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[Article]

Landscape-Level Sampling for Status Review of Great Basin Redband Trout

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Abstract.—In response to a petition to list Great Basin redband trout (subspecies of rainbow trout *Oncorhynchus mykiss*) as threatened or endangered, the U.S. Fish and Wildlife Service conducted a status review in 1998. To support that review, we conducted a survey of the abundances of redband trout in each of six subbasins of the Great Basin that included the states of Oregon, California, and Nevada. We used a generalized random-tessellation stratified algorithm to select a target sample size of 35 sites/subbasin. Out of a target number of 210 sites, 185 were visited by three-person crews that surveyed stream habitat and estimated the abundance of fish populations in sample reaches with lengths that were nearly 20 times the respective channel widths. A minimal sampling intensity was based on previously encountered levels of between-site variance in estimates of redband trout abundance. The total population estimate of age-1 and older (age-1+) redband trout in the Great Basin was 971,313 fish, with a 95% confidence interval equaling ±15% of the mean estimate; 95% confidence limits ranged from 15% to 31% for population estimates in individual subbasins. Age-1+ fish abundance in terms of numerical density showed no significant differences between any subbasins. However, there were significant differences in terms of biomass: Catlow Valley subbasin biomass was significantly higher than the Great Basin mean, whereas Goose Lake subbasin biomass was significantly lower than the basinwide mean. These comparisons were supported by like differences in average weight. Analysis of stream habitat characteristics and fish abundance revealed no relationships that were generally consistent throughout the Great Basin, although spatial patterns were evident within some stream systems where sampling intensity was sufficiently high.

Redband trout (subspecies of rainbow trout *Oncorhynchus mykiss*) occur in inland drainages of the Pacific Northwest, USA. Currens (1997; 2007) suggests that separate groups of redband trout evolved in large river systems, such as the Columbia, Klamath, and Sacramento rivers. Great Basin populations of redband trout (Figure 1) occur in basin-and-range geology and persist in fragmented habitats that are peripheral to and isolated from riverine core groups; these populations probably constitute unique evolutionary lineages. Redband trout populations connected to perennial lake systems have evolved adfluvial life histories. Such populations may have adaptations to unique habitats, and their importance as units of conservation could likely equal or exceed that of large riverine core populations (Li et al. 1995; 2007).

Great Basin populations of redband trout are found in arid forest and desert environments characterized by extreme fluctuations in streamflow and temperature. Information collected after droughts in 1992 and 1994 suggested that some populations exhibited depressed abundance. A 1997 Endangered Species Act (ESA) petition to list Great Basin redband trout as a threatened or endangered species prompted a population status review by the U.S. Fish and Wildlife Service (USFWS) in 1998. Redband trout have little commercial value and historically have supported only a small sport fishery. Hence, they have attracted less attention from managers, they have not been well researched, and their status has been less adequately documented compared with other salmonids in the Pacific Northwest. Although the distribution of Great Basin redband trout was generally known (Flitcroft and Dambacher 1999), particularly lacking were reliable estimates of population abundance and an understanding of critical habitat. The objective of this study was to help fill these information gaps.

Methods

Although population estimates of fishes throughout entire stream systems have effectively been carried out

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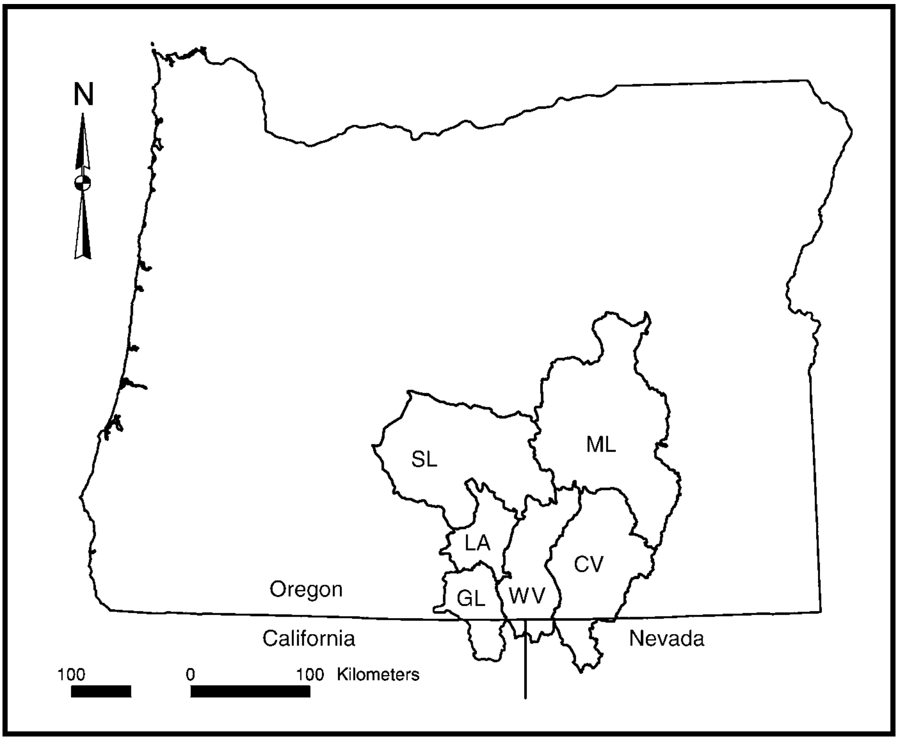

