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Kevin A. Meyer[a], Daniel J. Schill[a], Elizabeth R. J. M. Mamer[a], Christine C. Kozfkay[b] & Matthew R. Campbell[b]

[a] Idaho Department of Fish and Game, 1414 East Locust Lane, Nampa, Idaho 83686, USA

[b] Idaho Department of Fish and Game, 1800 Trout Road, Eagle, Idaho 83616, USA

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ARTICLE

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Kevin A. Meyer,* Daniel J. Schill, and Elizabeth R. J. M. Mamer
Idaho Department of Fish and Game, 1414 East Locust Lane, Nampa, Idaho 83686, USA

Christine C. Kozfkay and Matthew R. Campbell
Idaho Department of Fish and Game, 1800 Trout Road, Eagle, Idaho 83616, USA

Abstract
Redband Trout *Oncorhynchus mykiss gairdneri* are likely the most abundant and most widely distributed native salmonid in the Columbia River basin, yet their current distribution and abundance across the landscape have 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 in dry desert subbasins (49% of sites) than in montane subbasins (20%), and 25% of the dry "stream sites" had no discernible stream channel whatsoever, indicating a lack of flowing water for perhaps 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 *Salvelinus fontinalis* (128 sites), Bull Trout *Salvelinus confluentus* (37 sites), or Brown Trout *Salmo trutta* (16 sites). Redband Trout were also the most abundant species of trout, with an approximate abundance of 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 (the earliest year 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 catchable trout have been sterilized prior to stocking. Genetic results from 61 study sites suggest that hybridization with hatchery Rainbow Trout is more likely to occur in streams that were directly stocked with catchable trout 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.

The Columbia River Redband Trout *Oncorhynchus mykiss gairdneri* is a major assemblage of Rainbow Trout native to the Fraser and Columbia rivers east of the Cascade Range (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) and nonanadromous 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 (ESA), 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 about most other salmonids in the Intermountain West (Thurow et al. 1997). To help fill this information gap, we undertook an assessment of the distribution and abundance of Redband Trout in the upper Snake River basin of Idaho. For perspective, we also assessed the distribution and abundance of other native and nonnative salmonids in the study area except

*Corresponding author: kevin.meyer@idfg.idaho.gov
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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 × 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., the total number of fish stocked) are well correlated with current levels of introgression, then simple models can be used to characterize introgression at stream locations for which genetic information is lacking (e.g., Bennett et al. 2010).

Although genetic purity is obviously important, an evaluation of genetic risk is also common in status assessments. Genetic guidelines for population size typically rely on estimation of the effective population size (N_e) because it is an indication of the rate at which random genetic processes (such as genetic drift, inbreeding, and the 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 populations with $N_e \geq 500$ will likely maintain genetic diversity over the long-term (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 the most reliable data—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; McElhaney et al. 2000), compared with 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 thus 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 subbasins. 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 was used to delineate isolated Redband Trout populations within individual subbasins 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 km^2 (Figure 1). 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 their abundance. We also excluded the Burnt River, Powder River, Malheur River, and Pine Creek subbasins in Oregon, and all streams within the Shoshone-Paiute Indian Reservation, because they lie entirely outside of our management jurisdiction. In the Bruneau River subbasin, the portion of the Jarbidge River drainage in Nevada was also excluded. For the remaining subbasins along the border of Idaho, we sampled the subbasin in its entirety, including areas outside Idaho.

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 (the anadromous form of *O. mykiss*) are native to the study area but long ago were denied access to 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, measuring from the confluence of the Snake River with the Columbia River) 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 such trout began early in the last century in some streams using sub-catchable-sized fish (usually 25–100 mm 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 the poor return to creel for anglers (Meyer and Koenig 2011). Stocking of catchables increased through

