length of age-0 fish was inconsistent across reaches and between species. For these reasons we did not include fish <100 mm in any of our estimates of trout abundance. For both depletion and mark-recapture electrofishing, all trout were pooled for an overall estimate of trout abundance at the reach scale (e.g., Mullner et al. 1998; Isaak and Hubert 2004; Carrier et al. 2009), and point estimates for each species were then calculated based on the proportion of catch that each species comprised (Meyer et al. 2012). Since 2001 hatchery rainbow trout have been sterilized in Idaho to eliminate hybridization concerns (Kozfkay et al. 2006); the few hatchery rainbow trout we encountered during sampling were readily distinguishable from wild rainbow trout based on fin condition and were removed from further consideration in this study.

Yellowstone cutthroat trout, rainbow trout, and cutthroat x rainbow hybrids (hereafter hybrids) were differentiated using the phenotypic characteristics outlined in Meyer et al. (2003a). In short, any fish with (1) no spots on the head, (2) no white leading edge on the pelvic or anal fins, (3) spots that were large and concentrated posteriorly and dorsally, and (4) a faint or strong throat slash were considered Yellowstone cutthroat trout. Rainbow trout and hybrids were clustered into one group for analyses, and were visually identified by some combination of the presence of white edges on the pelvic or anal fins, smaller spots evenly distributed throughout the body, spots on the top of the head, or absence of a throat slash.

Because stream width was not measured at a number of reaches in various time periods, we standardized abundance to fish per 100 linear meters of stream. We compared abundance between time periods using two-tailed paired *t*-tests. To assess trends in abundance at individual reaches, we used linear regression to relate year to abundance (\log_e transformed). The resulting slope of this regression produces an estimate of the intrinsic rate of change (*r*) for the population (Maxell 1999). Following this methodology, we generated point estimates of *r* at each of the reaches sampled for any species detected in at least one of the sampling periods. We converted each point estimate of *r* to an estimate of population growth rate (λ) by raising Euler's number (*e*) to the power of *r*. We calculated an overall mean λ and an associated variance for each species, and estimated means and variances by species and by drainage. Mean estimates of λ whose 90% confidence intervals (CIs) did not overlap with unity were considered to have changed significantly.

We assessed whether population growth was associated with several basic stream habitat conditions, including stream width, stream order, elevation, and gradient, by use of correlation coefficients. However, because stream width and stream order were highly correlated (correlation coefficient = 0.74), and stream width is a more direct metric of stream size, we discarded stream order.

To assess whether drought negatively affected Yellowstone cutthroat trout in our study, we compared their abundance to the Palmer Drought Severity Index (PDSI) computed for southeast Idaho by the National Climatic Data Center (Heddinghaus and Sabol 1991; www.ncdc.noaa.gov). The PDSI is computed as a monthly value based on a balance between

moisture supply, soil characteristics, and evapotranspiration (Palmer 1965). Negative PDSI values of 0 to -0.5 are normal, -0.5 to -1 indicate incipient drought, -1 to -2 indicate mild drought, -2 to -3 moderate drought, -3 to -4 indicate severe drought, and less than -4 indicate extreme drought. Positive PDSI values follow a similar qualitative categorization for wet weather. We averaged monthly values to compute a mean PDSI for the year.

Because drought affects stream flow, which inherently affects stream width, the fish abundance metric we used (fish/100 m) could have potentially been lower (or higher) in some years if stream width was narrower (or wider) and territory size influenced abundance (Grant and Kramer 1990). To account for this, we transformed abundance data to fish/100m² and therefore discarded abundance estimates without accompanying measurements of stream width.

Abundance estimates for each of the three sampling periods at a reach were then normalized to a z-score based on the mean abundance at the reach across all sampling periods, so that each reach had a mean abundance z-score of zero and a standard deviation of 1. For each year of fish sampling, we estimated a mean z-score for all reaches surveyed in that year. We evaluated whether mean annual PDSI was related to mean annual z-scores for the same year using linear regression. However, because drought could have potentially affected recruitment or had other delayed impacts that outweighed effects on within-year abundance, we related drought to Yellowstone cutthroat trout abundance at time lags of up to four years because most cutthroat trout in eastern Idaho are four years old or less (Meyer et al. 2003b). Residuals of the linear regression were evaluated diagnostically, and there were no detectable issues regarding normality, outliers, influential data points, or unequal variance between the terms of the regression model.

We used SAS (SAS Institute 2009) to perform all statistical analyses. Throughout our analyses, we used a significance level of $\alpha = 0.10$ to increase the power of detecting trends or differences between time periods (Peterman 1990; Maxell 1999; Dauwalter et al. 2009).

RESULTS

Yellowstone cutthroat trout occupied all 74 reaches in the 1980s, compared to 70 reaches in 1999-2000, and 69 reaches in 2010-2011 (Table 1). In comparison, rainbow trout and hybrid occupancy increased from 23 reaches in the 1980s to 36 reaches in 1999-2000, and then declined back to 23 reaches in 2010-2011. The decline in rainbow trout and hybrid occupancy from 1999-2000 to 2010-2011 occurred in four of the seven drainages. Brown trout and brook trout occupancy was largely unchanged across all time periods.

Yellowstone cutthroat trout abundance increased from an average of 40.0 fish/100 m in the 1980s to 42.0 fish/100 m in 1999-2000, then declined to 32.8 fish/100 m in 2010-2011 (Table 2; Figure 1); the decline from 1999-2000 to 2010-2011 was statistically significant ($t = 2.36$; $df = 73$; $P = 0.02$). Declines in Yellowstone cutthroat trout abundance were evident in three of the seven drainages, including the Willow Creek (60% decline from the 1980s to 2010-2011), Portneuf River (44%), and Teton River (44%) drainages. Considering reaches individually, abundance was lower from the 1980s to 2010-2011 at 39 of the 74 reaches and higher at the remaining 35 reaches. Yellowstone cutthroat trout comprised 80% of the abundance of all trout in the 1980s, 76% in 1999-2000, and 69% in 2010-2011.

Abundance of rainbow trout and hybrids remained relatively unchanged for all time periods, with mean abundance (in reaches where they were present during at least one survey) of 8.9, 7.1, and 9.8 fish/100m in the 1980s, 1999-2000, and 2010-2011, respectively (Table 2; Figure 1). Brown trout abundance increased significantly ($t = -2.14$; $df = 27$; $P = 0.04$) from the 1980s (mean = 9.5 fish/100m) to 1999-2000 (21.6 fish/100m) and then declined slightly (but not statistically) by 2010-2011 (18.1 fish/100m). Brook trout abundance remained relatively unchanged from the 1980s (4.8 fish/100m) to 1999-2000 (2.9 fish/100m) but rose significantly ($t = -2.72$; $df = 18$; $P = 0.01$) from 1999-2000 to 2010-2011 (8.7 fish/100m).

Although abundance of Yellowstone cutthroat trout showed a clear decline from 1999-2000 to 2010-2011, this did not translate to a negative population growth rate across the entire time period. In fact, λ across all 74 reaches averaged 0.98 for Yellowstone cutthroat trout, and 90% CIs overlapped unity (0.96-1.00; Table 3). Within individual drainages, population growth rate for Yellowstone cutthroat trout showed a statistically significant decline in the Willow Creek (mean $\lambda = 0.85$; 90% CI = 0.73-0.97) and Teton River (mean $\lambda = 0.98$; 90% CI = 0.97-0.99) drainages.

In comparison, estimates of mean λ were above 1.00 for all nonnative salmonids, although 90% CIs overlapped unity in all cases (Table 3). However, significant increases or decreases were evident within individual drainages. For rainbow trout, λ declined significantly in the Portneuf River drainage (mean $\lambda = 0.79$; 90% CIs = 0.69 - 0.89) and the Willow Creek drainage (mean $\lambda = 0.80$; 90% CIs = 0.65 - 0.95), and increased significantly in the South Fork Snake River drainage (mean $\lambda = 1.23$; 90% CIs = 1.12 - 1.34). Brown trout declined significantly in the Willow Creek drainage (mean $\lambda = 0.74$; 90% CIs = 0.65 - 0.83) and increased significantly in the Portneuf River drainage (mean $\lambda = 1.58$; 90% CIs = 1.42 - 1.74) and the South Fork Snake River drainage (mean $\lambda = 1.20$; 95% CIs = 1.08 - 1.31). For brook trout, λ did not differ from unity in any drainage.

Population growth rates at individual stream reaches were rarely correlated with the stream habitat conditions that we measured at that reach (Table 4). In fact, the only statistically significant associations were a positive correlation for brook trout ($r = 0.45$) and a negative correlation for Yellowstone cutthroat trout ($r = -0.23$) with respect to reach gradient.

Mean PDSI over the entire time period (1980-2011) was 0.36, and during the years of fishing sampling, PDSI averaged 0.59 (Figure 2). The PDSI oscillated from a wet period from 1980 to 1986, to a dry period from 1987 to 1990, to a wet period from 1995-1999, and back to a dry period from 2000 to 2004.

The mean annual z-scores of Yellowstone cutthroat trout abundance were most strongly correlated to mean annual PDSI at a one year time lag, and this formed a statistically significant relationship ($F = 6.56$; $r^2 = 0.40$; $P = 0.02$; Figure 3) which indicated that more pronounced drought conditions in any given year resulted in lower cutthroat trout abundance one year later. In this relationship, all but one of the data points demonstrated above average cutthroat trout abundance when PDSI was >0 (wetter than normal) and below average abundance when PDSI was <0 (drier than normal). All other time lags (including no lag) produced much weaker and non-significant relationships with PDSI ($r^2 < 0.12$, $P > 0.27$)

DISCUSSION

Results from this study suggest that Yellowstone cutthroat trout continue to dominate the reaches in our study that were originally established in the 1980s to monitor cutthroat trout populations in the upper Snake River basin. Indeed, occupancy was generally unaltered (down 7%) and population growth did not differ from replacement. While abundance declined 18%, this was not statistically significant, and may simply reflect normal temporal fluctuations in trout populations (Dauwalter et al. 2009). Finally, Yellowstone cutthroat trout allopatry was equivalent in 2010-2011 (42% of reaches) as in the 1980s (45%).

Despite these positive findings, there are some causes for concern. First, Yellowstone cutthroat trout are no longer present in several reaches, including in Corral Creek (in the Willow Creek drainage) where they were formerly quite abundant. Second, Yellowstone cutthroat trout abundance was <10 fish/100m in the 1980s at four of the five reaches no longer occupied by cutthroat trout. If this pattern continues, future extirpations may be more likely at the eight reaches occupied by cutthroat trout in 2010-2011 where abundance was <10 fish/100m. Fortunately, nonnative trout do not appear to be expanding dramatically. Although they have experienced a 50% increase in total abundance from the 1980s to 2010-2011 across all these reaches, non-native trout at this time only constitute about 30% of the abundance of all trout at these reaches.

Rainbow trout and hybrid occupancy expanded from the 1980s to 1999-2000, but then contracted to 1980s levels by 2010-2011. Most of this early expansion and later contraction occurred in the 12 reaches sampled in Diamond Creek (Blackfoot River drainage) and Pine Creek (South Fork Snake River drainage), with rainbow trout and hybrid occupancy in these two streams increasing from 0 reaches in the 1980s to 9 in 1999-2000, and then declining to 4 reaches in 2010-2011. However, even excluding these two streams, occupancy by rainbow trout and hybrids contracted from 27 reaches in 1999-2000 to 19 reaches in 2010-2011. These contractions were not likely caused by misidentifying fish because rainbow trout and hybrids are readily distinguishable from Yellowstone cutthroat trout based on phenotype (Campbell et al. 2002; Meyer et al. 2006a), and hatchery fish are also readily distinguishable from wild fish based on fin condition. To our knowledge, natural declines in hybridization of wild native cutthroat trout populations have not been empirically demonstrated. The decline in occupancy by rainbow trout and hybrids in our study reaches from a high in 1999-2000 coincides with a decision by IDFG to discontinue stocking of catchable-sized hatchery rainbow trout in waters that support Yellowstone cutthroat trout populations, and where stocking has continued in lotic environments, to only stock rainbow trout that have been sterilized by pressure treatment to eliminate hybridization issues (Kozfkay et al. 2006; IDFG 2007). Continuing these policies and expanding management actions to control or remove rainbow trout and hybrids from streams in the upper Snake River basin (e.g., High 2010) may limit the expansion of rainbow trout introgression in streams occupied by native Yellowstone cutthroat trout.

Sympatric interactions with brook trout are also of concern for long-term conservation of Yellowstone cutthroat trout in the upper Snake River basin. Brook trout have frequently been shown to outcompete and often entirely displace native cutthroat trout populations in western North America (e.g., Peterson and Fausch 2003; Shepard 2004; Peterson et al. 2004). Interestingly, the only noteworthy associations between fish abundance and stream habitat conditions were that Yellowstone cutthroat trout population growth was negatively related to stream gradient whereas brook trout population growth was positively related to gradient. However, these associations were largely driven by data from two reaches (reaches 1 and 2 in Table 2), and the relationships were not statistically significant without these data. In an

electrofishing survey of 1,000 randomly distributed study reaches in the upper Snake River basin between 1999 and 2003, brook trout were widespread, occupying 27% of the stream reaches surveyed (Meyer et al. 2006a). In the present study, brook trout were sympatric with Yellowstone cutthroat trout in 14 reaches in the 1980s; by 2010-2011, the only one of these reaches where cutthroat trout were no longer present (Birch Creek) was at a reach where their original abundance was extremely low. Although Yellowstone cutthroat trout in our study appear to be persisting even with sympatric brook trout, results from previous studies suggest that the risk of extirpation is higher when brook trout are present (Peterson and Fausch 2003; Shepard 2004; Peterson et al. 2004). Unfortunately, removing brook trout mechanically is usually not effective (Thompson and Rahel 1996; Meyer et al. 2006b; but see Shepard et al. 2002), and biologists are often apprehensive of using chemicals to remove undesirable species due to a variety of issues including fear of negative public perception, government bureaucracy issues, and uncertain effectiveness (Finlayson et al. 2000).

Our results suggest that drought severity in any given year has a negative effect on Yellowstone cutthroat trout abundance the following year. Considering that age-0 fish in one year were large enough the following year to be included in our abundance estimates, and they would likely constitute the most abundant age class in the estimates, the negative relationship between drought and Yellowstone cutthroat trout abundance is perhaps the result of poor survival or production of age-0 fish during low-flow years. Such an effect on age-0 survival could stem from a number of mechanisms, including reduced reproductive success (Elliott et al. 1997), reduced habitat quality and availability (Hakala and Hartman 2004), poorer food resources for newly emerged fry (Cowx et al. 1984), intensified predation as age-0 fish are forced into closer proximity to predators due to less available space (Larimore et al. 1959), or lower winter flows which may reduce overwinter survival (Hakala and Hartman 2004). Regardless of the mechanism, the negative effect of drought on Yellowstone cutthroat trout abundance observed here suggests that if more frequent drought conditions occur in the future (Luce and Holden 2009), declines in Yellowstone cutthroat trout abundance may result.

All three trout species present at the reaches surveyed in the Willow Creek drainage showed statistically significant declines in population growth (Table 3). In the 1990s the Natural Resource Conservation Service (NRCS) identified the Willow Creek drainage as one of the ten worst soil erosion areas in the United States, and nearly every stream in the drainage is listed as an impaired water on the Clean Water Act's 303d list for excessive sedimentation (Thompson 2004). Although 49% of the watershed has been part of a conservation program during the last 30 years (Thompson 2004), stream habitat conditions remain degraded. Fortunately, Yellowstone cutthroat trout have been able to persist in the Willow Creek drainage under these conditions for many decades (Corsi 1988), and Willow Creek is the least hybridized drainage in Idaho relative to Yellowstone cutthroat trout populations (Meyer et al. 2006a). However, the long-term viability of Yellowstone cutthroat trout in such degraded habitat, especially if stream temperatures warm in the future within the drainage (Isaak et al. 2011), is tenuous.

Our study had limitations that may hinder making strong inferences regarding the occupancy and abundance of salmonids in drainages within the upper Snake River basin. The primary shortcoming was the non-random nature of reach selection by biologists in the 1980s. Since reaches were typically established near roads, bridges, culverts, or other easily accessible features, they may not be representative of conditions across the landscape. However, our sample size was quite large, the surveyed reaches were broadly distributed across the study area, and they encompassed a wide variety of physical habitat conditions; hence they are likely minimally biased in regards to spatial coverage, despite the nonrandom

nature of site selection (Kadmon et al. 2003; Wagner et al. 2007). Moreover, it could be argued that by concentrating study reaches in accessible areas, where detrimental stream alterations are typically more prevalent, and where stream reaches were more accessible to fish stocking trucks, our results may represent a worst-case scenario relative to the status of Yellowstone cutthroat trout.

An inherent limitation of our approach that may have contributed to our observed reduction in Yellowstone cutthroat trout occurrence is the fact that all 74 reaches contained Yellowstone cutthroat trout in the 1980s. Therefore, our study design could only have detected range contraction (not expansion). Had the original study site selection been done randomly across the landscape, with some sites containing cutthroat trout and some absent of cutthroat trout, we might have observed local extirpations as well as recolonizations at individual sites, in a pattern exemplified by stream-dwelling salmonids functioning within a meta-population (Rieman and Dunham 2000). Given that all sites contained cutthroat trout at the beginning of our study, we could only detect local extirpations.

With only three surveys over time at each reach, it is difficult to draw decisive temporal conclusions from our results. In fact, the coefficient of variation (CV) in Yellowstone cutthroat trout abundance in our study (63%) typifies temporal fluctuations frequently exhibited by trout populations across North America (Dauwalter et al. 2009). As such, the fluctuations we observed may not represent true changes in abundance, but instead may simply reflect inter-annual variation in population size that typifies many trout populations. These fluctuations emphasize the need to continue to monitor these populations over the next several decades to ascertain whether population growth rates truly differ from replacement, or whether they are simply oscillating around a relatively stable mean.

In conclusion, the results of this study suggest that Yellowstone cutthroat trout populations in the upper Snake River basin of Idaho may be declining slightly, although at a rate so slow as to not differ statistically from zero change in growth. Our sample reaches were not chosen at random, so caution should be used in extrapolating these results outside of our study area. However, our reaches did encompass a broad geographic range and a wide variety of habitats, so they likely provide a reasonable index of Yellowstone cutthroat trout population trends in southeastern Idaho. Further monitoring over time may help distinguish normal population fluctuations from actual changes in the distribution and abundance of trout populations in the upper Snake River basin. Coupling these reaches with repeat sampling of already established randomly located reaches (such as from Meyer et al. 2006a) may help validate any changes detected by repeating our study in the future.