FIGURE 1.—Map of Oregon, showing six subbasins that contain Great Basin redband trout: Silver Lake (SL), Lake Abert (LA), Goose Lake (GL), Warner Valley (WV), Catlow Valley (CV), and Malheur Lakes (ML). Extension of several subbasins into California and Nevada is also shown.

by systematic random sampling of habitat units (Hankin and Reeves 1988), this technique requires a complete a priori census of stream habitat in a basin to maximize survey efficiency. Where this is impractical, as in a landscape-level survey across many basins (e.g., this study), an alternative design is needed that provides a representative sample of sites at which fish densities and habitat characteristics are measured. Basin- and landscape-wide estimates are then inferred from the sample by application of the site inclusion probabilities. Although independent random sampling (IRS) and systematic sampling are two techniques that can provide representative samples, both have disadvantages when applied to natural resources (e.g., stream networks), as discussed by Stevens and Olsen (2004). As an alternative, Stevens and Olsen (2004) describe a spatially balanced site selection process that incorporates the advantages of IRS and systematic sampling, yet overcomes their disadvantages. The generalized random-tessellation stratified (GRTS) design has many features appropriate for sampling stream networks, including a capability for variable probability of site selection (e.g., we wanted to allocate an even number of sites to each of six subbasins across which the inhabited stream length differed), allowance for replacement of sites if the sites in the original sample could not be visited (e.g., site access denied), and post stratification of the sample (e.g., for investigating whether densities of redband trout differ between portions of the stream network that cross different land uses or geology).

Sample site selection.—The target stream population for this study was based on the known distribution of stream-resident Great Basin redband trout in Oregon, Nevada, and California, as documented by Flitcroft and Dambacher (1999; Figure 2). The goal was to estimate the numbers of age-1 and older (age-1+) redband trout in each of six subbasins (Silver Lake, Abert Lake, Goose Lake, Warner Valley, Catlow Valley, and Malheur Lakes) with a 95% confidence level that was within ±50% of the estimate. A minimal sampling intensity of 35 sites/subbasin was chosen (hence, 210 sites for the entire Great Basin) based on previously encountered levels of between-site variance in abundance estimates of age-1+ Great Basin redband trout (coefficients of variation as high as 150%; Oregon Department of Fish and Wildlife [ODFW], unpublished data). The U.S. Geological Survey's (USGS)