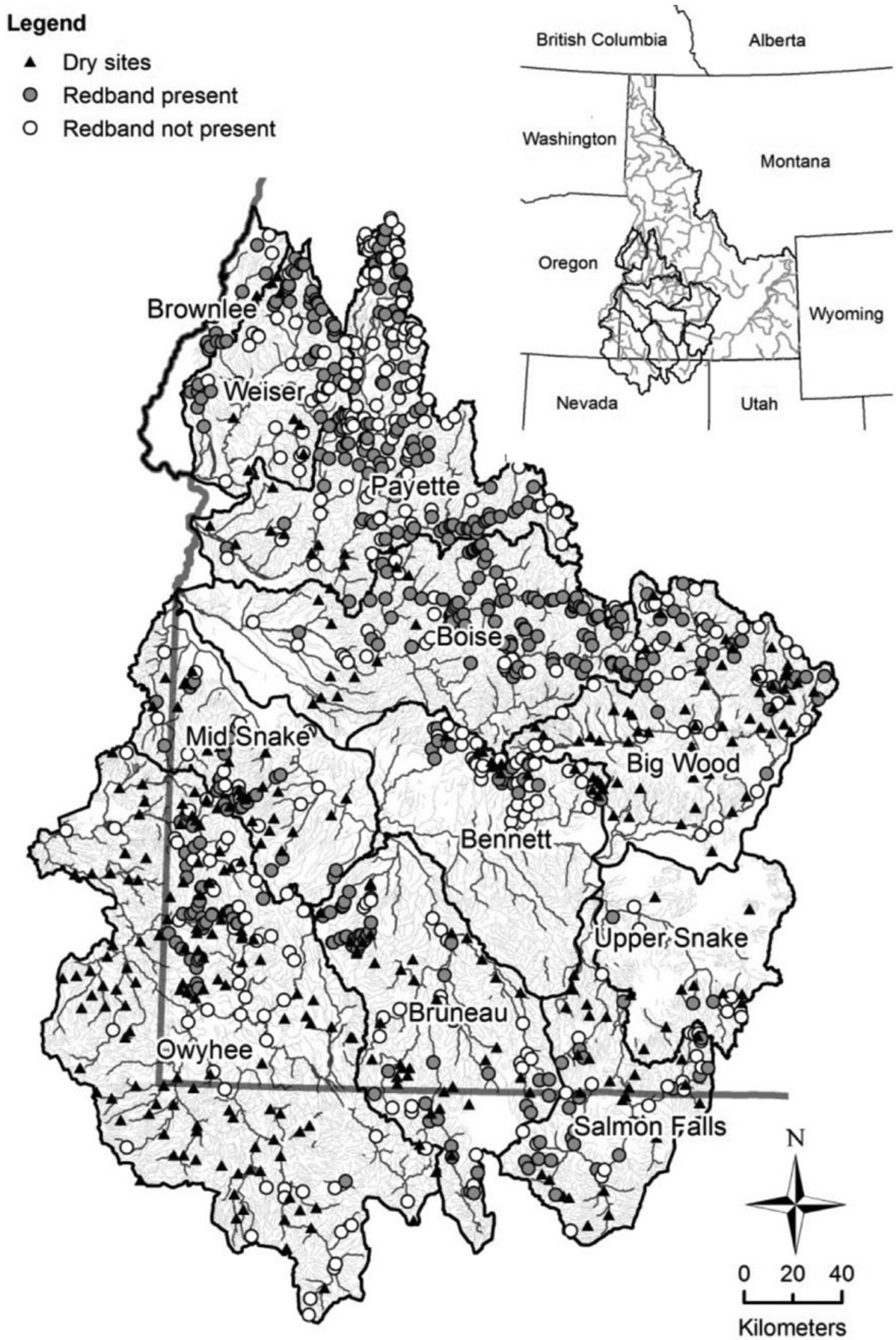

FIGURE 1. Locations and characteristics of the 1,032 study sites used for Redband Trout population assessments in subbasins of the upper Snake River basin, Idaho.

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 interact with native salmonids, since 2001 the IDFG has 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 the triploid induction rate in recent years has been 100% in all batches tested (A. Barfoot, Troutlodge, Inc., personal communication).