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TABLES

Table 1. Number of reaches occupied by Yellowstone cutthroat trout (≥ 100 mm TL) by drainage during the 1980s, 1999-2000 and 2010-2011.

Metric	Period	Drainages							Total
		Raft River/ Goose Creek	Portneuf River	Blackfoot River	Willow Creek	South Fork Snake River	Palisades Reservoir/ Salt River	Teton River	
Number of sites surveyed		4	10	9	5	16	26	4	74
Yellowstone cutthroat trout									
Number of sites occupied in:	1980s	4	10	9	5	16	26	4	74
	1999-2000	2	9	9	5	16	25	4	70
	2010-2011	2	9	9	3	16	26	4	69
Rainbow trout and hybrids									
Number of sites occupied in:	1980s	1	8	2	2	4	2	4	23
	1999-2000	1	8	8	0	11	4	4	36
	2010-2011	2	4	3	0	8	2	4	23
Brown trout									
Number of sites occupied in:	1980s	0	0	0	3	5	11	1	20
	1999-2000	0	1	0	2	7	8	0	18
	2010-2011	0	2	0	1	8	9	2	22
Brook trout									
Number of sites occupied in:	1980s	1	1	7	0	0	1	4	14
	1999-2000	2	0	2	0	0	0	4	8
	2010-2011	2	0	5	1	0	0	4	12

Table 2. Trout abundance (fish/100 m) by reach and species.

Reach	Stream	Reach length (m)	Mean width (m)	Estimate method ¹	Year of estimate		Trout abundance (fish/100 m)														
					1999-	2010-	Yellowstone cutthroat trout			Rainbow trout and hybrids			Brown trout			Brook trout					
					1980s	2000	1980s	1999-2000	2010-2011	1980s	1999-2000	2010-2011	1980s	1999-2000	2010-2011	1980s	2000	2011			
Raft River/Goose Creek drainages																					
1	Birch Creek	96	1.5	D	1987	2000	2010	1.3	0.0	0.0							1.3	30.6	27.5		
2	Cold Creek	72	2.1	D	1987	2000	2010	5.0	0.0	0.0	0.0	0.0	100.6				0.0	6.3	5.0		
3	Eighthmile Creek	83	1.1	D	1986	2000	2010	6.1	23.2	29.3											
4	Trout Creek	120	2.5	D	1987	2000	2010	3.9	6.9	18.7	50.8	0.9	3.1								
Portneuf River drainage																					
5	Pebble Creek	208	2.3	D	1986	2000	2011	43.9	14.0	2.6	14.0	1.0	4.7			1.0	0.0	0.0			
6	Pebble Creek	104	4.7	D	1986	1999	2011	32.5	44.8	44.9	6.3	7.1	0.0								
7	Pebble Creek	106	3.6	D	1986	1999	2011	75.8	44.2	34.9	4.0	13.5	7.4								
8	Pebble Creek NF	133	1.8	D	1986	1999	2011	34.7	15.1	6.0											
9	Big Springs Creek	105	4.4	D	1986	1999	2011	23.9	25.8	3.8	4.8	2.0	0.0								
10	King Creek	76	8.1	D	1986	2000	2011	7.1	0.0	0.0											
11	Toponce Creek	88	6.0	D	1986	2000	2011	7.5	4.5	10.4	104.9	1.1	1.2	0.0	29.2	27.8					
12	Toponce Creek, MF	73	4.7	D	1986	2000	2010	2.5	17.4	33.8	76.3	78.3	12.5	0.0	0.0	2.5					
13	Toponce Creek, SF	101	3.4	D	1987	2000	2011	115.5	46.0	19.2	18.8	1.0	0.0								
14	Toponce Creek, SF	113	6.0	D	1987	2000	2011	29.2	146.9	52.2	1.8	7.1	0.0								
Blackfoot River drainage																					
15	Blackfoot River	4,347	12.1	D/MR	1988	2000	2011	0.8	12.5	32.0	0.0	1.9	0.7			0.0	0.0	0.1			
16	Blackfoot River	1,698	16.3	MR	1988	2000	2011	15.1	36.6	32.7	0.2	7.0	0.0			0.0	0.1	0.7			
17	Blackfoot River	1,753	11.4	D/MR	1988	2000	2011	5.9	13.2	101.5	0.1	6.3	0.0			0.1	0.5	14.0			
18	Diamond Creek	183	5.1	D	1988	2000	2011	8.4	10.6	19.1						1.1	0.0	9.3			
19	Diamond Creek	153	5.6	D	1980	2000	2011	130.4	61.9	10.9	0.0	6.8	0.0			4.8	0.0	6.1			
20	Diamond Creek	167	3.7	D	1987	2000	2011	24.7	64.2	30.3	0.0	6.7	0.0			2.7	0.0	0.0			
21	Diamond Creek	87	3.5	D	1987	2000	2011	9.2	43.7	26.4	0.0	4.6	3.4			2.3	0.0	0.0			
22	Diamond Creek	66	2.5	D	1987	2000	2011	50.7	43.9	10.7	0.0	12.2	0.0			1.3	0.0	0.0			
23	Diamond Creek	162	3.4	D	1988	2000	2011	17.6	29.1	10.3	0.0	19.0	1.8			5.4	0.0	0.0			
Willow Creek drainage																					
24	Willow Creek	859	8.8	MR	1984	2000	2011	21.3	3.9	30.9	1.2	0.0		2.6	0.6	0.0					
25	Willow Creek	561	10.8	MR/D	1984	2000	2011	66.9	22.9	40.3	0.7	0.0	0.0	24.2	2.1	0.2	0.0	0.0			
26	Brockman Creek	93	5.7	D	1983	2000	2010	7.7	26.9	0.0				2.0	0.0	0.0					
27	Corral Creek	76	1.3	D	1982	2000	2011	64.8	6.3	0.0											
28	Corral Creek	134	1.9	D	1982	2000	2011	27.6	14.6	3.1											
South Fork Snake River drainage																					
29	Snake River	7,300	79.0	MR	1988	2000	2011	7.5	8.3	6.2	2.9	3.1	3.1	10.0	29.7	40.6					
30	Snake River, SF	4,800	46.0	MR	1989	1999	2011	14.9	34.3	33.4	0.2	0.7	3.9	28.2	113.5	96.1					
31	Snake River, SF	2,900	66.0	MR	1989	2000	2011	46.2	69.8	27.1	0.3	2.0	5.1	45.2	175.7	93.1					
32	Snake River, SF	4,900	71.0	MR	1989	1999	2011	161.0	184.7	122.5	6.3	65.4	119.0	19.1	51.2	79.6					
33	Burns Creek	82	5.9	D	1980	2000	2011	56.5	33.4	11.8	0.0	20.2	5.3	0.0	0.0	9.2					
34	Burns Creek	86	5.3	D	1980	2000	2011	7.0	31.4	10.5	0.0	2.3	0.0	0.0	3.5	2.3					
35	Pine Creek	66	11.1	D	1980	2000	2011	51.5	71.2	76.6	0.0	6.1	21.9								
36	Pine Creek	90	9.3	D	1988	2000	2011	77.8	24.4	58.9	0.0	0.0	26.7								
37	Pine Creek	76	6.0	D	1980	2000	2011	155.4	146.8	64.9	0.0	5.1	0.0								
38	Pine Creek	80	4.8	D	1988	2000	2011	53.8	82.5	56.3	0.0	7.5	0.0								
39	Pine Creek, NF	72	5.3	D	1982	2000	2010	22.3	18.1	30.6											
40	Pine Creek, NF	80	7.9	D	1981	2000	2011	43.8	8.8	5.0	0.0	1.2	0.0								
41	Rainey Creek	159	5.7	D	1980	2000	2010	1.3	37.5	14.3				0.0	1.9	10.0					
42	Rainey Creek	124	6.5	D	1980	2000	2011	6.5	4.1	22.8											
43	Rainey Creek	174	7.6	D	1980	2000	2010	9.0	40.0	38.3	0.0	1.7	9.0	4.2	11.0	18.6					
44	Fall Creek	130	6.2	D	1988	2000	2011	12.8	60.5	71.4											
Palisades Reservoir/Salt River drainages																					
45	Bear Creek	211	8.8	D	1980	2000	2011	17.9	71.6	56.7	0.0	0.4	0.0	0.0	0.0	3.1					
46	Elk Creek	146	4.1	D	1980	2000	2011	24.7	36.3	47.3											
47	Big Elk Creek	106	6.9	D	1980	2000	2010	8.2	33.0	17.5											
48	Big Elk Creek	148	7.9	D	1980	2000	2010	19.9	61.3	31.5											
49	McCoy Creek	373	9.2	MR	1986	2000	2010	72.3	35.5	59.2	0.0	0.3	0.0	1.1	0.8	0.0					
50	McCoy Creek	396	8.8	MR	1986	2000	2010	107.7	117.5	102.0				1.0	0.0	0.3					
51	McCoy Creek	148	3.2	D	1986	1999	2010	52.9	56.9	72.2											
52	Jensen Creek	81	3.3	D	1986	1999	2010	162.6	0.0	59.2											
53	Fish Creek	86	3.6	D	1986	1999	2010	48.4	167.0	39.2											
54	Fish Creek	92	3.1	D	1986	1999	2010	43.5	90.2	34.8											
55	Barnes Creek	100	3.0	D	1986	1999	2010	24.2	33.6	28.3											
56	Barnes Creek	77	3.2	D	1986	1999	2010	7.9	10.5	23.7	0.0	0.0	1.3								
57	Clear Creek	124	3.4	D	1986	1999	2010	61.5	31.1	41.8											
58	Iowa Creek	101	4.0	D	1986	2000	2010	25.8	31.3	41.2											
59	Jackknife Creek	109	6.1	D	1987	1999	2010	29.0	14.0	43.8				0.9	0.0	1.0					
60	Tincup Creek	153	5.9	D	1987	1999	2010	62.7	76.0	31.0	0.7	0.0	0.0	0.7	1.4	0.0					
61	Tincup Creek	123	6.8	D	1987	1999	2010	129.0	64.1	39.3	0.9	0.0	0.9	2.7	0.0	0.0					
62	Tincup Creek	101	5.1	D	1987	1999	2010	66.0	21.0	18.0											
63	Bear Canyon Creek	61	1.6	D	1987	1999	2010	87.8	32.3	1.9	0.0	1.9	0.0								
64	Stump Creek	454	7.0	MR	1986	2000	2011	44.2	123.6	32.5				9.5	25.5	16.9	0.7	0.0			
65	Horse Creek	86	2.2	D	1986	1999	2011	40.6	70.7	33.7				0.0	4.6	9.3					
66	Crow Creek	327	5.4	MR	1986	2000	2010	3.6	10.4	16.0				5.2	32.1	17.3					
67	Crow Creek	112	3.6	D	1986	1999	2010	83.6	117.1	71.5				0.9	9.0	15.9					
68	Sage Creek	206	5.3	D	1987	1999	2010	19.4	31.1	33.2	0.0	0.0	0.0	100.1	108.5	46.8					
69	Deer Creek	158	4.2	D	1986	1999	2010	37.1	78.6	109.6	0.0	0.6	0.0	7.6	5.7	15.3					
70	White Dugway Creek	84	1.6	D	1986	1999	2010	13.1	6.0	36.9	0.0	0.0	0.0	1.2	0.0	0.0	0.0	0.0			
Teton River drainage																					
71	Teton River	4,900	26.0	MR	1987	1999	2011	11.0	8.5	6.2	50.2	7.1	40.2	0.0	0.0	0.6	10.6	3.5			
72	Teton River	5,500	34.4	MR	1987	2000	2011	15.7	12.4	13.5	31.2	6.9	33.3	0							

Table 3. Mean, standard error (SE), and range of population growth rates (λ) for each trout species by drainage.

Drainage	Population growth rates (λ)											
	Yellowstone cutthroat trout			Rainbow trout and hybrids			Brown trout			Brook trout		
	Mean	SE	Range	Mean	SE	Range	Mean	SE	Range	Mean	SE	Range
Raft River and Goose Creek	0.85	0.13	0.61-1.07	1.32	0.45	0.88-1.77	None captured			1.39	0.24	1.15-1.63
Portneuf River	0.95	0.04	0.63-1.12	0.79	0.06	0.61-1.03	1.58	0.10	1.48-1.68	None captured		
Blackfoot River	1.03	0.03	0.93-1.18	1.15	0.12	0.73-1.56	None captured			0.96	0.11	0.62-1.47
Willow Creek	0.85	0.07	0.65-1.01	0.80	0.09	0.71-0.89	0.74	0.05	0.68-0.84	None captured		
South Fork Snake River	1.01	0.01	0.93-1.10	1.23	0.07	1.00-1.71	1.19	0.07	1.03-1.49	None captured		
Palisades Reservoir/Salt River drain	1.00	0.01	0.85-1.07	1.04	0.09	0.68-1.05	0.98	0.08	0.64-1.59	1.13	0.44	0.69-1.57
Teton River	0.98	0.01	0.97-0.99	1.00	0.01	0.99-1.03	1.23	0.20	1.02-1.43	1.01	0.01	1.01-1.03
Total	0.98	0.01	0.61-1.18	1.07	0.05	0.61-1.77	1.08	0.06	0.64-1.68	1.04	0.07	0.62-1.63

Table 4. Correlations between trout population growth rates (λ) and reach width, elevation, and gradient at 74 stream reaches. Asterisks indicate statistically significant correlations (at $\alpha = 0.10$).

Species	Reach width (m)	Reach elevation (m)	Reach gradient (%)
Yellowstone cutthroat trout	0.08	0.03	-0.23*
Rainbow trout and hybrids	-0.01	-0.04	0.02
Brook trout	0.07	-0.25	0.45*
Brown trout	-0.02	-0.19	0.22
All non-native trout	0.01	-0.19	0.16
All trout	0.13	-0.12	-0.01

FIGURES

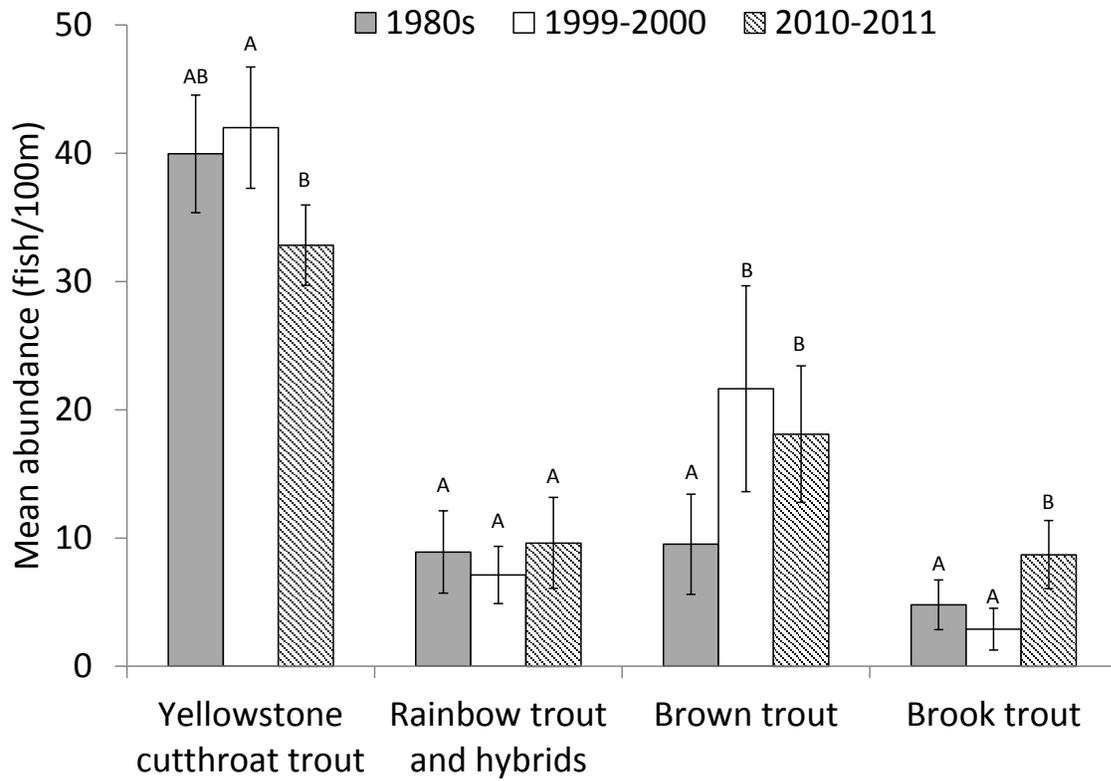


Figure 1. Estimates of mean abundance (± 1 SE) at 74 stream reaches in the upper Snake River basin by species and time period. Estimates only included reaches where a particular species was present in at least one time period. Letters that differ above the bars indicate statistical significance when comparing abundance with a paired *t*-test (at $\alpha = 0.10$).

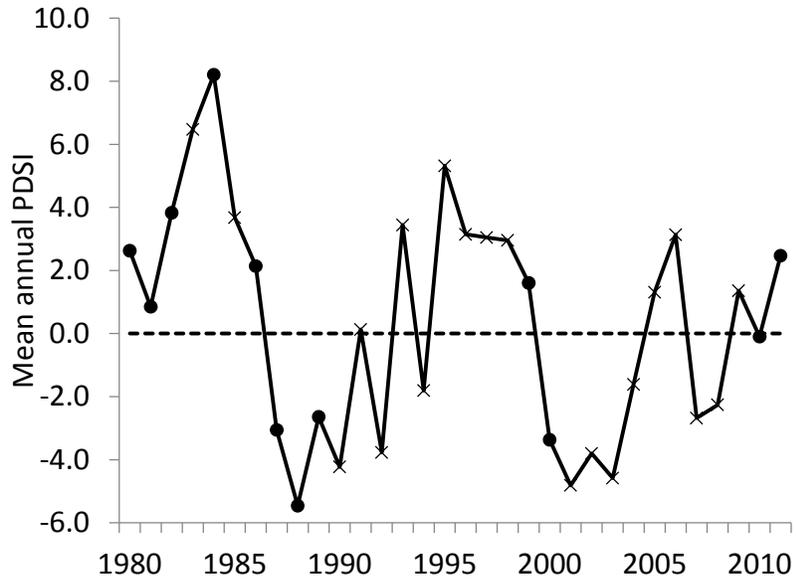


Figure 2. Mean annual Palmer Drought Severity Index (PDSI) for southeast Idaho during the study period. Filled circles indicate years when fish sampling occurred.