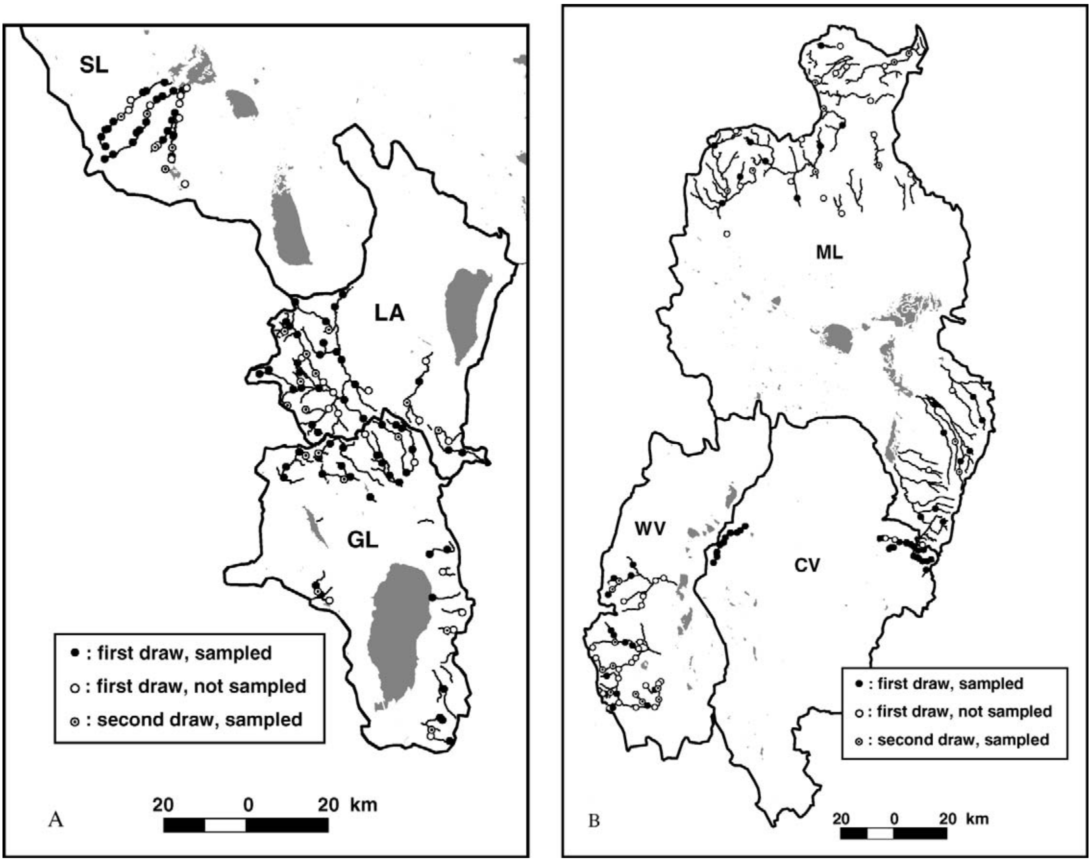

FIGURE 2.—Sites selected from first and second sample draws and sampled within the documented distribution of stream-resident Great Basin redband trout in **(a)** Silver Lake (SL), Lake Abert (LA), and Goose Lake (GL) subbasins; and **(b)** Warner Valley (WV), Catlow Valley (CV), and Malheur Lakes (ML) subbasins. Lakes and wetlands are denoted by shaded regions.

1:100,000-scale digital representation of the Great Basin stream network was used as the "frame" from which the GRTS algorithm selected sample sites and was used to calculate stream distances. A first sample draw of 35 sites (base sample) in each of the six basins was selected, along with a second draw of another 35 sites (oversample) to be used, if necessary, for replacing base sample sites that could not be visited. Initial weights assigned to each site were determined as the ratio of the stream length in the basin divided by the sample size. Weights were modified as required if the final and initial samples differed: for example, if the actual sample size were 30 or if the actual target stream network were smaller than represented in the frame, as from dry channels.

Replacement sites can be chosen in two ways. The second sample draw is structured as an ordered block of sites that retains the spatial balance of the first sample draw (Stevens and Olsen 2004). A disadvantage of this process is the possible introduction of bias resulting from, for example, the replacement of sites on private land (that might be differentially denied access and that might differ in condition) with sites on public land. A challenge for the field crews was that they did not know the number of sites to which access would be denied over the course of the survey season; hence, the crews were unable to determine whether they needed to sample the whole block to maintain spatial balance. It was logistically efficient to select a replacement site by following a second procedure, which involved selecting a site from the oversample that most closely matched the characteristics of the omitted site. We generally used this second approach, selecting sites from the oversample that were similar in location, size, elevation, and ownership to those of the base sample sites that were not visited; this was done both to preserve the spatial balance (by selecting nearby sites) and to avoid introduction of possible bias. To facilitate attainment of access to privately owned lands, we sought the support of our research objectives by the County Commissioners for Lake and Harney counties, Oregon. Their signatures and endorsements were included in access request letters that were mailed to all owners of private lands for sites in the base sample and oversample.