For several reasons, we divided our study streams into desert or montane categories by grouping all streams within the larger subbasins north of the Snake River (i.e., the Weiser, Payette, Boise, and Big Wood rivers) into the montane category and all the remaining subbasins into the desert category. First, as mentioned above, Redband Trout were petitioned for ESA listing only within the desert portion of their range in the upper Snake River basin. Second, dividing subbasins into desert and montane categories corresponds well with the 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 subbasins have higher annual precipitation; are characterized geologically by the Idaho Batholith and younger Tertiary granitic intrusions; and have upland vegetation that is a mixture of coniferous forest, sagebrush *Artemesia* spp. and mesic forbs, and streamside vegetation dominated by willows *Salix* spp. In contrast, desert subbasins have lower annual precipitation; are characterized geologically by broken plateaus, barren rocky ridges, cliffs, and deep gulches and ravines within rhyolite and basalt formations; and have 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. Thus, 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 the variance of subsequent population estimates, we sampled the likely present reaches about twice as often (in terms of the percent of total stream kilometers sampled) as the unknown reaches and about 10 times more often than the 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 sampling frequency per stream kilometer to help ensure adequate sample sizes for subpopulation abundance extrapolations within these smaller tributaries.

About 74% of the sites selected in the above sampling scheme were on public land and 26% on private land. When study site locations were completely on private property, access was requested from landowners; this was denied less than 2% of the time. Additionally, constraints such as unwadable 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 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 V, 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 millimeter, 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., <100 mm and ≥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 V, 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 d later. We assumed that 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 ≥ 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 with an average depth of < 0.7 m, 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 sightability 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/m^2) for comparison with other studies.

Abundance extrapolation.—For each distribution stratum (i.e., likely present, unknown, or likely absent), we estimated total trout abundance separately by stream order. With ArcGIS software we summed the total length of the 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 ($\overline{y}_i$) 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):

$$N_{\text{census}} = \sum_{i=1}^{L} N_i \overline{y}_i .$$

For variance of N_{census} we used the formula

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

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 subbasin. Using the above formulas, we calculated 90% confidence intervals (CIs) around total abundance estimates by subbasin. 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 subbasins but were only present at 2% of the likely absent sites outside these subbasins. Because Redband Trout (and all other trout) were indeed virtually absent from these likely absent stream kilometers outside the Boise, Payette, and Weiser subbasins, the values for the remaining subbasins were considered numerically insignificant and consequently the estimates of occupancy and abundance in the likely absent category were not extrapolated except for the Boise, Payette, and Weiser subbasins.

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 subbasin. 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 (McElhaney 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 with 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-size Redband Trout (N_{adult}) residing in subbasins and populations within subbasins were estimated following an approach described in more detail by Meyer et al. (2006a).

TABLE 1. 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.

		Logistic regression coefficients				
Desert or montane	Sex	Constant	Total length (m)	Stream 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. A. Meyer, unpublished data
Montane	Female	−5.933	0.067	−1.765	0.59	Meyer, unpublished data

Briefly, 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 subbasins and 53% and 59% across the montane subbasins (Table 1). Based on the logistic regression coefficients in Table 1, Redband Trout size at maturity in first- to fifth-order streams varied from 122 to 215 mm TL in desert subbasins and from 122 to 227 mm in montane subbasins, depending on stream order.

At each study site, the length frequency of captured Redband Trout was compared with 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 that the overall sex ratio was 50:50 (Schill et al. 2010) and divided Redband Trout abundance by 2 to account for both sexes. Estimates of N_{adult} at each site were then extrapolated for each subbasin and population using the formulas above and the same approach as Meyer et al. (2006a).

To approximate N_e, we assumed that the ratio 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 endpoint of the 90% CI of N_{adult} by the lower ratio and the upper endpoint 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, 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 that 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, 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-size 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 with the stocking of catchable trout only as well as with all hatchery Rainbow Trout combined (including catchables, fry, and fingerlings).

We summed the total number of Rainbow Trout and the number of catchable-size 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 transformed the data on the independent variable (i.e., $\log_e$[number of fish stocked + 1]) because it was highly skewed. We used Akaike's information criterion (AIC) to judge the strengths of the 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 streams at the 1:100,000 scale. The stream network included 39,364 km (65% of all stream kilometers) of first-order streams, 10,569 km (17%) of second-order streams, and 5,357 km (9%) of third-order streams, with the remaining 6,113 km (10%) of streams being fourth through seventh order (Figure 2).