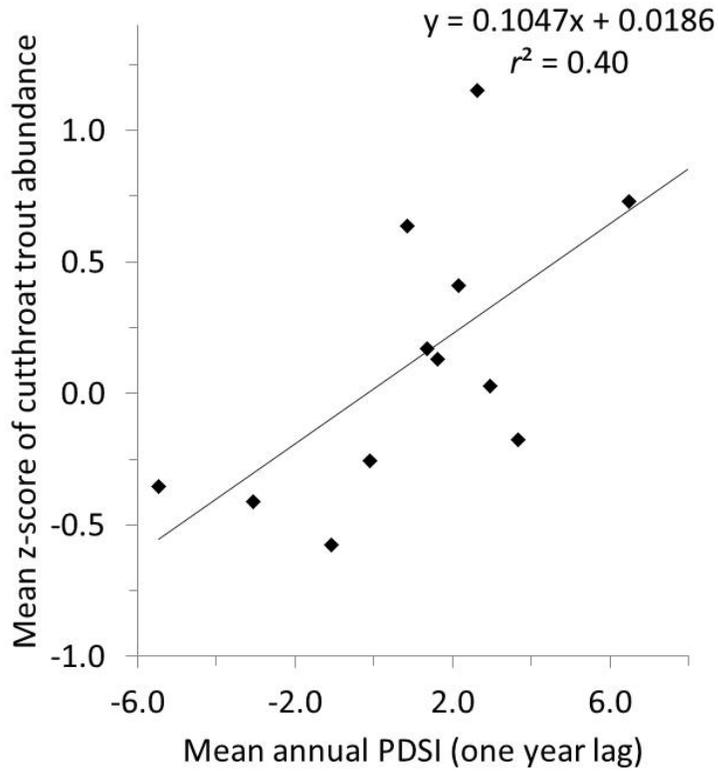


Figure 3. Relationship between mean annual Palmer Drought Severity Index (PDSI) in a given year and mean annual z-scores of the abundance of Yellowstone cutthroat trout one year later.

CHAPTER 2: STATUS OF REDBAND TROUT IN THE UPPER SNAKE RIVER BASIN OF IDAHO

ABSTRACT

Redband trout *Oncorhynchus mykiss gairdneri* are likely the most abundant and widely distributed native salmonid in the Columbia River basin, yet their current distribution and abundance across the landscape has not been well documented. We sampled 1,032 randomly distributed stream sites (usually 100 m in length) across more than 60,000 km of stream network to assess redband trout occupancy, abundance, and genetic purity in the upper Snake River basin of Idaho. Study locations were more often dry in desert sub-basins (49% of sites) than montane sub-basins (20%), and 25% of the dry “stream sites” had no discernible stream channel whatsoever, indicating a lack of flowing water perhaps for millennia. Redband trout were estimated to occupy 13,485 km of stream (22% of the total), and were captured more often (389 sites) than brook trout (128 sites), bull trout (37 sites), or brown trout (16 sites). Redband trout were also the most abundant species of trout, with an approximate abundance of roughly 3,449,000 ± 402,000 (90% confidence interval) of all sizes, followed by brook trout (1,501,000 ± 330,000), bull trout (159,000 ± 118,000) and brown trout (43,000 ± 25,000). Approximately 848,000 ± 128,000 redband trout were adults. From 1913 (oldest period of record) to 2001, roughly 43 million hatchery rainbow trout were stocked in streams in the study area, 17.5 million of which were of catchable size (i.e., ≥200 mm total length); since 2001 all catchables have been sterilized prior to stocking. Genetic results from 61 study sites suggest that redband trout hybridization with hatchery rainbow trout was more likely to occur in streams that were directly stocked with catchables from 1913 to 2001. Applying these results across the landscape, we estimated that redband trout likely remain pure in about 68% of the streams occupied in the upper Snake River basin.

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INTRODUCTION

The Columbia River redband trout *Oncorhynchus mykiss gairdneri* is a major assemblage of rainbow trout native to the Fraser and Columbia rivers each of the Cascade Mountains (Behnke 2002). They reside in a variety of habitats ranging from high-desert rivers in arid landscapes to forested montane streams, and include both anadromous (i.e., steelhead trout) and non-anadromous forms. While redband trout remain the most widely distributed native salmonid in the Columbia River basin, the species has declined both spatially and numerically from historical levels (Thurow et al. 1997, 2007). These declines have been largely attributed to (1) hybridization stemming from historical hatchery trout stocking and (2) anthropogenic disturbance resulting in habitat fragmentation, alteration, and desiccation (Thurow et al. 2007). In 1995, redband trout in the arid portion of the Snake River basin above Hell's Canyon Dam were petitioned for protection under the Endangered Species Act, but the petition was deemed unwarranted at that time (USOFR 1995). In general, less is known about the distribution and abundance of redband trout than for most other salmonids in the Intermountain West (Thurow et al. 1997). To help fill this information gap, we undertook an assessment of redband trout distribution and abundance in the upper Snake River basin of Idaho. For perspective we also assessed the distribution and abundance of other native and non-native salmonids in the study area, except for mountain whitefish *Prosopium williamsoni* whose status in the upper Snake River basin has been summarized elsewhere (Meyer et al. 2009).

Because hatchery rainbow trout *O. mykiss* of coastal origin have been stocked extensively throughout the upper Snake River basin, a concurrent assessment of their genetic introgression with native redband trout in the study area was also deemed a high priority. Redband trout in the upper Snake River basin are introgressed in some areas of the basin, and introgression is more likely to take place where historical stocking of fertile hatchery rainbow trout has occurred (Kozfkay et al. 2011). Unfortunately, visual identification of redband trout x rainbow trout hybrids is not possible, and genetic analyses are too costly to perform in all streams. However, if detailed stocking history is known, and stocking metrics (e.g., total number of fish stocked) are well correlated to current levels of introgression, then simple models could be used to characterize introgression at stream locations where genetic information is lacking (e.g., Bennett et al. 2010).

Beyond the obvious importance of genetic purity, an evaluation of genetic risk is also common in status assessments. Genetic guidelines for population size typically rely on estimation of effective population size (N_e) because it is an indication of the rate at which random genetic processes such as genetic drift, inbreeding, and loss of alleles occur in wildlife populations (Waples 2004). The 50/500 N_e rule-of-thumb is widely accepted for evaluating genetic risk because populations with $N_e \geq 50$ are thought to be impervious to short-term genetic concerns such as inbreeding depression, while $N_e \geq 500$ will likely allow for long-term maintenance of genetic diversity in the population (Franklin 1980). Unfortunately, accurately estimating N_e is difficult using either genetic (Waples 1991; Schwartz et al. 1998; Araki et al. 2007) or demographic approaches (Caballero 1994; Ardren and Kapuscinski 2003). For example, demographic estimation often involves parameters that are difficult to obtain such as lifetime family size (Harris and Allendorf 1989; Araki et al. 2007), while genetic approaches can suffer from resolution issues for all but the smallest populations (Waples 2006). Because population abundance estimates, expressed as either total population size (N_{census}) or adult abundance (N_{adult}), are often the most reliable or the only data available for many populations, the ratio of N_e to either N_{census} or N_{adult} is conceptually an important variable for monitoring genetic diversity within populations (Frankham 1995; Waples 2004). Ratios of N_e/N_{adult} have been approximated to be 0.2-0.3 for Pacific salmon (Allendorf et al. 1997; McElhany et al. 2000)

compared to 0.4-1.0 for nonanadromous trout in the region (Rieman and Allendorf 2001; Schill and Labar 2010). These ratios appear to be applicable to redband trout populations (Schill and Labar 2010), and as such, may be useful in approximating N_e across the landscape once estimates of N_{adult} have been made (e.g., Meyer et al. 2006a).

The primary objective of this paper was to summarize the current status of redband trout in the upper Snake River basin in southern Idaho and surrounding states. Specifically, we estimated the distribution, total population size, and adult breeder abundance for redband trout within individual sub-basins. In addition, genetic purity was assessed for 61 streams and related to historical stocking, so that in streams lacking genetic data, introgression could be inferred from stocking records alone. Information on redband trout distribution and known migration barriers were used to delineate isolated redband trout populations within individual sub-basins and to estimate their abundance where feasible.

STUDY AREA

The study area encompassed the Snake River basin upstream of Hell's Canyon Dam to the natural fish barrier of Shoshone Falls, an area of roughly 84,000 km² (Figure 4). The main stem of the Snake River was not included in the study because, for most of this river, redband trout are too scarce to accurately estimate abundance. We also excluded the Burnt River, Powder River, Malheur River, and Pine Creek sub-basins in Oregon, and all streams within the Shoshone-Paiute Indian Reservation, because they lie entirely outside of our management jurisdiction. In the Bruneau River sub-basin, the portion of the Jarbidge River drainage in Nevada was also excluded. For the remaining sub-basins along the border of Idaho, we sampled the sub-basin in its entirety, including areas outside the Idaho state boundary.

The historical range of redband trout in the Snake River basin likely included all of the Snake River and its tributaries below Shoshone Falls (Behnke 2002). Chinook salmon *O. tshawytscha*, sockeye salmon *O. nerka*, and steelhead trout (the anadromous form of *O. mykiss*) were native to the study area but long ago were denied upstream access in the upper Snake River basin and its tributaries by the construction of a series of dams lacking fish ladders, beginning with Swan Falls Dam in 1901 (river kilometer 739) and culminating with Hell's Canyon Dam in 1967 (river kilometer 398). Bull trout *Salvelinus confluentus* and mountain whitefish are also native to the upper Snake River basin below Shoshone Falls, as are a number of nongame fish species including five species of Cottidae, three species of Catostomidae, and seven species of Cyprinidae (Simpson and Wallace 1982). Nonnative brook trout *Salvelinus fontinalis* and brown trout *Salmo trutta* were previously introduced in the basin and have established some self-sustaining populations in streams within the study area.

A number of streams across the study area have been stocked with hatchery rainbow trout, typically of coastal origin. Stocking of hatchery rainbow trout began early in the last century in some streams using sub-catchable-sized fish (usually 25 to 100 mm total length [TL]). By 1950, the Idaho Department of Fish and Game (IDFG) began stocking catchable-sized fish (≥ 200 mm TL), and by the late 1960s, fry and fingerlings were no longer stocked in Idaho streams due to poor return to creel for anglers (Meyer and Koenig 2011). Stocking of catchables increased through the 1970s, but from 1985 to 2008, catchable stocking in Idaho streams was reduced by 50% in quantity and more than 50% in kilometers stocked, and now occurs in <2% of the 44,000 fishable kilometers in Idaho (IDFG, unpublished data). Moreover, in areas where catchables could potentially interact with native salmonids, the IDFG has since 2001 only stocked catchables that have been treated to induce sterility (Kozfkay et al. 2006); currently

these are produced largely from all-female triploid eggs purchased from Troutlodge, Inc., where triploid induction rate in recent years has been 100% on all batches tested (A. Barfoot, Troutlodge, Inc., personal communication).

For several reasons we divided streams into desert or montane categories by grouping all streams within the larger sub-basins north of the Snake River (i.e., the Weiser, Payette, Boise, and Big Wood rivers) into the montane category and all the remaining sub-basins into the desert category. First, as mentioned above, redband trout in the desert streams as identified in this study were petitioned for ESA listing only within the desert portion of their range in the upper Snake River basin. Second, dividing sub-basins into desert and montane categories corresponds well with differences in stream habitat characteristics such as elevation, gradient, substrate, shading, and temperature (Meyer et al. 2010). Finally, this division also corresponds to differences in geology, vegetation, and precipitation (Orr and Orr 1996). For example, montane sub-basins have higher annual precipitation, and are characterized geologically by the Idaho Batholith and younger Tertiary granitic intrusions, with upland vegetation that is a mixture of conifer forest, sagebrush *Artemisia spp.* and mesic forbs, and streamside vegetation dominated by willow *Salix spp.* In contrast, desert sub-basins have lower annual precipitation and are characterized geologically by broken plateaus, barren rocky ridges, cliffs, and deep gulches and ravines within rhyolite and basalt formations, with upland vegetation dominated by sagebrush and western juniper *Juniperus occidentalis*, and streamside vegetation of willows and mesic forbs.

METHODS

Study Site Selection

To develop a sampling framework, we examined stream courses on 1:100,000 scale maps of the study area and assigned *a priori* distribution categories for redband trout based on past experience or professional judgment. As such, all stream reaches were coded for redband trout presence as 1) likely present, 2) likely absent, or 3) unknown.

Study sites were selected from a GIS-layer of stream courses at the same 1:100,000 scale with personnel assistance from the Environmental Protection Agency's Environmental Monitoring and Assessment Program (EMAP). The EMAP approach uses GIS to arrange stream reaches in a randomized order, after which they are systematically sampled, resulting in a spatially balanced, random design (Stevens and Olsen 2004). Study sites were stratified in two ways, the first consisting of the three *a priori* distribution categories noted above. Within these strata, stream order (Strahler 1964) was used as a secondary stratification. Each stratum was considered a distinct sample frame, and within each stratum, sample sites were drawn in a spatially balanced and random manner. To minimize variance of subsequent population estimates, we sampled 'likely present' reaches about twice as often (in terms of the percent of total stream kilometers sampled) as 'unknown' reaches, and about 10 times more often than 'likely absent' reaches.

In a few small, isolated tributaries of the Snake River, the EMAP-derived study site selection process was replaced with a simple random sample procedure with increased sample frequency per stream km to help ensure adequate sample size for sub-population abundance extrapolations within these smaller tributaries.

About 74% and 26% of sites selected in the above sampling scheme were on public and private land, respectively. When study site locations fell completely on private property, access was requested from landowners and was denied less than 2% of the time. Additionally, constraints such as unwadeable beaver ponds or physically inaccessible canyon geology precluded sampling some other reaches, although these restrictions occurred rarely (i.e., <1% of the time). To replace unsampled reaches, we initially drew more random samples than we intended to sample, and substituted the next overdraw sample site (within the same stratum) for replacement.

Fish sampling

Fish sampling occurred between 1999 and 2005, after spring runoff, at moderate flow to base flow conditions (typically from June to October). At most study sites (92%), fish were captured with backpack electrofishing gear. Depending on stream width, 2-5 people conducted 2-3 pass removal sampling (Zippin 1958) using 1-3 backpack electrofishers (Smith Root Inc., Model 15D). We used a pulsed DC waveform operated at a range of 30-60 Hz, 200-500 volts, and a 2-5 ms pulse width. Block nets were installed at both ends of most electrofishing study sites to prevent fish movement out of the site during sampling. Removal electrofishing sites were typically 80-120 m in length (mean = 93 m, range = 20-180 m). Trout collected by electrofishing were anesthetized, identified to species, enumerated, measured for total length to the nearest mm, and released. The few hatchery rainbow trout collected were readily identifiable based on fin condition and were not considered further.

Trout abundance and associated variance were estimated via the maximum likelihood model in the MicroFish software package (Van Deventer and Platts 1989). If all trout were captured on the first pass, we considered that catch to be the estimated abundance. Because electrofishing is known to be size selective (Reynolds 1996), separate estimates were made for two size groups (i.e., trout <100 mm TL and those \geq 100 mm TL).

At sites too large to perform removal electrofishing (<1% of sites), mark-recapture electrofishing was conducted with a canoe- or boat-mounted unit (Coffelt Model Mark-XXII) using a pulsed DC waveform operated at 60 Hz, 400-500 volts, and a duty cycle of 20-40%. All trout were marked with a caudal fin clip during the marking run, and marked and unmarked trout were captured during a single recapture run usually 1-2 days later. We assumed there was no movement of marked or unmarked fish into or out of the study site, and attempted to reduce the likelihood of movement by lengthening the study sites to 213-1,705 m long (mean = 990 m). Estimates of abundance and variance were made with the modified Petersen estimate using the Fisheries Analysis + software package (Montana Fish, Wildlife and Parks 2004). Estimates were made for the smallest size groups possible (usually 25-50 mm) based on the need for a minimum of three recaptures per size group. As a result of low capture efficiencies for small fish in these larger rivers, we could not estimate fish <100 mm (TL) at the mark-recapture sites. For both depletion and mark-recapture electrofishing, all trout were pooled for an overall estimate of trout abundance at the site (e.g., Mullner et al. 1998; Isaak and Hubert 2004; Carrier et al. 2009), and point estimates for each species were then calculated based on the proportion of catch comprised by each species (Meyer and High 2011).

At the remaining sites (7%), where the stream channel was too large for removal electrofishing and too small or remote for boat electrofishing, daytime snorkeling was conducted to count trout (Northcote and Wilkie 1963; Schill and Griffith 1984). Wetted width at the snorkel sites averaged 19 m (range 2-43 m). Snorkeling was not conducted unless visibility was \geq 2 m. One to three snorkelers were used depending on stream width, and we attempted to count all

trout >100 mm (TL) and binned them into 25 mm size classes. In general, in streams <0.7 m average depth, upstream snorkeling was conducted, whereas for deeper streams, downstream snorkeling was conducted. Total counts were used as minimum abundance estimates with no correction for any sight-ability bias.

The area sampled by either electrofishing or snorkeling was estimated by measuring stream length (m) along the thalweg and mean stream width (nearest 0.1 m) from ten equally spaced transects within each site. Both electrofishing and snorkeling abundance estimates were converted to linear density (fish/100 m) for abundance extrapolations and areal density (fish/m²) for comparison with other studies.

Abundance Extrapolation

For each distribution stratum (i.e., likely present, unknown, and likely absent), we estimated total trout abundance separately by stream order. With ArcGIS software we summed the total length of stream (in meters) for each stream order within a stratum and divided this total by 100 m (roughly equivalent to the typical study site length) to calculate the total number of sampling units (N_i) in each stream order stratum (L). Using the abundance estimates standardized to 100 linear meters of stream, we calculated a mean abundance (\bar{y}_i) and associated variance (s_i^2) within each particular stratum. For total population size (N_{census}), we used the stratified random sampling formulas of Scheaffer et al. (1996): (elsewhere in the document you centered formulas)

$$N_{census} = \sum_{i=1}^L N_i \bar{y}_i$$

For variance of N_{census} we used the formula:

$$\hat{V}(N_{census}) = \sum_{i=1}^L N_i^2 \left(\frac{N_i - n_i}{N_i} \right) \left(\frac{s_i^2}{n_i} \right)$$

where n_i is the sample size within stratum i . Considering the *a priori* distribution categories and stream order, there were typically 9-15 strata within each sub-basin. Using the above formulas, we calculated 90% confidence intervals (CIs) around total abundance estimates by sub-basin. All sample sites, including fishless and dry sites, were included in the estimates.