A total of 1,032 study sites were surveyed for trout occupancy and abundance (Table 2; Figure 1). 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 in montane subbasins (20%). Our sampling framework resulted in 0.2% of the entire stream network being sampled (Table 2).

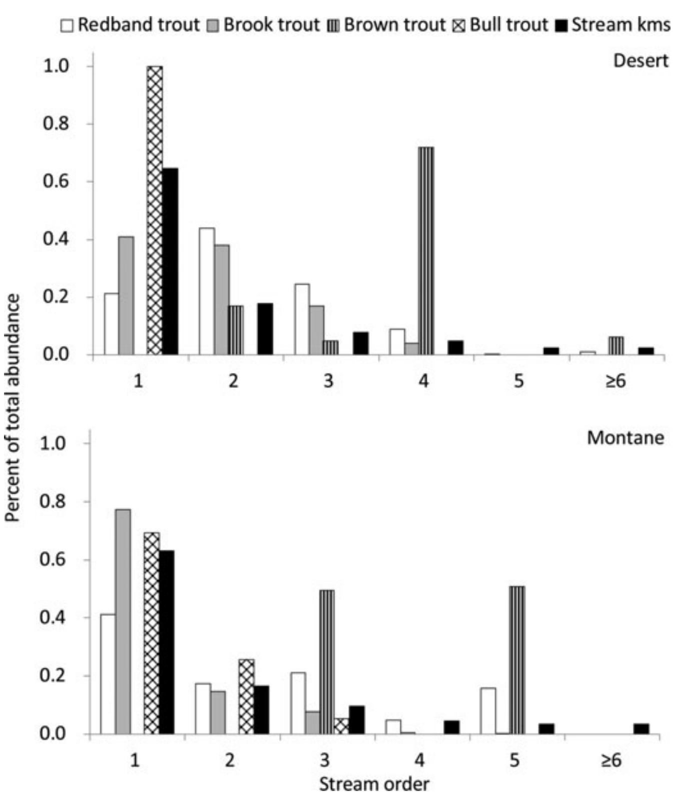

FIGURE 2. Proportions of trout species abundance and stream kilometers by stream order in desert and montane streams of the upper Snake River basin, Idaho.

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 subbasins. Outside these three subbasins, 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 streams in the study area, with a much higher rate of occupancy in montane subbasins (39% of all stream kilometers) than in desert subbasins (11%).

Redband Trout were the most abundant salmonid in the upper Snake River basin, with approximately 3,450,000 ± 402,000 of all sizes (90% confidence interval about the mean; Table 3). Brook Trout were the next most abundant at approximately 1,501,000 ± 330,000, followed by Bull Trout at 159,000 ± 118,000 and Brown Trout at 43,000 ± 25,000. Redband Trout were captured in all subbasins, Brook Trout were present in 8 of 12 subbasins, and Brown Trout and Bull Trout were captured in 4 and 3 subbasins, respectively. Ninety-nine percent of the total abundance of Brook Trout occurred in the four montane subbasins.

We identified 46 individual populations of Redband Trout in the upper Snake River basin, including 26 desert populations and 20 montane populations (Table 4). The average total population size was about 35,000 and 140,000 for individual desert and montane populations, respectively. Estimates of individual populations were mostly complete, in that (1) they summed to 85% of the total abundance for all subbasins 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 2). 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.

The mean abundance of all trout (both size-classes) at all sites combined (including dry and troutless sites) was 0.07 fish/m^2, whereas for Redband Trout alone the mean abundance was 0.06 fish/ m^2 (Figure 3). Fish <100 mm and ≥100 mm made up 46% and 54%, respectively, of the abundance for

TABLE 2. Stream network and distributional extent of Redband Trout in subbasins of the upper Snake River basin, Idaho.

Variable	Bennett Mountain	Big Wood	Boise	Brownlee	Bruneau[a]	Mid-Snake	Owyhee[b]	Payette	Salmon Falls	Upper Snake	Weiser	Total
Desert or montane subbasin	Desert	Montane	Montane	Desert	Desert	Desert	Desert	Montane	Desert	Desert	Montane	
Total estimated km ranked a priori as likely present	169	654	2,061	217	788	237	734	1,833	591	126	249	7,660
Total estimated km ranked a priori as unknown	501	2,829	894	42	700	497	2,228	785	601	320	671	10,068
Total estimated km ranked a priori as likely absent	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 Rainbow Trout	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 Rainbow Trout	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 Rainbow Trout	0	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 subbasin 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

[a]Excludes the Jarbidge River drainage in Nevada.
[b]Excludes the Duck Valley Indian Reservation.

Redband Trout, compared with 48% and 52% for all trout. Trout density (all species and sites combined) was equivalent in montane subbasins (mean = 0.07 fish/m^2) and desert subbasins (0.07 fish/m^2) but only because the higher percentage of dry sites in desert subbasins 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/m^2) than in montane streams (0.14 fish/ m^2). Considering only sites that contained Redband Trout, the density of Redband Trout was over twice as high in desert streams (mean = 0.21 fish/m^2) than in montane streams (0.10 fish/m^2).

TABLE 3. Abundance (N_{census}) and 90% confidence limits (CLs) of Redband Trout and other trout species in the upper Snake River basin, Idaho; NA = not available.

			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	
Subbasin	Desert or montane	Sample code[a]	N_{census}	±90%CLs	N_{census}	±90%CLs	N_{census}	±90%CLs	N_{census}	±90%CLs	N_{census}	±90%CLs	N_{census}	±90%CLs	N_{census}	±90%CLs	N_{census}	±90%CLs
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								
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	NA			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	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		

[a]LP is likely present, UK is unknown, and LA is likely absent; see Methods for further description.
[b]Excludes the Jarbidge River drainage in Nevada.
[c]Excludes the Duck Valley Indian Reservation.

TABLE 4. Estimated total abundance (N_{census}), number of adults (N_{adult}), and effective population size (N_e) for individual populations of Redband Trout in the upper Snake River basin, Idaho. The proportion of kilometers (km) included in the estimates is an indication of how complete each estimate is.

				Redband Trout abundance			Proportion of km included in estimates by sample code		
Desert/montane	Subbasin	Population[a]	n	N_{census}	N_{adult}	N_e	Likely present	Unknown	Likely absent[b]
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 tributaries	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			

[a] EF = East Fork, NF = North Fork.
[b] Estimates applied only to Boise, Payette, and Weiser subbasins (see Methods).