A total of 71% of all stream kilometers in the study area were categorized as 'likely absent', and 276 sites (27% of the total) were sampled in this category. Redband trout were actually present at 41% of the 'likely absent' sites in the Boise, Payette, and Weiser sub-basins, but were only present in 2% of the 'likely absent' sites outside these three sub-basins. Because redband trout (and all other trout) were indeed virtually absent from these 'likely absent' stream kilometers outside the Boise, Payette, and Weiser sub-basins, values were considered numerically insignificant for the remaining sub-basins and consequently, estimates of occupancy and abundance in the "likely absent" category were not extrapolated except for the Boise, Payette, and Weiser sub-basins.

We identified individual redband trout populations based on our sampling results and local biologists' knowledge regarding potential isolating mechanisms, such as hanging culverts, waterfalls, and stream channel desiccation. Populations were delineated based on whether they were likely to be physically disconnected from or experiencing negligible gene flow with other

populations within the sub-basin. While this admittedly resulted in inexact delineations, deciding whether a stream contains a marginally independent population or is part of a larger one is rarely straightforward (McElhany et al. 2000).

We estimated total abundance for individual redband trout populations by the same methods and formulas as above. However, because few surveys were made within some individual populations, small sample size often precluded estimates for one or more strata within some populations. For these, minimum abundance was computed by adding the estimates for all strata for which calculations could be made. The number of kilometers within strata that were included in the estimates was compared to the total kilometers for all strata within the population to characterize the completeness of the overall estimate. Small sample size also precluded calculations of variance (and therefore confidence intervals) for individual populations. Nonetheless, these abundance estimates were included as a management-level indicator of approximate size for individual redband trout populations across the landscape.

Estimation of N_{adult} and approximation of N_e

The number of breeding-sized redband trout (N_{adult}) residing in sub-basins, and populations within sub-basins, was estimated by following an approach described in more detail by Meyer et al. (2006a). Briefly here, we used logistic regression models relating stream order and fish length to male and female maturity (dummy response variables; 0 = immature, 1 = mature) to predict, at any given study site, based on stream order at that site, the length at which the probability of a redband trout being mature was 0.5 (hereafter ML50). Based on the adjusted R^2 for discrete models (Nagelkerke 1991), these models explained 49% and 67% of the variation in male and female redband trout ML50 across the desert sub-basins and 53% and 59% across the montane sub-basins (Table 5). Based on the logistic regression coefficients in Table 5, redband trout size-at-maturity in first- to fifth-order streams varied from 122-215 mm TL in desert sub-basins and 122-227 mm in montane sub-basins, depending on stream order.

At each study site, the length frequency of captured redband trout was compared to estimates of ML50 at the site for both males and females to estimate how many of the redband trout at the site were likely mature. We assumed the overall sex ratio was 50:50 (Schill et al. 2010) and divided redband trout abundance by two to account for both sexes. Estimates of N_{adult} at each site were then extrapolated for each sub-basin and population using the formulas above and the same approach as Meyer et al. (2006a).

To approximate N_e , we assumed that N_e/N_{adult} for redband trout in the upper Snake River basin ranged from 0.4 to 0.7 (Schill and Labar 2010), and multiplied estimates of N_{adult} by the midpoint of this range. To approximate bounds for these estimates, we multiplied the lower 90% CI of N_{adult} by the lower ratio, and the upper 90% CI by the higher ratio.

Genetic analyses

Our attempts to quantify the distribution and abundance of genetically unaltered redband trout were hampered by the fact that no fixed diagnostic markers are currently available to genetically differentiate rainbow trout from redband trout, nor can phenotype be used to visually identify hybridization between these two subspecies. Instead, the detection of intraspecific hybridization in this study was based on allele frequency differences between the stocking sources and native populations (Sprowles et al. 2006; Small et al. 2007; Brunelli et al. 2008).

Initially, fin samples were collected at 139 study sites, but due to cost considerations genetic analyses were only conducted at a subset ($n = 61$) of these sites. Inclusion of sites for genetic analyses was not determined at random but rather to jointly accommodate the objectives of this study and those of Kozfkay et al. (2011). To investigate introgression, 13 polymorphic microsatellite loci were used, along with 5 nuclear DNA Single Nucleotide Polymorphisms (SNPs) and 1 mitochondrial DNA (mtDNA) SNP. Details regarding genetic markers, respective laboratory protocols, and data analyses can be found in Kozfkay et al. (2011). In the current study, we also added 30 samples from Dworshak Hatchery steelhead trout, a known pure redband trout population within the Snake River basin. Reference “pure” redband trout populations and reference hatchery rainbow trout populations from Kozfkay et al. (2011) provided guidelines on a detection threshold for redband trout introgression, which were based on an admixture coefficient (i.e., a q -value, established from microsatellite loci and nuclear DNA SNPs) and the frequency of the coastal mtDNA haplotype (see Kozfkay et al. 2011). There was a strong correlation at any given site between mtDNA haplotype frequencies and the admixture coefficient ($r = 0.89$), indicating that both methods provided similar information relative to genetic introgression.

Kozfkay et al. (2011) found that redband trout introgression with hatchery-origin rainbow trout was 2.6 times as likely at sites where historical records indicated that stocking had occurred. To refine this finding, we summarized the stocking of hatchery rainbow trout in the study area by the IDFG from 1913 (the oldest records available) to 2001 (after which only sterile fish have been stocked in study area streams). In that period of time, over 43 million hatchery rainbow trout were stocked in streams alone (not including lakes and reservoirs). However, most (63%) fish were stocked prior to 1968 and were usually fry or fingerlings (i.e., fish <200 mm TL). Because fry and fingerling plants typically demonstrate very poor survival rates relative to catchable-sized fish (Wiley et al. 1993), especially in flowing water (Cresswell 1981), we suspected that they would contribute minimally to introgression in the study area. Nevertheless, we compared introgression results to the stocking of catchable trout only, as well as to all hatchery rainbow trout combined (including catchables, fry, and fingerlings).

We summed the total number of rainbow trout and the number of catchable-sized rainbow trout stocked in each of the 61 streams included in our genetic analyses, and used logistic regression to compare whether these totals were related to redband trout purity at the genetic sampling locations. We used a binary response variable (0 = pure, 1 = introgressed), and used a data transformation on the independent variable (i.e., $\log_e(\text{number of fish stocked} + 1)$) because it was highly skewed. We used Akaike’s information criterion (AIC) to judge the strength of competing models (Akaike 1973).

RESULTS

Distribution and abundance

The study area within the upper Snake River basin contained a total of 60,869 km of stream at the 1:100,000 scale. The stream network included 39,364 km (65% of all stream kilometers) of first-order stream, 10,569 km (17%) of second-order stream, and 5,357 km (9%) of third-order stream, with the remaining 6,113 km (10%) of stream being fourth- through seventh-order (Figure 5).

A total of 1,032 study sites were surveyed for trout occupancy and abundance (Table 6, Figure 4). A total of 377 sites (37%) were dry or nearly dry (i.e., contained too little water to

support any species of fish), and the percentage of dry sites was much higher in desert (49% of sites) than montane sub-basins (20%). Our sampling framework resulted in 0.2% of the entire stream network being sampled (Table 6).

Redband trout were the most widely distributed species of trout, being captured at 389 sites, whereas brook trout were captured at 128 sites, bull trout at 37 sites, and brown trout at 16 sites. Our *a priori* categorization of redband trout occupancy portrayed their distribution somewhat accurately, as they were caught at 63% of the study sites within the “likely present” reaches, 20% of the study sites within the “unknown” reaches, and 17% of the study sites within the “likely absent” reaches. Although occupancy was therefore very similar between the “unknown” and “likely absent” reaches, as mentioned above, this similarity was caused by a high frequency of redband trout occurrence (41%) in “likely absent” reaches within the Boise, Payette, and Weiser montane sub-basins. Outside these three sub-basins, redband trout were present at only 2% of the remaining “likely absent” reaches. Redband trout were estimated to occupy a combined total of 13,485 km (22%) of stream in the study area, with a much higher rate of occupancy in montane sub-basins (39% of all stream kilometers) compared to desert sub-basins (11%).

Redband trout were the most abundant salmonid in the upper Snake River basin, with approximately $3,450,000 \pm 402,000$ of all sizes (Table 7). Brook trout were next most abundant at approximately $1,501,000 \pm 330,000$, followed by bull trout at $159,000 \pm 118,000$, and brown trout at $43,000 \pm 25,000$. Redband trout were captured in all sub-basins, brook trout were present in 8 of 12 sub-basins, and brown trout and bull trout were captured in 4 and 3 sub-basins, respectively. Ninety-nine percent of the total abundance of brook trout occurred in the four montane sub-basins.

We identified 46 individual populations of redband trout in the upper Snake River basin, including 26 desert populations and 20 montane populations (Table 8). Average total population size was about 32,000 and 125,000 for desert and montane sub-basins, respectively. Estimates of individual populations were mostly complete, in that (1) they summed to 85% of the total abundance for all sub-basins combined, and (2) there was sufficient data to extrapolate abundance to 78% of the ‘redband present’ kilometers, 75% of the ‘redband unknown’ kilometers, and 86% of the ‘redband absent’ kilometers.

In terms of total abundance, most trout resided in the smallest streams for all species except brown trout (Figure 5). First- and second-order streams, which comprised 81% of all stream kilometers, accounted for 60% of the abundance for redband trout, 92% for brook trout, and 95% for bull trout. In contrast, third- to fifth-order streams, which comprised only 16% of the total stream kilometers, accounted for 96% of the abundance for brown trout. This relationship was fairly consistent between desert and montane streams.

Mean abundance of all trout (both size classes) at all sites combined (including dry and trout-less sites) was 0.07 fish/m², whereas for redband trout alone, mean abundance was 0.06 fish/m² (Figure 6). Fish <100 mm and ≥100 mm made up 46 and 54%, respectively, of the abundance for redband trout, compared to 48 and 52% for all trout. Trout density (all species and sites combined) was equivalent in montane sub-basins (mean = 0.07 fish/m²) and desert sub-basins (0.07 fish/m²), but only because the higher percentage of dry sites in desert sub-basins reduced to a greater degree the mean abundance for all sites. At sites that contained at least one species of trout, the density of all trout combined was higher in desert streams (mean = 0.21 fish/m²) than montane streams (0.14 fish/m²). When considering only sites that contained

redband trout, the density of redband trout was over twice as high in desert streams (mean = 0.21 fish/m²) than in montane streams (0.10 fish/m²).

Estimates of mature adults and N_e

We estimated that approximately 848,000 ± 128,000 of the redband trout in the upper Snake River basin were breeding-sized adults (Table 9), which was 25% of all redband trout and 42% of those ≥100 mm TL. Within the 46 designated individual populations of redband trout, N_e for desert populations averaged about 4,700 per population, compared to about 14,800 per population for montane populations (Table 8). Effective population size was approximated to be <50 for only 3 populations.

Introgression with hatchery rainbow trout

Based on the IDFG's historical and current fish stocking databases, 43 million hatchery rainbow trout have been stocked in streams in the study area, 17.5 million of which have been of catchable size. Based on mtDNA haplotype frequencies and the admixture coefficient generated from SNP and microsatellite results, redband trout were considered pure in 34 of the 61 streams where genetic samples were collected and analyzed. There was general agreement between catchable stocking and hybridization in streams, in that catchables were stocked in only 7 (23%) of the 34 streams where redband trout were considered pure, but 19 (73%) of the 27 streams where redband trout were considered hybridized.

The number of stocked catchables alone (transformed to log_e(number stocked + 1)) produced a statistically significant logistic regression model (Wald $X^2 = 15.2$, $df = 1$, $P < 0.0001$, Figure 7), explained 36% of the variation in the presence or absence of redband trout introgression at a particular location, and correctly classified site-specific presence or absence of introgression over 75% of the time. The model that included stocked fry and fingerlings along with catchable stocking explained less of the variation in the presence or absence of introgression (22%), correctly classified introgression less often (66% of the time), and produced a poorer (i.e., higher) AIC score (AIC = 76.6 for all stocked fish, compared to 68.6 for catchables alone). Based on results from the model including only catchable stocking information, we estimated that stocking only about 300 hatchery catchable rainbow trout (across all years) resulted in a probability of 0.5 for a particular stream being introgressed at some level.

The stocking record indicated that a total of 139 individual streams were stocked with catchable rainbow trout in the upper Snake River basin from 1913 to 2001, which constitutes 6% of the 2,204 named streams and 8% of the total kilometers of stream in the study area (assuming stocking impacted the entire stream that was stocked, but none of the adjacent streams). Catchable stocking occurred much more often in montane streams (15% of the total stream kilometers) than in desert streams (5%). We used the logistic regression results to approximate the extent of introgression by assuming that (1) only streams stocked with catchables contained introgressed populations of redband trout, and (2) redband trout were introgressed throughout the entire course of each stream stocked with catchables (regardless of stream length, stocking location, or the location from which genetic samples were analyzed). Although it is obvious that neither assumption was entirely true, making these assumptions resulted in an approximation that redband trout were likely pure in 9,124 km of stream, or 68% of the estimated 13,485 km they currently occupy in the upper Snake River basin.

DISCUSSION

Distribution and abundance

Population abundance has long been recognized as a crucial measure of the ecology of a species (Andrewartha 1961) and is an important metric in present-day status and risk assessments (McElhany et al. 2000; Morris and Doak 2002). Considering this, our results suggest that redband trout are abundant and widespread in the upper Snake River basin, far outnumbering other native and non-native salmonids in the basin. Data sets on trends in redband trout abundance are generally lacking across the basin, although redband trout appear relatively stable in those desert streams for which temporal data sets are available (Zoellick et al. 2005). Although brook trout are next most abundant in the upper Snake River basin, and often negatively impact native salmonids in western North America (reviewed in Dunham et al. 2002), there is no evidence that they affect redband trout in a negative manner. At present, it appears that redband trout are demographically secure in many areas of the upper Snake River basin, both in desert and montane sub-basins. Montane sub-basins constituted only 40% of the stream kilometers but accounted for 73% of the abundance of redband trout. Moreover, redband trout resided in fewer, larger individual populations in montane sub-basins than in desert sub-basins. These findings suggest that montane populations of redband trout may be more robust and secure. However, redband trout constituted 97% of the total trout abundance in desert sub-basins compared to only 60% in the montane sub-basins, suggesting the long-term threat posed by non-native salmonids may be much lower in desert sub-basins.

Redband trout were not isolated in headwater streams. In fact, we found that redband trout abundance was lower in first-order streams and higher in second- and third-order streams than the number of stream kilometers would have predicted (Figure 5), indicating a concentration in these intermediate-sized streams. In contrast, brook trout and bull trout were concentrated in headwater streams, with brown trout concentrated in lower elevation, larger rivers. Similar partitioning along a longitudinal stream network for these particular species has been documented previously (e.g., Rahel and Nibbelink 1999; Torgersen et al. 2006) and is likely related to differences in habitat requirements and life history behaviors between species.

Mean densities of trout in our study, although taken from randomly distributed sites, are difficult to compare directly to other studies because we sampled stream reaches likely to have trout at a much higher rate than streams reaches we felt would not have trout present. Thus, our estimates of mean trout abundance are higher than if we had sampled stream reaches completely at random. Nevertheless, mean abundances reported in our study were similar to those reported in the few other randomly-sampled extrapolation efforts undertaken for stream salmonids in the Intermountain West. For example, mean density in this study for all trout at all sites (including dry and fishless locations) was 0.07 fish/m², similar to the estimate of 0.06 fish/m² for trout in eastern Idaho (Meyer et al. 2006a). Platts and McHenry (1988) summarized trout density in the western United States, and found a mean of 0.04 fish/m² for trout in 39 streams within the Intermountain West. For only those sites that contained redband trout in the present study, mean density of redband trout ≥ 100 mm in desert streams of southwest Idaho was 0.12 fish/m², similar to a mean of 0.18 fish/m² for age-1 and older redband trout in desert streams of south-central Oregon (Dambacher et al. 2009).

For a number of reasons we regard our estimates of total abundance as almost certainly biased in a negative direction. One source of negative bias was the use of a 1:100,000-scale stream hydrography layer, which inherently reduced our total population estimates by reducing the total number of stream kilometers in the study area. Although streams existing on both the

1:100,000 and 1:24,000 scale were probably of similar length (Firman and Jacobs 2002), many first-order streams that appear at the 1:24,000 scale are absent at the 1:100,000 scale. In a rangewide status assessment of westslope cutthroat trout *O. clarkii lewisi*, this resulted in 35% more stream kilometers at the 1:24,000 scale than the 1:100,000 scale (Shepard et al. 2005). Another source of negative bias was using removal electrofishing with backpack shockers as the primary sampling technique. This method of population estimation has consistently been shown over the last several decades to underestimate true population abundance of stream-dwelling salmonids and other fish species (e.g., Junge and Libosvsky 1965; Riley and Fausch 1992; Rodgers et al. 1992). Based on self-evaluation of our own crew's sampling efficiency, our estimates are probably negatively biased by about 22-25% for fish ≥ 100 mm TL and 27-37% for fish < 100 mm TL (Meyer and High 2011). Snorkeling has also been shown to underestimate stream abundance of trout (Thurrow and Schill 1996; Thurrow et al. 2006) with the latter authors suggesting that snorkeling density estimates for *O. mykiss* average only 32% of the actual population size. These potential sources of bias suggest that estimates of total trout abundance across the entire study area likely far exceed the values reported herein.

We also undoubtedly underestimated the actual number of kilometers that redband trout occupied, since we assumed that all 13,485 km of streams *a priori* categorized as "absent" were actually unoccupied (not including the Boise, Payette, and Weiser sub-basins, for which we estimated occupancy), yet we caught redband trout in 2% of the study sites in these categories. Also, the probability of detecting redband trout in our study was obviously not equal to one, and thus we falsely concluded that redband trout were absent from an unknown number of locations. However, backpack electrofishers were used to sample fish 92% of the time in the present study, and we previously estimated our field crew's capture efficiencies to be 20-60% (depending on pass number and fish size) for salmonids using this gear (Meyer and High 2011). At those efficiencies, if abundance was as low as two fish in 100 meters of stream, the likelihood of catching at least one of these fish with three depletion passes would be about 95%. Accordingly, we believe that our occupancy results were negatively biased, but only to a small degree.