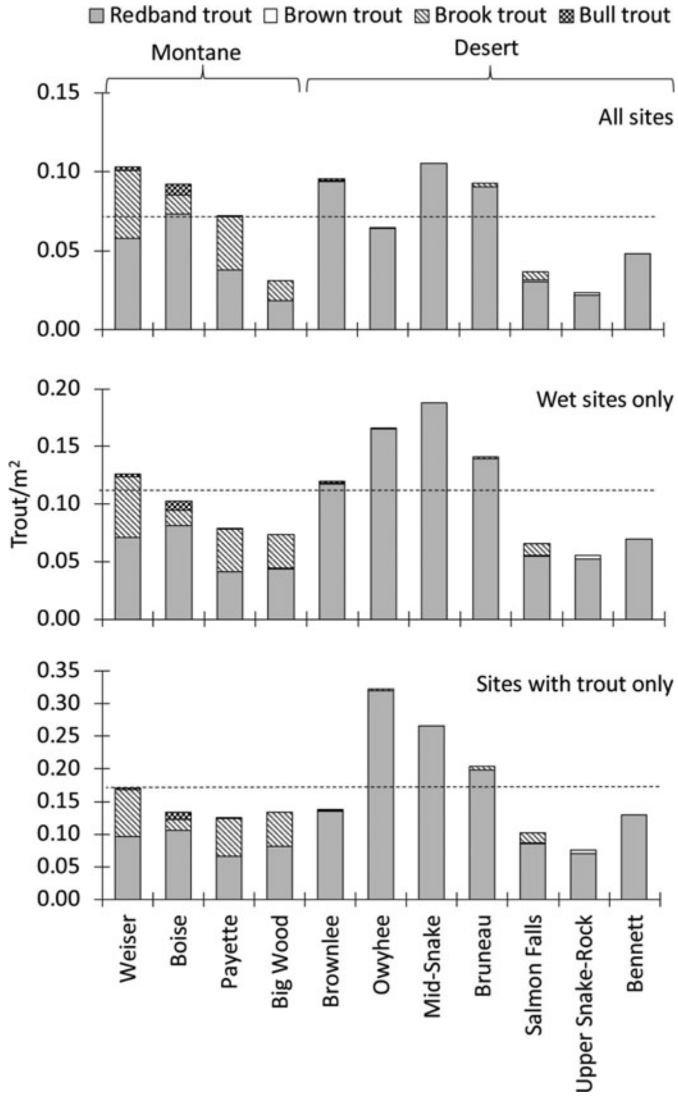

FIGURE 3. Mean densities of trout species in desert and montane subbasins of the upper Snake River basin, Idaho. The dashed lines indicate the mean abundance.

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-size adults (Table 5), which was 25% of all Redband Trout and 42% of those ≥100 mm TL. Within the 46 individual populations of Redband Trout, the value of N_e for desert populations averaged about 5,100 per population, compared with about 15,600 per population for montane populations (Table 4). Effective population size was estimated to be <50 for only 3 populations.

Introgression with Hatchery Rainbow Trout

Based on the IDFG's historical and current fish stocking databases, a total of 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 in 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 $\chi^2 = 15.2$, df = 1, $P < 0.0001$; Figure 4), explained 36% of the variation in the presence or absence of Redband Trout introgression at a particular location, and correctly classified the 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 with 68.6 for catchables alone). Based on the 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 of 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

TABLE 5. Estimated total number of adults (N_{adult}) with 90% confidence limits (CLs) for Redband Trout in each subbasin of the upper Snake River basin, Idaho.

Subbasin	Estimate	± 90% CLs
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

[a]Excludes the Jarbidge River drainage in Nevada.
[b]Excludes the Duck Valley Indian Reservation.

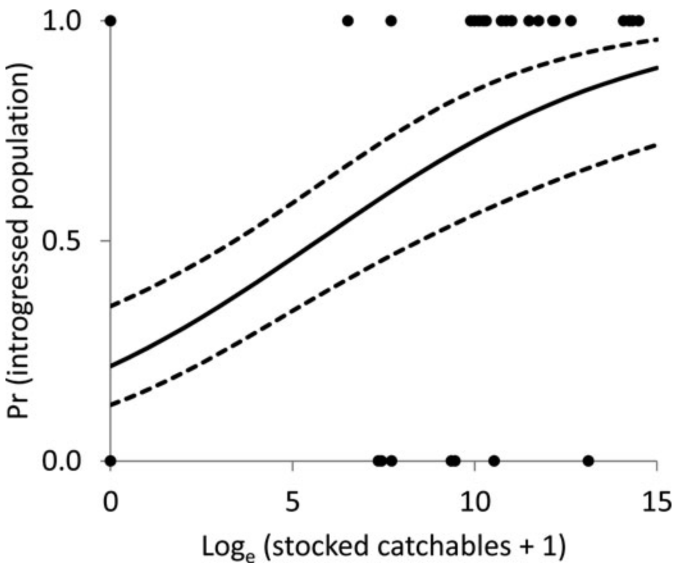

FIGURE 4. Logistic regression relationship (solid asymptotic line) between the number of catchable Rainbow Trout stocked in a stream (log$_e$ transformed data) and whether the Redband Trout in the stream were introgressed. The dotted asymptotic lines indicate the 90% confidence interval for the relationship.