The higher density of redband trout we observed in desert streams was not caused by differences in annual sampling intensity between desert and montane environments (such as might have occurred if, for example, desert streams were more often sampled in wetter years) because both desert and montane streams were sampled somewhat equally across all years. Besides a difference in redband trout density, we observed several other differences between streams in desert and montane sub-basins, most notably that study sites in desert sub-basins (1) were more often dry, (2) more often lacked a stream channel altogether, (3) were less likely to contain redband trout, and (4) less frequently contained non-native salmonids. Stream habitat conditions also differ between desert and montane streams in metrics such as stream gradient, elevation, substrate, shading, and summer water temperature, which results in dissimilar fish-habitat relationships between these disparate environments (Meyer et al. 2010). Consequently, different management strategies and monitoring programs may be required for redband trout in desert compared to montane sub-basins, although at present redband trout appear to be abundant in both environments. At a minimum, we recommend that trends be monitored separately for desert and montane streams, to assess differences in the stability of these populations.

Estimates of mature adults and N_e

The average proportion of redband trout ≥ 100 mm TL that were mature (42%) was quite high, as is typical of stream-dwelling salmonids that mature at a small size and early age.

Equivalent estimates include 30% for Yellowstone cutthroat trout *O. clarkii bouvieri* in eastern Idaho streams (Meyer et al. 2006a), and 40% (with a range of 24- 53%) over a 4 year period for brook trout in a small southwestern Idaho stream (Meyer et al. 2006b). Fish in these two studies matured at two to three years of age, similar to redband trout in our study area (Schill et al. 2010). Such early maturation resulted in much higher approximated values of N_e than would otherwise be expected. Although few comparable approximations of N_e exist for non-anadromous salmonid populations, our approximations of N_e for redband trout populations were higher than approximated ranges reported for resident Yellowstone cutthroat trout populations in southeastern Idaho (Meyer et al. 2006a). This discrepancy is due in part to smaller size at maturation for redband trout in southern Idaho relative to Yellowstone cutthroat trout in eastern Idaho (Meyer et al. 2003; Schill et al. 2010), and also to smaller lengths of stream reaches for individual redband trout populations compared to individual cutthroat trout populations.

Although the subpopulation estimates of mature adults and N_e reported in this study are no more than “approximations based on approximations” (Rieman and Allendorf 2001), we concur with Harris and Allendorf (1989) that, for management purposes, assessing relative risk among populations does not necessarily require great precision in estimating N_e . We therefore suggest that, if population boundary delineations were reasonably accurate in this study, then current genetic risk in terms of inbreeding or genetic drift for most redband trout populations in the upper Snake River basin appears to be relatively low based on the 50:500 rule of thumb. However, determining boundaries for redband trout populations across such a large spatial scale was difficult, and our delineations were admittedly based on limited empirical data. Consequently, we likely overestimated population sizes and N_e for some of the larger populations. However, many of the estimates for smaller populations (e.g., populations in the Snake River tributaries sub-basin), known to be reproductively isolated and therefore at greatest risk, are likely to be the strongest estimates of N_e , and a strong majority of these exceeded an N_e of 50.

We did not use genetic results to help delineate populations or estimate N_e for two reasons. First, we typically collected fin clips from within or very near the 100-m study sites, and the sites chosen for genetic analyses were too distant from each other and limited in sample size to expect gene flow measurements to be meaningful. Second, because stream-dwelling trout populations often exhibit limited dispersal, at least in regards to gene flow (Hudy et al. 2010), using our fin clipping sampling scheme to estimate N_e would likely have led to drastic underestimations of this parameter (Whiteley et al. 2012). In fact, because of the difficulty in estimating N_e using genetic methods, Whiteley et al. (2012) recommend foregoing genetic estimates of N_e altogether, and instead focusing on estimates of the effective number of breeders, or N_b , which can be more reliably estimated for stream-dwelling trout populations. Such estimates would also be more directly comparable to our method of estimating the number of breeders via population dynamics.

Introgression with hatchery rainbow trout

Considering that redband trout remain the most widely distributed and abundant salmonid in the upper Snake River basin despite more than a century of extraction-based land-use activities in the area, we believe that intraspecific introgression with hatchery rainbow trout is one of the primary threats to redband trout persistence in the upper Snake River basin. Fortunately, introgression is not ubiquitous across the study area, nor do we consider it likely to become so in the future. At this time, based solely on which streams were historically stocked with fertile catchable hatchery rainbow trout, we estimate that about 32% of the stream kilometers in the basin are likely to currently contain redband trout introgressed with non-native

rainbow trout. Because the stocking records have no site-specific stocking location tied to the stocking event, the calculation of this percentage required that we assume catchable stocking (1) resulted in introgression over the entire course of the stocked stream, and (2) resulted in no introgression in any adjacent or nearby tributaries. The strong relationship between catchable stocking and introgression suggests that in general these are reasonable assumptions to make, but neither assumption is entirely true because a portion of the stocked streams remained pure while a similar proportion of unstocked streams were hybridized. Some of this discrepancy was perhaps due to errors in the stocking record. Regardless, while some spread of introgression (from the original stocking locations) has likely occurred and will likely continue to occur (e.g., Rubidge and Taylor 2005; Bennett and Kershner 2009), the agreement we observed between historical catchable stocking and current introgression suggests that, to date, hybridization has expanded minimally outside the locations where catchables were historically stocked. Such resiliency of the native redband trout genotype in drainages with decades of hatchery rainbow trout stocking is not an uncommon occurrence (e.g., Small et al. 2007; Matala et al. 2008) and indeed at times should be expected if theory on locally adapted stocks is correct.

In the Big Wood River sub-basin, no pure redband trout populations were found. The Big Wood River, near its confluence with the Snake River, flows over a 20-meter natural waterfall that is probably of similar age as the nearby natural fish barrier on the Snake River created by Shoshone Falls, which blocked upstream invasion by redband trout. The waterfall on the Big Wood River resulted in one endemic fish species in the sub-basins (the Wood River sculpin *Cottus leiopomus*), and seven other fish species present in other nearby sub-basins are absent from the Big Wood River sub-basin (Simpson and Wallace 1982). Based on this evidence, we suggest that redband trout are not native to the Big Wood River sub-basin. Further genetic samples collected throughout the sub-basin may help confirm or refute this assertion.

There was a strong correlation between the number of fry and fingerlings compared to the number of catchables stocked in individual streams over the period of record ($r = 0.81$), but our results suggest that the stocking of catchables (not fry and fingerlings) resulted in introgression in the study area. In fact, of the 15 sites where redband trout apparently remain pure despite previous records of stocking hatchery rainbow trout, 13 of these sites were stocked either entirely ($n = 9$) or mostly ($n = 4$) with fry and fingerlings only. Moreover, although catchable trout have extremely poor survival rates when stocked in streams (Miller 1952; Bettinger and Bettoli 2002; High and Meyer 2009), hatchery fry and fingerling survival is even lower (Schuck 1948; Cresswell 1981), and therefore has largely been discontinued in flowing waters across the U.S. (Halverson 2008).

Since the available genetic markers are not fixed between rainbow trout and redband trout, quantitatively estimating introgression is a difficult task, and it is nearly impossible to differentiate purportedly pure populations from those with low levels of introgression (Pritchard et al. 2007). Thus, we may have underestimated the extent of introgression in redband trout populations in the upper Snake River basin. However, our results indicated that we had sufficient resolution to differentiate coastal hatchery strains from inland redband trout and identify populations with greater than 10% admixture, a threshold supported in other studies detecting intra-specific hybridization (Simmons et al. 2009; Kozfkay et al. 2011; Neville and Dunham 2011). There was a strong correlation between stocking history and the presence of hybridization, which lends further support to our extrapolations of the amount of introgressive hybridization in the basin. Given the detected level of resolution and management implications of introgressive hybridization, all populations are considered valuable because at the scale of most existing data, it is usually impossible to know the extent of introgression throughout an entire population, and populations are often not hybridized throughout the entire extent of their

distribution (e.g., Meyer et al. 2006a; Ostberg and Rodriguez 2006). Our estimate that redband trout were likely pure in 68% of their current range in the upper Snake River basin was meant only as an approximation and should not be used to infer purity or introgression at untested sites. Rather, we encourage additional genetic work to characterize redband trout introgression across the basin, which could help (1) test and refine the stocking vs. introgression logistic regression model developed herein, (2) further clarify redband trout introgression levels across the basin, and (3) focus management and recovery strategies for redband trout in the near future.

This study has demonstrated that redband trout in the upper Snake River basin are widespread and abundant, and remain genetically pure in large portions of the basin. Knowledge gained from this study required sampling only 0.2% of the entire stream network, yet produced population abundance estimates with 90% CIs within $\pm 50\%$ of the estimate for many of the sub-basins in the study area. Future studies of status assessments for widespread species in flowing waters may benefit from following our method of using the EMAP study site selection process and stratifying by stream order and an *a priori* categorization of species occupancy (i.e., “likely present,” “likely absent,” or “unknown”). Nevertheless, our approach had several shortcomings. First, each site was sampled only once, thus temporal variability inherent in distribution and abundance data for stream-dwelling fishes (Decker and Erman 1992; Dauwalter et al. 2009) was not captured by our snapshot study design. Second, population boundaries could only be weakly delineated, and much more refined surveying and genetic sampling may be required to estimate N_{census} and N_b precisely within individual populations. Third, genetic purity was not well refined, and additional genetic samples would be useful to confirm the accuracy of the hybrid model and more definitively assess introgression across the landscape. Finally, our design did not address trends across time; clearly there is a need for more information on trends in redband trout abundance both in the upper Snake River basin (but see Zoellick et al. 2005) and across their range in the Intermountain West. These efforts would help further clarify the status of redband trout in the upper Snake River basin and elsewhere.

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TABLES

Table 5. Coefficient estimates and the amount of variation (\tilde{R}^2 , or the adjusted R^2 for discrete models; see Nagelkerke 1991) explained by logistic regression models relating the probability of being mature (dependent variable) to redband trout total length and stream order.

<u>Logistic regression coefficients</u>						
Desert or			Total	Stream		
montane	Sex	Constant	length (m)	order	\tilde{R}^2	Source
Desert	Male	-4.238	0.047	-0.998	0.49	Schill et al. 2010
Desert	Female	-10.100	0.090	-1.742	0.67	Schill et al. 2010
Montane	Male	-5.556	0.056	-0.887	0.53	K. Meyer, unpublished data
Montane	Female	-5.933	0.067	-1.765	0.59	K. Meyer, unpublished data

Table 6. Stream network and distributional extent of redband trout in sub-basins of the upper Snake River basin, Idaho.

	Bennett Mountain	Big Wood	Boise	Brownlee	Bruneau ^a	Mid- Snake	Owyhee ^b	Payette	Salmon Falls	Upper- Snake	Weiser	Total
Desert or montane sub-basin	Desert	Montane	Montane	Desert	Desert	Desert	Desert	Montane	Desert	Desert	Montane	
Total estimated km ranked <i>a priori</i> as "known"	169	654	2,061	217	788	237	734	1,833	591	126	249	7,660
Total estimated km ranked <i>a priori</i> as "unknown"	501	2,829	894	42	700	497	2,228	785	601	320	671	10,068
Total estimated km ranked <i>a priori</i> as "not"	3,481	2,997	5,093	254	4,134	3,421	12,488	4,178	2,924	1,954	2,216	43,141
Total km	4,151	6,480	8,049	513	5,622	4,156	15,450	6,795	4,116	2,400	3,137	60,869
Total km estimated as occupied	210	1,246	4,567	121	884	1,452	927	2,911	137	107	923	13,485
Number of sites within "likely present" range	31	27	68	7	76	23	68	79	34	4	27	444
Number of sites within "likely present" range with RBT	19	15	55	4	46	15	38	47	19	1	21	280
Number of sites within "unknown" range	23	66	13	3	24	26	65	30	22	15	25	312
Number of sites within "unknown" range with RBT	5	9	6	2	4	10	3	6	5	3	9	62
Number of sites within "likely absent" range	2	21	42	0	14	19	86	50	15	13	14	276
Number of sites within "likely absent" range with RBT	0	-	23	0	0	2	2	18	0	0	2	47
Number of dry sites	13	65	12	2	47	30	134	12	31	19	12	377
Total number of sites	56	114	123	10	114	68	219	159	71	32	66	1,032
Amount of sub-basin sampled (%)	0.1	0.2	0.2	0.2	0.2	0.2	0.1	0.2	0.2	0.3	0.2	0.2

^aExcludes the Jarbidge River drainage in Nevada.

^bExcludes the Duck Valley Indian Reservation.

Table 7. Abundance (N_{census}) and 90% confidence intervals (CI) of redband trout and other trout in the upper Snake River basin, Idaho.

Sub-basin	Desert or montane	Sample code ^a	Rainbow trout				Brook trout				Brown trout				Bull trout			
			≥100 m TL		< 100 mm TL		≥100 m TL		< 100 mm TL		≥100 m TL		< 100 mm TL		≥100 m TL		< 100 mm TL	
			N_{census}	±90% CI	N_{census}	±90% CI	N_{census}	±90% CI	N_{census}	±90% CI	N_{census}	±90% CI	N_{census}	±90% CI	N_{census}	±90% CI	N_{census}	±90% CI
Bennett	Desert	LP	21,926	12,888	11,148	7,958												
		UK	35,351	32,037	8,243	10,434												
Big Wood	Montane	LP	175,617	153,544	10,246	662	27,244	19,565	62,412	74,463	24,130	24,526						
		UK	20,933	9,642	77,842	78,352	19,511	11,311	25,427	20,029	0							
Boise	Montane	LP	325,638	52,844	158,331	56,734	26,612	12,827	48,844	27,149	6,122	5,648			34,256	18,503	17,104	21,962
		UK	38,377	16,407	80,512	13,579												
		LA	414,295	136,815	267,885	119,891					130				91,525	113,956	3,059	5,031
Brownlee	Desert	LP	32,165	21,791	12,015	12,824	1,264	2,076										
		UK	19,135	NA	3,283	NA												
Bruneau ^b	Desert	LP	113,163	36,871	50,966	20,783	1,650	1,700	1,206	1,471								
		UK	6,349	5,517	41,076	62,817												
Mid-Snake	Desert	LP	50,493	31,793	40,566	43,082												
		UK	35,960	26,785	62,171	57,225												
Owyhee ^c	Desert	LP	136,796	42,024	112,888	51,650	379	492										
		UK	11,964	15,392	21,547	25,611												
Payette	Montane	LP	148,786	45,346	90,206	37,553	98,170	36,306	66,709	36,887					8,552	5,653	201	329
		UK	9,368	8,189	33,854	35,851	36,379	24,029	82,337	69,187								
		LA	137,956	52,859	197,559	140,529	364,897	198,106	325,534	181,850								
Salmon Falls	Desert	LP	44,561	16,920	13,368	10,527	1,387	2,273	1,526	2,500	1,779	1,441	616	1,010				
		UK	4,623	5,667	6,486	9,657	896	1,472	8,961	14,724	1,686	2,766	187	307				
Upper-Snake	Desert	LP	10,601	NA	25,157	NA					6,478	NA	1,935	NA				
		UK	4,456	4,963	1,606	2,213												
Weiser	Montane	LP	62,146	16,836	31,062	10,331	12,877	10,557	42,321	61,039					1,755	1,439	2,228	2,018
		UK	31,104	19,405	14,472	9,141	7,366	6,855	16,453	14,712								
		LA	121,069	180,383	64,203	105,576	181,215	125,277	39,181	34,686								
Subtotal	LP	LP	1,121,892	183,770	555,953	100,153	169,583	44,604	223,018	106,661	38,510	25,209	2,551	1,010	44,562	19,401	19,533	22,057
		UK	217,620	53,606	351,092	125,602	64,152	27,468	133,178	74,975	1,686	2,766	187	307				
		LA	673,319	232,487	529,648	212,764	546,112	234,394	364,714	185,129	130	NA			91,525	113,956	3,059	5,031
Total by size class			2,012,832	301,157	1,436,693	266,599	779,848	240,176	720,911	226,430	40,326	25,360	2,738	1,056	136,087	115,595	22,592	22,624
Total			3,449,525	402,207			1,500,758	330,083			43,064	25,382			158,679	117,789		

^aLP is "likely present", UK is "unknown", and LA is "likely absent"; see methods for further description.

^bExcludes the Jarbidge River drainage in Nevada.

^cExcludes the Duck Valley Indian Reservation.

Table 8. Estimated total abundance (N_{census}), number of adults (N_{adult}), and effective population size (N_e) of redband trout in each sub-basin of the upper Snake River basin, Idaho. Proportion of kilometers (kms) included in the estimates is an indication of how complete each estimate is.

Desert/Montane	Sub-basin	Population	<i>n</i>	Redband trout abundance			Proportion of kms included in estimates by sample code			
				N_{census}	N_{adult}	N_e	Likely Present	Likely Unknown	Likely Absent ^a	
Desert	Bruneau	Big Jacks	36	26,261	3,582	1,970	100	100		
		Bruneau	37	60,768	3,676	2,022	96	42		
		EF Bruneau	14	41,396	6,637	3,650	80	77		
		Little Jacks	8	40,006	24,526	13,489	100	100		
		Sheep	19	1,692	0	0	93	59		
	Owyhee	Cow	2							
		Jordan	72	129,704	42,924	23,608	100	95		
		NF Owyhee	41	84,384	22,073	12,140	87	72		
		Upper Owyhee	104	104,100	33,676	18,522	100	100		
	Rock	Rock	32	50,936	4,206	2,313	62	65		
	Salmon Falls	Cedar	6	11,288	3,312	1,822	91	48		
		Lower Salmon Falls	9	4,110	0	0	100	71		
		Upper Salmon Falls	56	51,216	11,850	6,518	100	97		
	Snake Tribs	Bennett	9	1,610	254	140	100	55		
		Brownlee	10	72,857	21,917	12,054	100	0		
		Canyon	13	14,189	4,786	2,632	72	94		
		Castle	11	41,405	18,204	10,012	100	76		
		Clover	12	45	45	25	5	100		
		Cold Springs	7	5,207	3,580	1,969	100	100		
		Jump	9	14,896	921	507	100	6		
		King Hill	13	4,773	3,426	1,884	100	100		
		Little Canyon	14	6,978	2,284	1,256	100	100		
		Reynolds	15	7,718	2,918	1,605	22	88		
			Shoofly	2						
			Sinker	13	53,243	5,521	3,037	82	93	
		Succor	6	1,424	1,142	628	21	33		
	Montane	Big Wood	Big Wood	45	237,261	55,250	30,388	98	99	
			Camas	19	20,798	962	529	79	68	
			Fish Creek	5						
			Lower Little Wood	10	1,923	1,349	742	33	100	
Lower Wood			14							
		Upper Little Wood	21	26,765	2,527	1,390	92	99		
Boise		Anderson Ranch	55	418,399	140,623	77,343	84	95	99	
		Arrowrock	39	179,576	58,161	31,989	99	25	92	
		Lower Boise	13	16,659	9,054	4,980	3	100	100	
		Lucky Peak	16	61,931	5,600	3,080	73	100	92	
Payette		Cascade	38	68,907	10,798	5,939	43	100	92	
		Little Payette Lake	11	10,561	3,316	1,824	100	100	84	
		Lower Payette	8							
		Payette	43	761,023	59,806	32,893	90	99	99	
		Payette Lake	35	23,450	5,665	3,116	90	46	99	
		Squaw	24	43,914	7,926	4,359	90	50	97	
Weiser		Crane Creek	7							
		Lost Valley	3							
		Main Weiser	51	139,494	39,409	21,675	100	74	79	
		Mann Creek	5	93,442	24,217	13,319	100	24	100	
Total				2,934,309	646,123	355,368				

^aEstimates applied only to Boise, Payette, and Weiser sub-basins (see methods).

Table 9. Estimated total number of adults (N_{adult}) with 90% confidence intervals (CI) for redband trout in each sub-basin of the upper Snake River basin, Idaho.

Sub-basin	N_{adult}	
	Estimate	\pm 90% CI
Bennett	20,158	10,243
Big Wood	46,232	51,468
Boise	366,179	35,544
Brownlee	19,105	4,245
Bruneau ^a	51,562	19,861
Mid-Snake	36,757	20,134
Owyhee ^b	76,785	26,177
Payette	103,591	30,105
Salmon Falls	13,759	6,466
Upper-Snake	8,332	4,508
Weiser	105,316	98,941
Totals	847,775	127,585

^aExcludes the Jarbidge River drainage in Nevada.

^bExcludes the Duck Valley Indian Reservation.

FIGURES

Legend

- ▲ Dry sites
- Redband present
- Redband not present

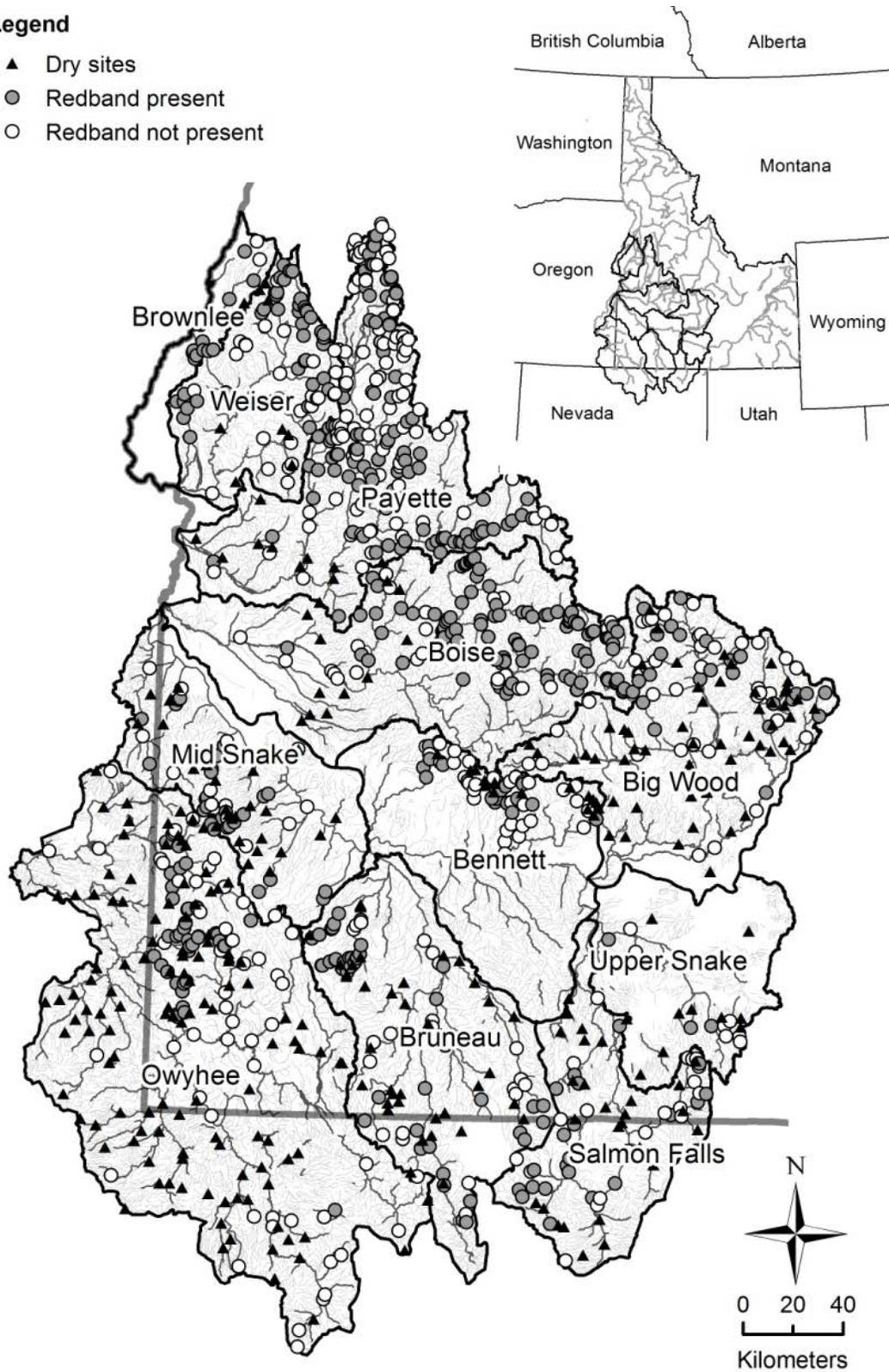


Figure 4. Distribution of the 1,032 study sites used for redband trout population assessments in sub-basins of the upper Snake River basin, Idaho.

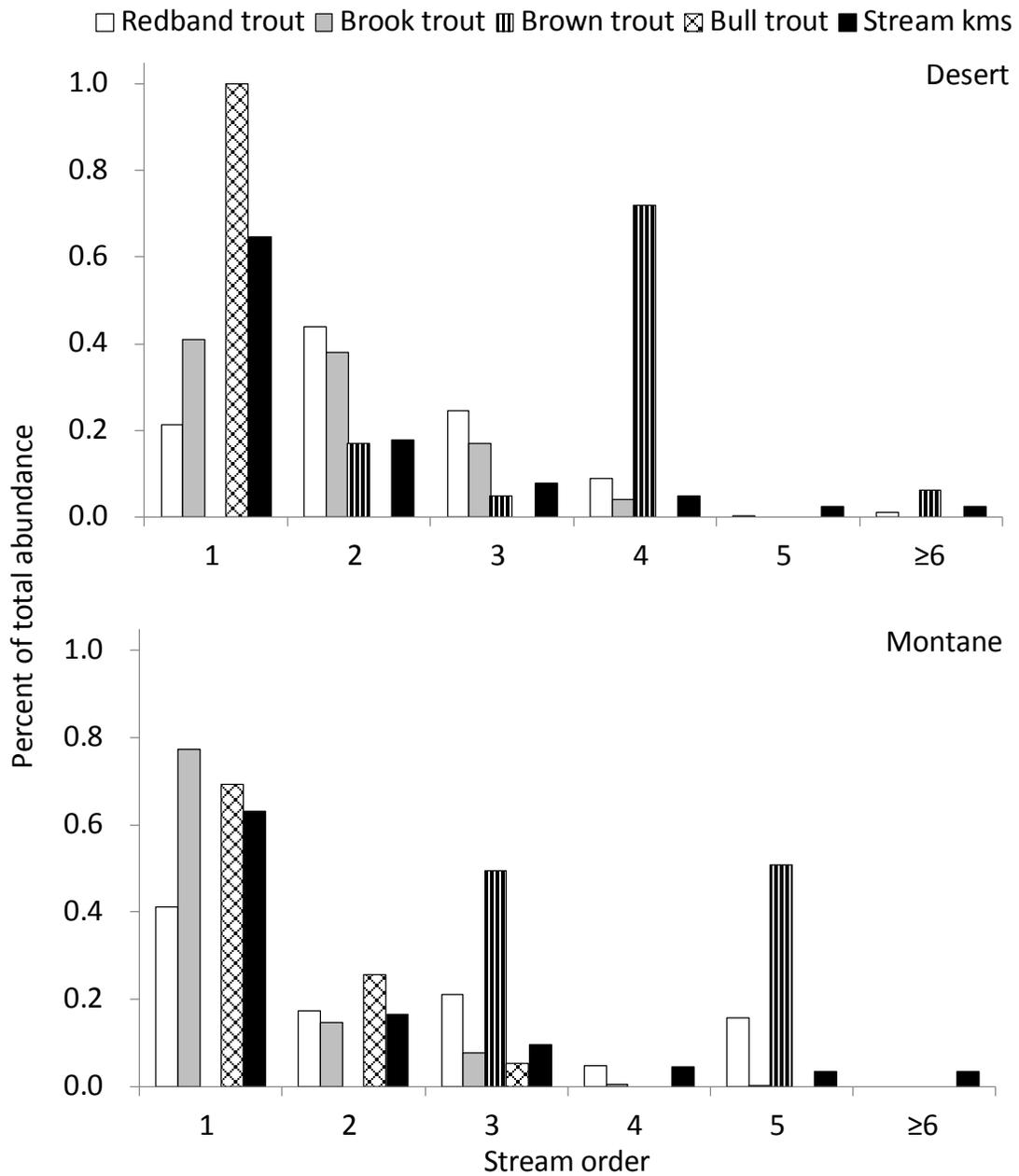


Figure 5. Proportion of total trout abundance and stream kilometers by stream order in desert and montane streams of the upper Snake River basin, Idaho.

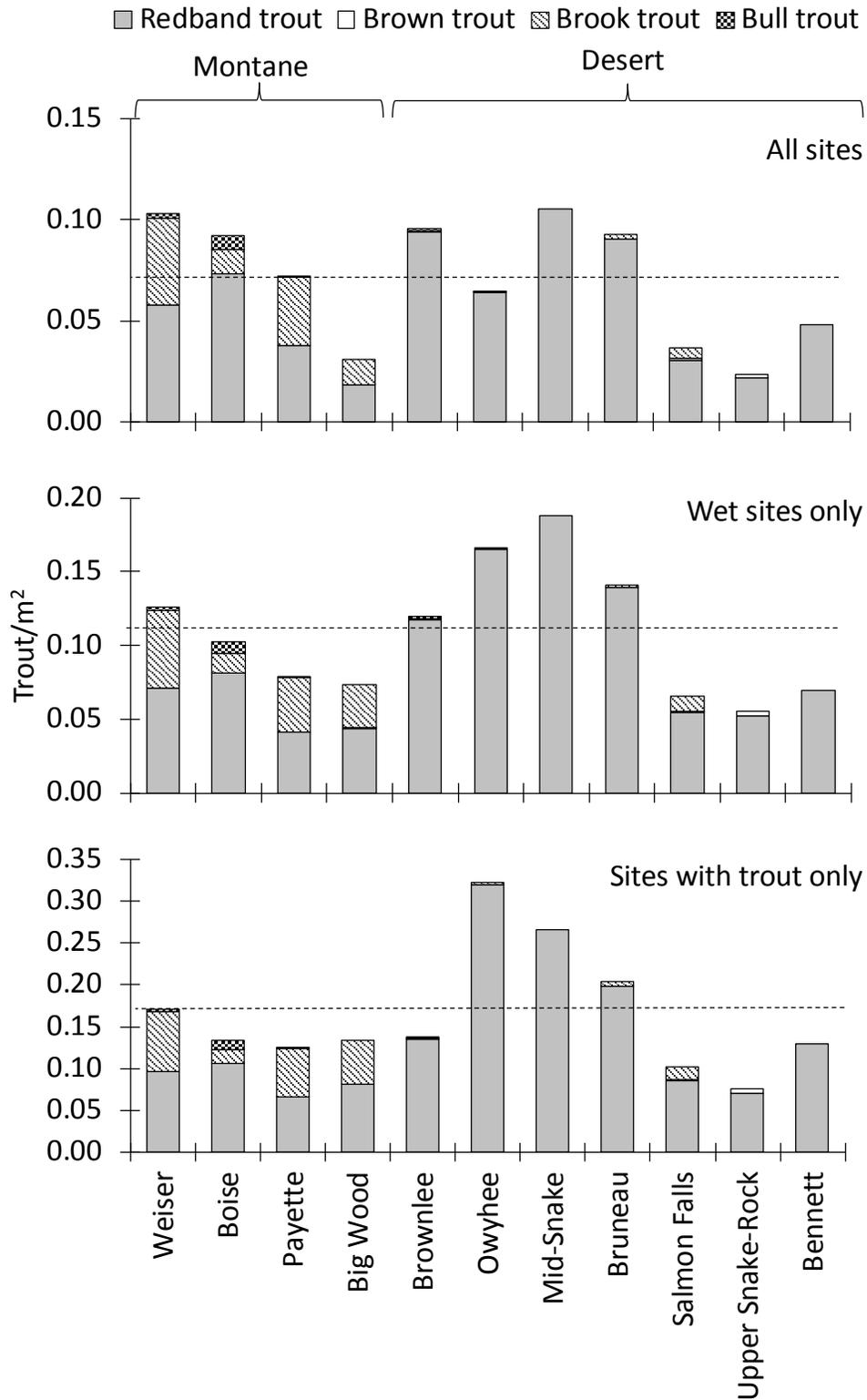


Figure 6. Mean density (fish/m²) of trout in desert and montane sub-basins of the upper Snake River basin, Idaho. Dashed lines depict mean abundance for each scenario.

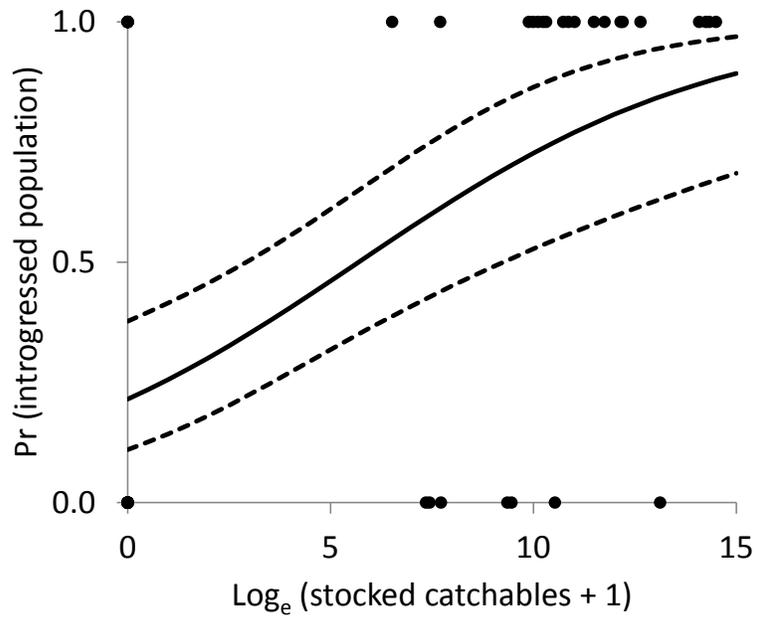


Figure 7. Logistic regression relationship (solid asymptotic line) between the number of catchable rainbow trout stocked in a stream (\log_e -transformed data) and whether the redband trout in the stream were introgressed. Dotted asymptotic lines indicate the 95% confidence intervals for the relationship.

CHAPTER 3: BULL TROUT TRENDS IN ABUNDANCE AND PROBABILITIES OF PERSISTENCE IN IDAHO

ABSTRACT

We estimated bull trout *Salvelinus confluentus* population growth rates and used population growth models to evaluate observation error and estimate bull trout persistence probabilities 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 since 1994, substantially more population growth rates trended statistically upward ($n = 13$) than downward ($n = 3$). Average (SE) intrinsic rates of population change were 0.01 (0.03) prior to 1994 and 0.07 (0.02) since 1994; across all years of data, rate of change averaged 0.07 (0.02). Forty-five percent of the data sets had zero to minimal estimated 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 fit for bull trout population growth. Moreover, few of the most reliable model 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 time periods before or after 1994, and generally was not trending positively or negatively through time. Parametric bootstraps predicted that mean (median) probability of falling below quasi-extinction levels of 20 adults in the next 30 years was 9.8% (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 risk of extirpation is low in the foreseeable future.

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INTRODUCTION

Concerns about the status of bull trout *Salvelinus confluentus* in the western United States have been expressed since at least the mid-1980s (see Federal Register 50 FR 37958) when the species was first considered for listing under the Endangered Species Act (ESA). The species was listed with a threatened designation in the coterminous U.S. in 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 basin and the Klamath basin, and concluded that although bull trout were more widely distributed in the region than many other native salmonids, bull trout subpopulations were 'strong' (i.e., >500 adults, all life stages present, abundance stable or increasing, spawning and rearing habitat not limited) in only 6% of their potential range. Using a similar definition of 'strong populations', the U.S. Fish and Wildlife Service (USFWS) concluded that bull trout in the Columbia basin were 'strong' in only 13% of their potential range (USFWS 1998). However, within parts of the Columbia basin, particularly in Idaho, bull trout appear to be relatively abundant and stable (High et al. 2008), with 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 trends in abundance 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 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 techniques 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).