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 streams, or 68% of the estimated 13,485 km that 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 (McElhaney 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 nonnative salmonids. Data sets on trends in Redband Trout abundance are generally lacking across the basin, although Redband Trout appear to be relatively stable in those desert streams for which temporal data sets are available (Zoellick et al. 2005). Although Brook Trout are the next most abundant species 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 subbasins. Montane subbasins 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 subbasins than in desert subbasins. 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 subbasins, compared with only 60% in the montane subbasins, suggesting that the long-term threat posed by nonnative salmonids is much lower in desert subbasins.

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 2), indicating a concentration in these intermediate-sized streams. In contrast, Brook and Bull trout were concentrated in headwater streams, with Brown Trout being 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.

The mean densities of trout in our study, although taken from randomly distributed sites, are difficult to compare directly with those of other studies because we sampled stream reaches that were likely to have trout at a much higher rate than stream reaches that we felt would not have trout. Thus, our estimates of mean trout abundance are higher than if we had sampled stream reaches completely at random. Nevertheless, the mean abundances reported in our study are similar to those reported by the few other randomly sampled extrapolation efforts undertaken for stream salmonids in the Intermountain West. For example, the mean density in this study for all trout at all sites (including dry and fishless locations) was 0.07 fish/m^2, similar to the estimate of 0.06 fish/m^2 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/m^2 for trout in 39 streams within the Intermountain West. For only those sites that contained Redband Trout in the present study, the mean density of Redband Trout $\geq$ 100 mm in desert streams of southwestern Idaho was 0.12 fish/m^2, similar to a mean of 0.18 fish/m^2 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 lewisii, this resulted in 35% more stream kilometers at the 1:24,000 scale than at the 1:100,000 scale (Shepard et al. 2005). Another source of negative bias was the use of removal electrofishing with backpack shockers as the primary sampling technique. Over the last several decades, this method of population estimation has consistently been shown to underestimate the true population abundance of stream-dwelling salmonids and other fish species (e.g., Junge and Libosvarsky 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 the stream abundance of trout (Thurow and Schill 1996; Thurow 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 total trout abundance across the entire study area likely exceeds the estimates 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 subbasins, 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 1.0, 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 m 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 are negatively biased, but only to a minimal degree.

The higher density of Redband Trout that 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 sampled more often 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 subbasins, most notably that study sites in desert subbasins (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 nonnative salmonids. Stream habitat conditions also differ between desert and montane streams in terms of such metrics 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 subbasins than in montane subbasins, 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 bouvierii* 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 2 to 3 years of age, similar to the 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 nonanadromous salmonid populations, our approximations of N_e for Redband Trout populations were higher than the ranges reported for resident Yellowstone Cutthroat Trout populations in southeastern Idaho (Meyer et al. 2006a). This discrepancy is due in part to the 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 to the smaller lengths of stream occupied by 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 the population boundary delineations were reasonably accurate in this study, the current genetic risk in terms of inbreeding or genetic drift for most Redband Trout populations in the upper Snake River basin is 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 subbasin), which are known to be reproductively isolated and therefore at greatest risk, are likely to be the strongest estimates of N_e.

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 analysis were too distant from each other and limited in sample size for 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 is a more reliable estimate 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 nonnative 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 that 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).

In the Big Wood River subbasin, no pure Redband Trout populations were found. The Big Wood River, near its confluence with the Snake River, flows over a 20-m 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 subbasin (the Wood River Sculpin *Cottus leiopomus*), and seven other fish species present in other nearby subbasins are absent from the Big Wood River subbasin (Simpson and Wallace 1982). Based on this evidence, we suggest that Redband Trout may not be native to the Big Wood River subbasin. Further genetic samples collected throughout the subbasin may help confirm or refute this assertion.

There was a strong correlation between the number of fry and fingerlings and 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 United States (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 to identify populations with greater than 10% admixture, a threshold supported in other studies detecting intraspecific 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 versus 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.

CONCLUSION

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. The knowledge gained from this study required sampling only 0.2% of the entire stream network, yet such sampling produced population abundance estimates with 90% CIs within 50% of the estimate for many of the subbasins 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, so any temporal variability inherent in the 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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