However, 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 and 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 >0.95 probability. 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 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; CRFPO 2005; Muhlfeld et al. 2006; Thurow et al. 2006). For the purposes of our study, we follow the definition of observation error by Dennis et al. (2006) as the amount of error inherent in the observation or sampling methods by which population abundance is being monitored. This error is in addition to real fluctuations in population abundance caused by demographic and environmental noise, termed process noise. Inclusion of data sets with significant observation error in PVAs inflates estimates of population variability, leading to

pessimistic estimates of population viability (Morris and Doak 2002). This 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 viability of animal populations (Garton et al. 2011; Russell et al. 2012). Our second study objective was to compare several population growth models in 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

Delineating population boundaries

Bull trout are found in numerous drainages throughout Idaho (Figure 8), totaling about 103,000 km². Within this area, the USFWS has unofficially designated 272 local bull trout populations within 30 core areas (USFWS 2002), although these designations continue to be refined. According to the USFWS, a local bull trout population describes a unit which 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 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 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 subpopulations (McElhany et al. 2000; Theobald and Hobbs 2002), we assessed the status of bull trout at the population level even though we recognize that not all subpopulations are interconnected within each bull trout population in Idaho.

Available bull trout data

Altogether, 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 on their upstream spawning migrations at salmon weirs (Schill et al. 1994; Stark et al. 2012), which were generally operated from May through 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 outmigration (e.g., Copeland and Venditti 2009). Screw traps were deployed as early as possible in the spring, usually in the last week of February or the first week of March, and operated until ice-up (usually the first week of December). Bull trout of all sizes were counted at the screw traps, but average length was 178 mm, and <1% of fish were <75 mm in length. Redd counts were used to monitor bull trout abundance in six populations, and methods followed the descriptions in 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, but in general, from one to five observers (depending on stream width) snorkeled slowly upstream counting all salmonids ≥ 75 mm total length (TL). During snorkeling surveys, visibility (i.e., distance to distinguish patterns on an object the size of an average fish) averaged 4.3 m and

water temperature averaged 14.5°C, with <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). Within two populations, multipass electrofishing was conducted within the same sections of river, using pulsed DC electrical output. Finally, angler creel was conducted within one population, with mean annual bull trout catch rates (fish/hour) 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; Thurow et al. 2006; Muhlfeld 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 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 fit to the \log_e -transformed abundance data is equivalent to the intrinsic rate of change (r) for the population (Maxell 1999) and produces unbiased estimates of r despite the potential presence of observation error within the data (Humbert et al. 2009). Values of $r < 0$ indicate negative population growth whereas $r > 0$ indicates positive population growth. We used a significance level of $\alpha = 0.10$ to increase the probability of detecting trends (Peterman 1990; Maxell 1999). Previous work has suggested that bull trout abundance in Idaho had an inflection point in about 1994 (High et al. 2008; Copeland and Meyer 2011), so we estimated r for three periods: pre-1994, post-1994, and the entire time period. Data from 1994 were included in both the early and late time periods.

Fitting 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 the abundance of adult bull trout in these same populations (Table 10). For the Lake Pend Oreille population, adult abundance was estimated from a 2008 mark-recapture estimate of all bull trout ≥ 400 mm total length (TL) (M. Hansen, University of Wisconsin-Stevens Point, unpublished data). For the Lower Kootenai, Coeur d'Alene Lake, and Priest Lakes populations, adult abundance was estimated from the maximum number of redds counted in 2009 in these populations (Idaho Department of Fish and Game (IDFG), unpublished data). We assumed that all redds were counted in these populations and that there were 3.2 adults for each redd counted (Downs and Jakubowski 2006). For the remaining populations, adult abundance was approximated from the estimated abundance of bull trout ≥ 70 mm in High et al. (2005, 2008), which compiled over 2,500 snorkeling and electrofishing surveys to produce abundance estimates across Idaho. To approximate adult abundance based on estimates of abundance for all bull trout ≥ 70 mm, we assumed that 10% of all bull trout ≥ 70 mm in length (reported in High et al. 2005, 2008) 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 details in Garton et al. 2011) based on the

finite rate of change ($\hat{\lambda}_t$) estimated for that population from sequential, paired annual indices of abundance using the formula:

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

where $M_i(t+1)$ and $M_i(t)$ were indices of abundance for year $t + 1$ and year t , respectively (e.g., total number of bull trout captured in two consecutive years at a particular screw trap). An index to 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 using the formula:

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

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, because 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 spatio-temporal 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 of 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, 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 snorkel reaches were used to estimate trends in adult bull trout abundance for the snorkel data sets.

We fit a suite of stochastic population growth models to the time series population reconstructions for each bull trout population using maximum likelihood methods. Thorough descriptions of these models can be found in 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), which is a stochastic version of the Gompertz model that 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 model is as follows:

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

where \hat{r}_t = estimated instantaneous rate of change in year t ($\ln N_{t+1} - \ln N_t$),

\hat{a} = estimated intercept,

\hat{b} = estimated slope (a measure of the strength of density dependence),

$\hat{\tau}^2$ = estimated observation error, and

$\hat{\sigma}^2$ = 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, which results in pessimistic estimates of population viability (Morris and Doak 2002). The Gompertz state space model was therefore used to identify data sets estimated to have no observation error, which theoretically produced uninflated estimates of extinction risk. Secondly, we identified data sets with estimates of minimal observation error, which we arbitrarily set at $\hat{\tau}^2 < 0.10$; we assumed that minimal observation error would only slightly inflate extinction risk. We assumed that estimates of extinction risk for data sets where $\hat{\tau}^2 \geq 0.10$ were potentially inflated substantially; they 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); 3) the Gompertz-type model of density dependence in population growth (Dennis et al. 2006); and 4) either a “period effect” or a “time effect” in population carrying capacity 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 Ricker and Gompertz models is that the Ricker model assumes population growth rates are linearly (negatively) related to population size, whereas the Gompertz model assumes a log (negative) relationship and thus larger density-dependent effects at small population sizes. Both models provide an estimate of carrying capacity defined as the quasi-equilibrium abundance, or the population size at which the growth rate is zero (Garton et al. 2011). Models that included a “period effect” in our study inferred that carrying capacity differed between the pre-1994 and post-1994 periods; “period” was consistently not significant in any of the models and this variable was eventually discarded. Models that included a “time effect” inferred that carrying capacity was changing linearly through time, either increasing or decreasing depending on the sign of the estimated coefficient.

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

Population persistence projections

We performed parametric bootstraps (Efron and Tibshirani 1998) on minimum population size by projecting 100,000 replicate abundance trajectories for 10 and 30 years into the future for each population using the formula:

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

where $\hat{N}(t+1)$ = estimated population abundance at time $t+1$,

$\hat{N}(t)$ = estimated population abundance at time t , and

$\hat{r}(t)$ = 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 and 30 years. The quasi-extinction threshold of 20 adult bull trout 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 all models 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 estimated 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 dataset (Garton et al. 2011).

We assumed that bull trout population viability was independent between populations. We deemed this was a reasonable assumption to make because correlations in abundance between bull trout populations were generally low, as evidenced by correlations (Pearson's r) of the rates of change between all populations that 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 10). Approximations of starting adult bull trout population size averaged 2,485 (median = 884) and ranged from a low of 109 (Priest Lakes population) to a high of 12,513 (Lake Pend Oreille population) (Table 10). Most populations included in our analyses (57%) 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 have increased in abundance since 1994 (Table 11). Prior to 1994, the intrinsic rate of change was zero for 3 data sets, positive for 4 data sets, and negative for 5 data sets (one of which was significant at $\alpha = 0.10$). Since 1994, the intrinsic rate of change was zero for 2 data sets, positive for 18 data sets (14 significant), and negative for 5 data sets (3 significant). Average (SE) rates of change were 0.01 (0.03) prior to 1994 compared to 0.07 (0.02) since 1994. Across all populations and all years of data, average (SE) rate of change was 0.07 (0.02).

Observation error

Three of the 25 bull trout trend data sets were not monitored annually, thus density-dependent population growth models could only be fit to the remaining 22 data sets. Of these, 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 12). Snorkeling data were most prone to high observation error, with 70% of the snorkeling data sets with estimates of $\hat{\tau}^2 \geq 0.10$. In

contrast, only 17% of the redd count data sets and 25% of the screw trap data sets contained estimates of $\hat{t}^2 \geq 0.10$.

Population growth models

The suite of population growth models generally fit well to Idaho bull trout trend data sets, with the best models on average explaining about half the variation in annual rates of change (excluding EGPE models, which inherently explain none of the variation; Table 12). The Gompertz model was nearly always (19 of 22 instances) the best fitting model (Table 12). Essentially none of the best models contained a period effect, suggesting that carrying capacity generally did not differ for the time period before or after 1994. In addition, only a few of the best models with zero or minimal observation contained a time (i.e., year) effect, suggesting that carrying capacity generally was not trending positively or negatively through time. For the trend data sets estimated to have high observation error, all but one model contained a year effect, suggesting that carrying capacity was trending positively or negatively through time for these data sets, although the presence of high observation error reduces the reliability of this result. For the data sets 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 ($r = 0.00$).

Population persistence projections

Parametric bootstraps based on model averaged parameter estimates predicted that, for the abundance data sets estimated to have zero or minimal observation error, mean (median) probability of falling below 20 adults in 10 years and 30 years was 3.5% (1.7%) and 9.8% (4.7%), respectively (Figure 9). In comparison, for data sets estimated to have high observation error, mean (median) probability of falling below 20 adults in 10 years and 30 years was 16.2% (4.4%) and 34.3% (11.0%), respectively. Thus, declining below quasi-extinction levels 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 those with zero or minimal observation error.

For the data sets with zero or minimal observation error, there was a negative exponential relationship between the ending adult population size (after \ln 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 10); for the data sets with high observation error, no such relationship existed ($r^2 = 0.02$; $F = 0.11$; $P = 0.75$; Figure 10).

DISCUSSION

Data limitations

More than half of the available long-term bull trout trend monitoring data sets were estimated to have a statistically significant amount of observation error. This finding supports repeated assertions that bull trout trend monitoring data, being composed frequently of redd counts or snorkeling surveys, is often rife with sampling error (Dunham et al. 2001; CRFPO 2005; Muhlfeld et al. 2006; Thurow et al. 2006) and has therefore been suggested to be inappropriate for use in PVA modeling. 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 likely produce more accurate estimates of

persistence. But realistically, even for data sets with high observation error, PVA model results should still be considered useful in the instances where extinction probabilities are predicted to be low, since observation error can only inflate the estimated risk of extinction.

Our results suggest that for monitoring trends in adult bull trout abundance in stream settings, data collected from snorkeling short index reaches (typically 100 m in length in our study) will likely contain more sampling error than other traditional fish sampling techniques. This is not surprising considering that most fish counted during snorkel surveys are juveniles and sub-adults that are subject to higher variability because of inter-annual fluctuations in recruitment. However, 11% of the bull trout observed during snorkel surveys for the data we included in our study were ≥ 400 mm TL. Since bull trout of this length are usually considered mature (Downs et al. 2006; Muhlfeld et al. 2011), and 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), spawning adults probably comprised a similar proportion of fish observed during snorkeling as they comprised within the actual populations. For this reason, we believe that the use of snorkel data sets in viability analyses is appropriate as long as observation error is not high, or if observation error is high but projected extinction risk is low (since, as mentioned above, observation error can only bias 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 the screw traps in our study were ≥ 400 mm TL). The two types of data sets that monitored adult bull trout abundance most directly (i.e., weirs and redd counts) were usually reliable insofar as they infrequently had high observation error. Regardless of the population monitoring method, we considered all data sets estimated to have no measurable observation error to have produced the most reliable estimates of persistence.

Overestimating adult population sizes would likely have resulted in overestimating probabilities of persistence, but we believe that, if anything, our adult abundance approximations were likely underestimates for most populations we evaluated. For instance, when redds were extrapolated to estimate adult population size, we assumed that all redds produced by the population were actually counted, and all 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 within this population, 3.2 adults exist for every redd constructed, and 93% of adults are repeat spawners (Downs and Jakubowski 2006; Downs et al. 2006). Assuming these findings are applicable throughout this population, adult abundance in the Lake Pend Oreille population would be estimated to have been 6,430 fish in 2008. However, an unrelated mark-recapture study conducted in Lake Pend Oreille in 2008 produced an estimate of 12,513 bull trout ≥ 400 mm (M. Hansen, University of Wisconsin-Stevens Point, unpublished data). Since fish of this length are mostly mature in this population (Downs et al. 2006; also see Muhlfeld et al. 2011), we used that estimate for adult abundance in the present study. Even the mark-recapture estimate assumes there is no resident or fluvial component to the population. The difference between the mark-recapture estimate and redd count extrapolation suggests that some bull trout redds were missed in the Lake Pend Oreille population sampling in 2008. Similarly, redds were undoubtedly missed in the other three populations where approximations of adult population size were based entirely on redd counts extrapolations (i.e., Lower Kootenai, Coeur d'Alene Lake, and Priest Lakes populations), suggesting those abundance approximations may have been similarly underestimated.

The remaining approximations of adult population size in Table 10 were derived from estimates of abundance for bull trout ≥ 70 mm TL published in 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 made using 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 in High et al. (2005, 2008), we assumed that 10% of all bull trout ≥ 70 mm in length were adults. This assumption was deemed reasonable and possibly conservative because, as mentioned above, previous studies that used population modeling exercises to simulate metrics such as bull trout population structure and effective population size assumed that 17% of all bull trout were adults (Rieman and McIntyre 1993) or 6-13% of bull trout > 50 mm were adults (Rieman and Allendorf 2001).

We assumed that the trend data sets available within a population were unbiased representations of the true trend within that population. For most populations this assumption is tenuous, since the trend data were obtained from only a portion of the population. Nonetheless, for the five bull trout populations where multiple trend data sets were available, there was agreement between trend directions within the same population in 21 of 26 direct comparisons (Table 11). Further, many of the trend data sets were initiated to monitor species other than bull trout, such as the screw trap and snorkel data sets in the Salmon and Clearwater basins. Although these data sets contain data on all salmonids encountered, they were established to monitor salmon and steelhead trends, and it therefore seems unlikely that their use would have resulted in bull trout data that was 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 rates of change, but CIs were correct only when process noise was absent or small in relation to observation error. Since this condition fit few of our data sets, some of the statistically significant trends in Table 11 (both positive and negative) may not have been significant if the CIs were correct, or vice versa for the non-statistically significant trends. However, since the estimates of 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 to negative post-1994 estimates (5) suggests that, regardless of statistical significance, bull trout have been at least stable if not increasing since 1994 for many populations in Idaho. We considered including a more comprehensive random coefficients regression model (using PROC MIXED in SAS and following the modeling recommendations of Piepho and Ogutu 2002) to produce statewide trend estimates by time period; however, the resulting estimates (SE) of trends were 0.01 (0.03) prior to 1994, 0.08 (0.02) since 1994, and 0.07 (0.02) across all years, which are essentially identical estimates as already reported herein using the more simplistic approach of Maxell (1999).

Although this 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 this correspondence may be largely coincidental. Indeed, other sympatric native salmonids (Chinook salmon *O. tshawytscha*, steelhead trout, *O. mykiss*, mountain whitefish, and westslope cutthroat trout) and nonnative salmonids (brook trout *S. 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). The latter authors suggest that salmonids in central Idaho, including bull trout,

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 stream flow.

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 at least portions of the range of bull trout in Idaho since at least 1980 (Isaak et al. 2010, 2011), and (2) bull trout are expected to be one of the most sensitive fish species 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 we are not suggesting that continued stream warming will not at some point become measurably detrimental to bull trout, the disconnect between more than three decades of climate-induced stream warming and a positive trend in bull trout abundance for many Idaho populations over this same time period is paradoxical. This apparent inconsistency suggests that other abiotic or biotic stream conditions may currently be mitigating some negative impacts on bull trout due to climate change, at least within the range of climate alteration observed to date. For example, winter is often a stressful period of high mortality for stream-dwelling salmonids in temperate climates (reviewed in Cunjak 1996). Although predicted changes in winter ice and flow dynamics due to climate change are complex (reviewed in 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 to estimate the relative magnitude of observation error compared 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 best fit 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 long-term bull trout monitoring data sets. The finding of zero or minimal observation error for most 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 in effect in the population (and in the data), 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 are conservative because they are ascribing all the error to process noise even though in some cases some or most of it might be due to observation error.

For the data sets estimated to have zero or minimal observation error, the lack of a period or a time effect in our modeling results suggest that over the last several decades, carrying capacity has not changed for bull trout populations. 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 under-seeded with bull trout. Because bull trout have a long developmental period (Pratt 1992), filling 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 either carrying capacity or ending population size (or both) were not reliable when observation error was high.

Population persistence projections

We assumed that the population level (not the sub-population level) was the appropriate scale to apply PVA models for bull trout in Idaho because population viability is more appropriately linked to populations than to sub-populations (Ruggiero et al. 1994; McElhany et al. 2000; Theobald and Hobbs 2002). However, PVA modeling has been applied at nearly every scale imaginable, including sub-populations, populations, states, evolutionarily significant units, sub-species, and species. The scale at which population growth model projections are applied affect 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 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 are obviously not the same for Sage-Grouse and bull trout populations, the spatial scales used in these previous studies suggests that at a minimum, the scale at which we applied our analyses was probably not too large for bull trout.

Our estimated probabilities of persistence would obviously 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), setting quasi-extinction levels is essentially a subjective decision (Morris and Doak 2002) concerning how much extinction risk is considered acceptable or tolerable (Shaffer et al. 2002; Wilhere 2008). Higher values than we used, such as 100 adults, would likely translate to an effective population size of 50 for bull trout (Rieman and Allendorf 2001), above which 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 in small populations (Lande 1988), and demographic stochasticity is generally considered to be a critical factor in population viability only if a population is smaller than about 20 adults (Goodman 1987; Lande 1993; Morris and Doak 2002). Regardless of what quasi-extinction threshold is 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 serve best to highlight which bull trout populations in Idaho are more secure or more vulnerable to extirpation in the next several decades.

The probability of populations declining below quasi-extinction levels was over three times higher for data sets with high observation error than for those with zero or minimal observation error, supporting our premise that observation error would artificially inflate

extinction risk. Nevertheless, extinction risk was relatively low for most bull trout, regardless of whether the data sets had measurably high observation error or not. Our results highlight the need for better trend monitoring data sets in some bull trout populations, such as the Lemhi and Middle Fork Salmon River populations, where the only existing data has high observation error. Moreover, 13 bull trout populations have no long-term abundance monitoring data that we are aware of. Describing trends and persistence probabilities for bull trout in Idaho cannot be completed until additional abundance time series are available where they are now lacking.

We recognize that some of the assumptions we made are arguable, that some sampling methods had shortcomings, and that accurately characterizing trends and abundance for every bull trout population presents challenges considering their sparse abundance and the vast and remote landscape they occupy. We also recognize that our PVA model 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 bull trout populations in Idaho are generally at low risk of extirpation in the foreseeable future. Assuming our results pragmatically reflect persistence probabilities for the bull trout populations in Idaho where trend data were available, it is hoped that our results help focus management efforts on long-term maintenance of strong populations and those at-risk populations with the best prospects of persistence or most in need of management intervention.

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TABLES

Table 10. Description of trend monitoring data sets and estimates of adult abundance for bull trout populations in Idaho.

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

Table 11. Intrinsic rates of change for bull trout populations in Idaho. Shaded estimates indicate statistically significant trends (i.e., those that do not overlap zero). Missing estimates indicate where data were insufficient for that period of record.

Bull trout population	Data type	Intrinsic rate of change (<i>r</i>)								
		Pre-1994			Post-1994			All years		
		Esti- mate	90% CI Lower Upper		Esti- mate	90% CI Lower Upper		Esti- mate	90% CI Lower Upper	
Lower Kootenai	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	- ^a		
North Fork Clearwater	Redd count				0.18	0.13	0.23	- ^a		
Lochsa	Redd count				0.10	0.05	0.15	- ^a		
Lochsa	Snorkeling	0.25	-0.15	0.65	0.18	0.11	0.25	0.17	0.12	0.22
Lochsa	Screw trap				0.01	-0.04	0.07	0.01	-0.04	0.07
Selway	Snorkeling	0.00	-0.37	0.36	0.04	-0.02	0.10	-0.02	-0.07	0.02
South Fork Clearwater	Screw trap				0.16	0.08	0.24	- ^a		
South Fork Clearwater	Snorkeling	-0.25	-0.35	-0.15	-0.07	-0.12	-0.01	-0.11	-0.14	-0.08
Little-Lower Salmon	Snorkeling	0.05	-0.06	0.16	-0.04	-0.09	0.00	-0.01	-0.03	0.02
Little-Lower Salmon	Weir	-0.01	-0.04	0.01	0.06	0.03	0.09	0.01	0.00	0.02
South Fork Salmon	Screw trap				0.17	0.11	0.22	0.14	0.09	0.20
South Fork Salmon	Snorkeling	-0.02	-0.20	0.16	0.20	0.10	0.30	0.16	0.11	0.21
Middle Fork Salmon	Snorkeling	0.00	-0.11	0.12	-0.15	-0.23	-0.08	-0.15	-0.19	-0.12
Mid-Salmon (Chamberlain)	Snorkeling	0.05	-0.11	0.22	0.20	0.16	0.24	0.16	0.13	0.20
Lemhi	Snorkeling	-0.09	-0.28	0.10	0.05	-0.04	0.14	0.08	0.03	0.13
Upper Salmon	Snorkeling	0.11	-0.17	0.39	0.04	-0.11	0.19	0.15	0.08	0.22
Upper Salmon	Weir	0.00	-0.09	0.10	0.05	0.02	0.09	0.06	0.04	0.08
Upper Salmon	Creel				0.09	0.02	0.16	- ^a		
Upper Salmon	Screw trap				0.10	0.01	0.19	- ^a		
Anderson Ranch	Electrofishing				0.18	0.04	0.31	- ^a		
Weiser	Snorkeling				0.35	0.01	0.69	- ^a		
Little Lost	Electrofishing				-0.04	-0.09	0.02	- ^a		

^aEstimates are equivalent to post-1994 estimates due to a lack of pre-1994 data.

Table 12. Parameter estimates fitting adult bull trout abundance data sets from Idaho to the Gompertz state space model (which estimates observation error as $\hat{\tau}^2$ and process noise as $\hat{\sigma}^2$), and best-fitting population growth models with resulting model statistics. Data sets were separated by those having no observation error, minimal observation error (i.e., $\hat{\tau}^2 < 0.10$), or high observation error (i.e., $\hat{\tau}^2 \geq 0.10$).

Bull trout population	Data type	Gompertz state space model parameter estimates				Population growth model results				Ending adult population size
		$\hat{\tau}^2$	$\hat{\sigma}^2$	\hat{a}	\hat{b}	Best model	AIC		Estimated adult carrying capacity (SE)	
							r^2	w_i		
Data sets estimated to have no observation error										
Lower Kootenai	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 O'reille	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	Screw trap	0.00	0.70	2.60	-0.41	EGPE	0.00	0.67	- ^a	1,998
Lochsa	Screw trap	0.00	0.31	4.40	-0.66	Gompertz	0.32	0.38	1,511 (118)	2,170
Selway	Snorkeling	0.00	0.49	2.22	-0.76	Gompertz	0.45	0.71	181 (6)	153
Little-Lower Salmon	Snorkeling	0.00	0.22	4.98	-0.76	Gompertz	0.40	0.52	682 (19)	316
Little-Lower Salmon	Weir	0.00	0.14	2.56	-0.47	Gompertz	0.28	0.48	1,345 (53)	1,677
Upper Salmon	Creel	0.00	0.51	9.71	-1.24	Gompertz+Year	0.59	0.44	4,074 (1,440)	9,569
Data sets estimated to have minimal observation error										
Lochsa	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
South Fork Salmon	Snorkeling	0.07	0.28	0.15	-0.09	EGPE	0.00	0.43	- ^a	722
Data sets estimated to have high observation error										
North Fork Clearwater	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	Snorkeling	0.16	0.99	0.49	-0.08	Gompertz+Year	0.39	0.69	62 (154)	77
Lochsa	Snorkeling	0.47	0.21	0.67	-0.13	Gompertz+Year	0.63	0.99	1,659(1,525)	543
Middle Fork Salmon	Snorkeling	0.36	0.17	0.16	-0.04	Gompertz+Year	0.53	0.99	1,503 (17,329)	10,728
Mid-Salmon (Chamberlain)	Snorkeling	0.36	0.08	0.19	-0.03	Gompertz+Year	0.55	0.99	715 (655)	554
Lemhi	Snorkeling	0.33	0.25	1.67	-0.22	Ricker +Year	0.54	0.89	7,979 (326)	1,431
Upper Salmon	Screw trap	0.35	0.68	4.11	-0.61	Gompertz	0.37	0.47	1,815 (707)	2,218
Weiser	Snorkeling	1.22	0.26	3.89	-0.62	Gompertz+Year	0.86	0.97	121,885 (118,891)	2,399
Upper Salmon	Snorkeling	0.32	1.08	3.11	-0.45	Gompertz+Year	0.40	0.48	6,776 (3,839)	548

^aExponential growth with process error (EGPE) model does not produce an estimate of carrying capacity.

FIGURES

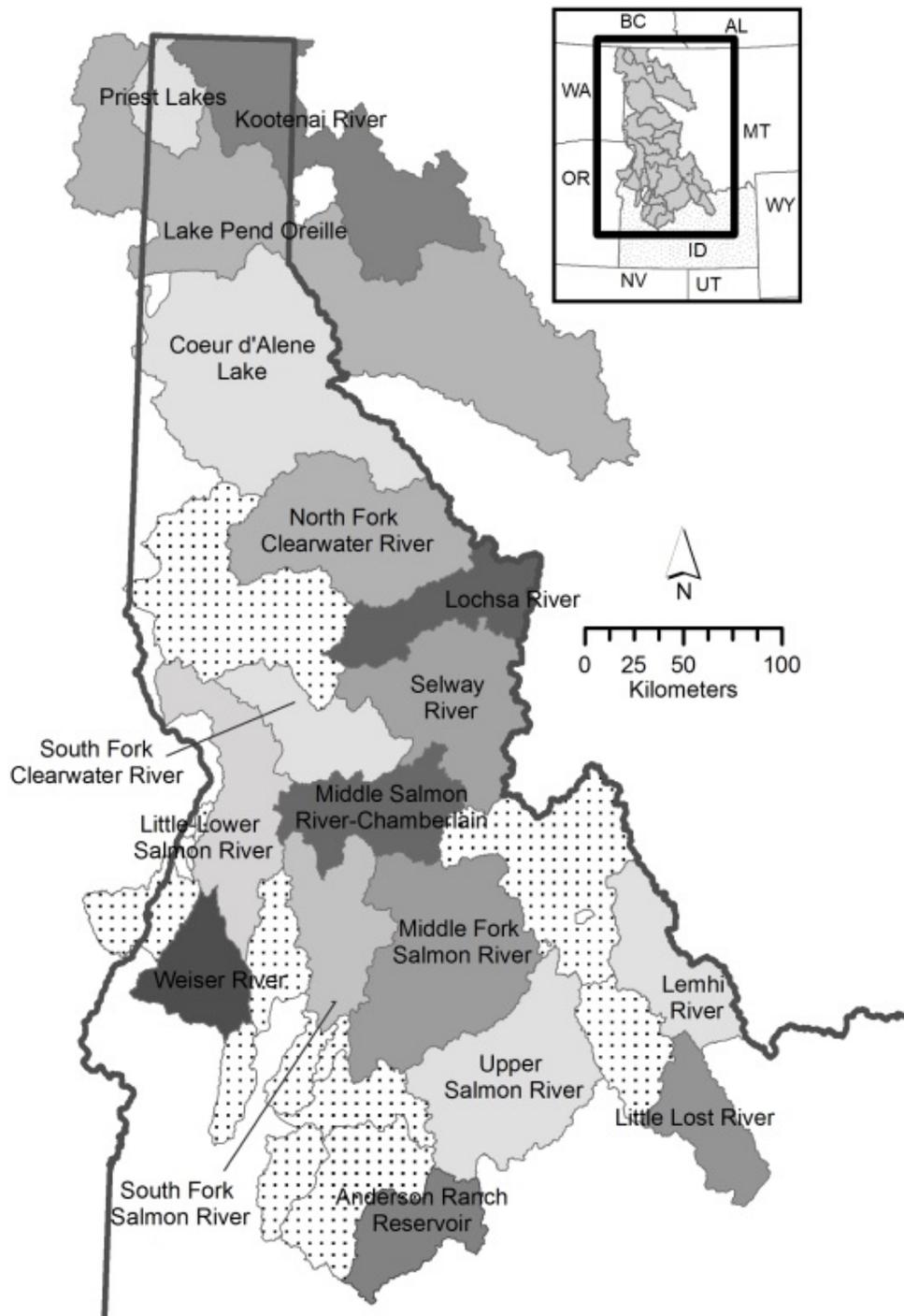


Figure 8. Study area depicting the 17 designated bull trout populations in Idaho for which trend data were available. Hatched, unlabeled populations indicate the 13 designated populations where trend data was lacking.

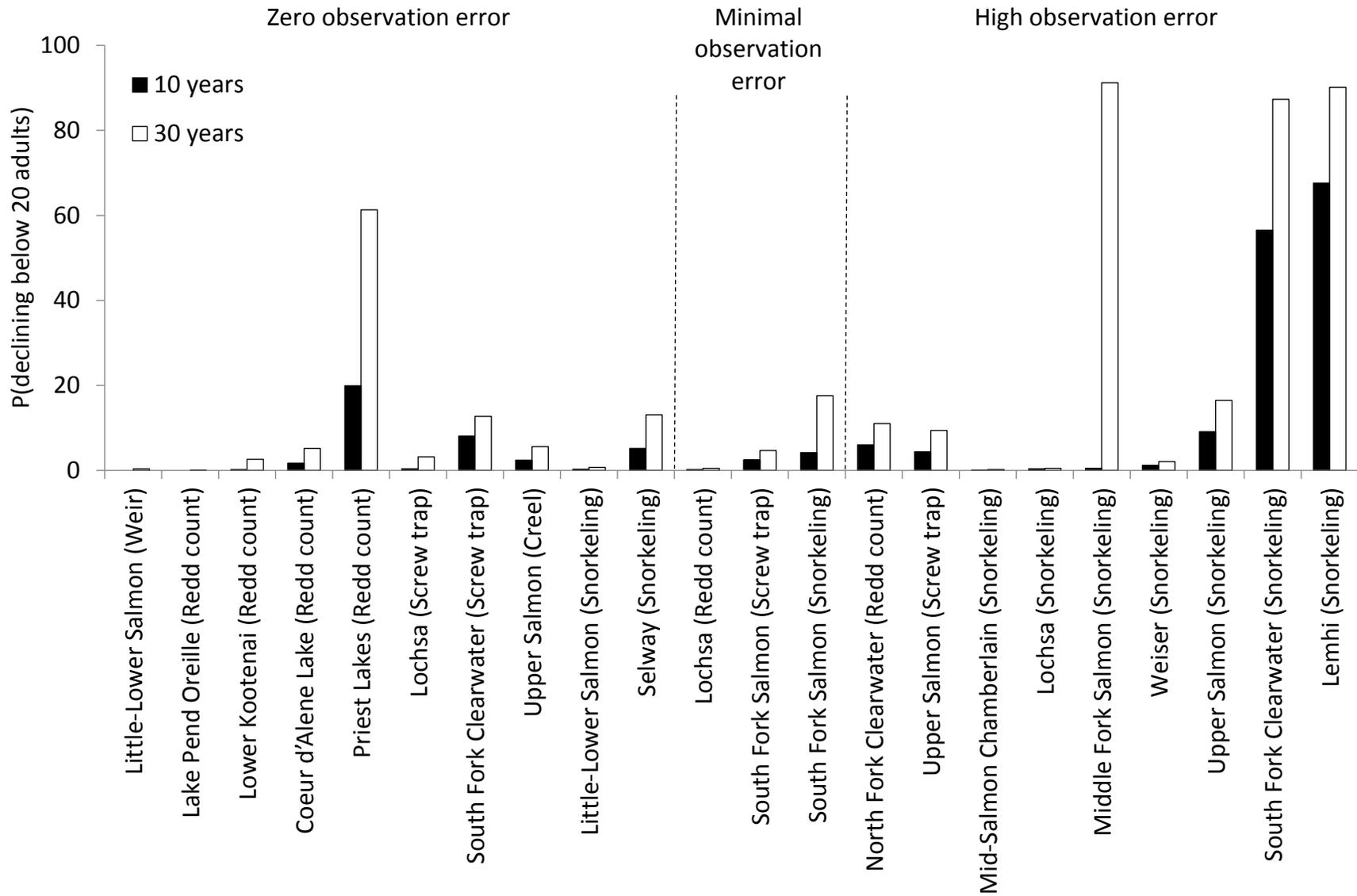


Figure 9. Estimated probability of bull trout populations in Idaho declining below 20 adults in 10 and 30 years.

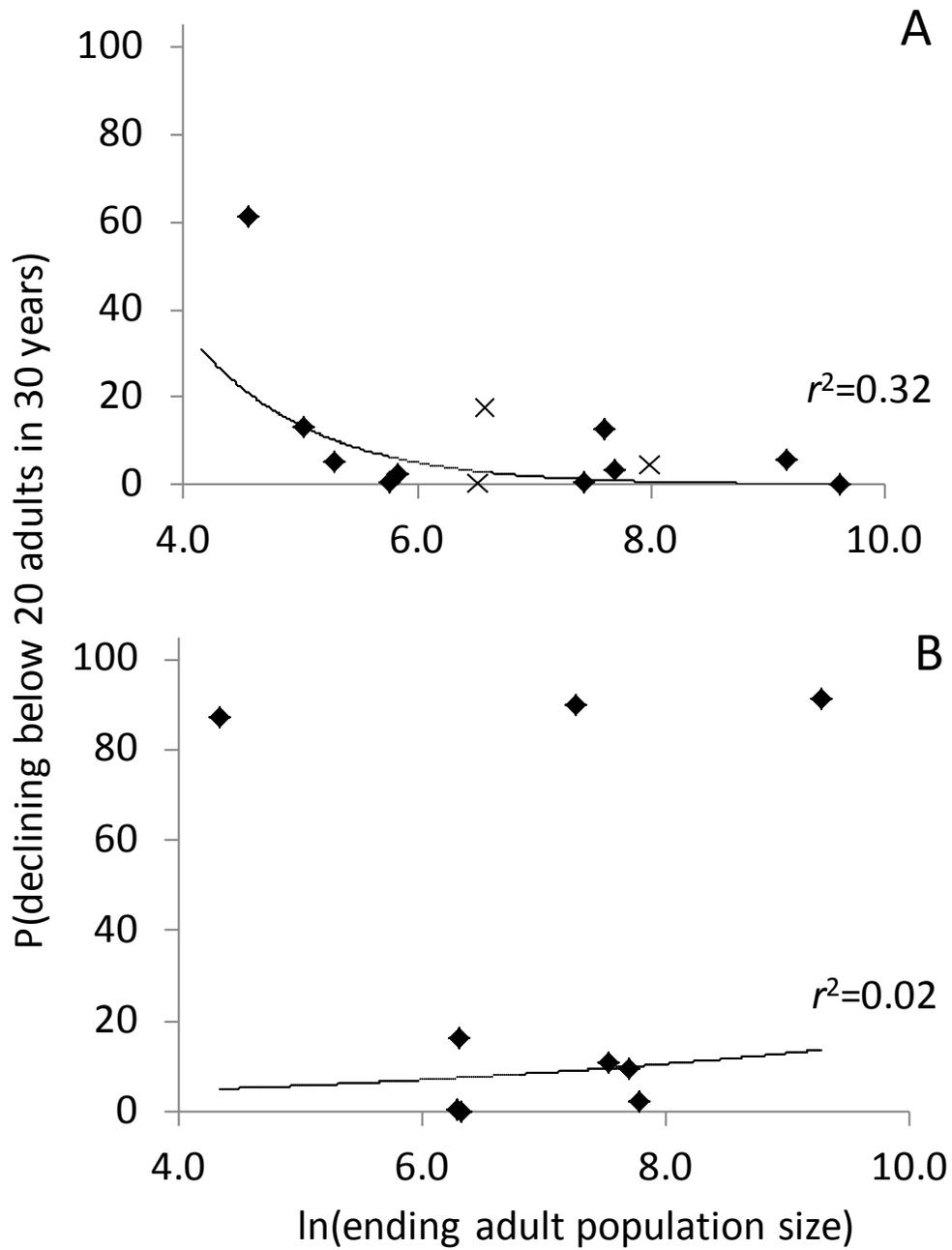


Figure 10. Relationships between ending adult population size and the risk of extirpation (i.e., the probability of declining below 20 adults in 30 years) for bull trout populations in Idaho. Upper panel (A) depicts results from trend monitoring data sets with zero (♦) and minimal (×) observation error, and lower panel (B) depicts results from data sets with high observation error. Dashed lines and coefficients of determination (r^2) depict negative exponential regression results.

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