Sample site reference points were located in the field by use of hand-held Global Positioning System (GPS) units. Due to error in the electronic base maps and random error of GPS units, reference point locations could be as much as 100 m from the actual stream channel, and therefore the nearest portion of stream channel was chosen as an adjusted reference point for each sample site. Stream sample areas were 20 or more times the active channel width and were enclosed by block nets (6-mm mesh) set in fast-water habitat units. Care was taken to avoid scaring or herding fish in or out of the sample area during site selection and placement of block nets.

Fish population estimates.—Removal-depletion estimates (Zippin 1958) were made using backpack electroshockers in wadeable streams and a raft-mounted electroshocker in channels that were too deep to wade. After two removal passes, the decision to cease sampling or proceed with an additional sampling pass was made based on the criterion of having attained at least a 50% reduction in age-1+ redband trout between successive passes. While this criterion targeted only numbers of captured age-1+ redband trout, equal effort was made to collect age-0 redband trout and all other species. Each sampling pass started at the downstream block net and proceeded systematically upstream. Anode probes were activated in discrete sections of the channel so as not to herd fish by pushing activated probes through the sample area. Stunned fish were collected by dip nets and held in buckets of stream water. Upon reaching the upstream block net, the pass was continued back towards the lower block net with approximately one-fourth of the upstream effort but this time by sweeping a continuously activated probe downstream so as to herd fish into the lower block net. These two separate efforts constituted a single pass. Captured fish were identified by species and apparent age-class, their lengths were measured to the nearest millimeter, and weights were recorded to the nearest 0.1 g. Length-frequency analysis was later used to categorize redband trout as either age 0 or age 1+. Separate age-class designations were made in each of the six subbasins. These designations were putative and were not corroborated by scale or otolith analysis. Population estimates of other species were made without distinction of size or age.

Habitat assessment.—Stream habitat of sample sites was characterized by 27 variables at the basin, reach, and habitat-unit levels (Table A.1). In general, descriptions were recorded for channel dimension, streambed composition, amount of large woody debris, and riparian characteristics according to ODFW stream survey protocols (Moore et al. 1997). Stream habitat was surveyed within the sample site and upstream to a distance that included 30 habitat units, which analyses of previous surveys have shown to provide a robust characterization of habitat at a reach level (ODFW, unpublished data). Habitat variables that describe fish habitat capacity (e.g., wetted area, depth, volume, and cover) were summarized only for the habitat units that were within the channel sampled for fish population estimates (Table A.1). Additional reach- and watershed-level variables were obtained from geographical information system analyses of digital line graphs and elevation models.

Stream water temperature was measured by grab samples at each sample site. However, since these measurements were made from morning to late afternoon hours and from the months of June to September, they could not be used to typify the stream temperature experienced by the sampled fish population. Due to the large spatial extent of the sites targeted in this study and due to budget constraints, which limited the number of field crew members and the number of times each site was visited, it was not possible to obtain more robust samples of stream temperature. Elevation and distance from watershed divide for each site were treated as potential surrogates for stream temperature. Also, conductivity (total dissolved solids [TDS]) of stream water was to be measured at each site; however, frequent malfunction of meters precluded inclusion of this variable in the multivariate analyses described below.

Data analysis.—Fish population estimates were made by extrapolating average number of fish per meter in sample sites to total length of stream channel occupied in each subbasin. Uncertainty in population estimates arises from two sources. A minor component of variance comes from the relative precision of the field sampling method (here, electroshocking removal-depletion estimates within sampled units), while the dominant source of variance typically arises from extrapolating a subsample (of size n units) to the entire stratum (of size N total units). This latter source is minimized when a population is distributed evenly among sampled units or when the sample size is relatively large (i.e., when n approaches N). Variance can be estimated using the routine sum-of-squares calculation typical of IRS schemes (Horvitz and Thompson 1952); however, for spatially balanced designs like the GRTS design, the IRS variance estimator yields a biased (high) estimate of variance, where the magnitude of bias is a function of the spatial pattern in the data (i.e., uneven spatial distribution among sample units). A local neighborhood (NBH) estimator that Stevens and Olsen (2003) describe yields unbiased estimates of variance. Compared with IRS schemes, a GRTS sample design coupled with the NBH variance estimator takes advantage of any spatial patterns in the distribution of a species, thereby yielding comparatively lower variance. We used both methods to estimate 95% confidence intervals (CIs) for population estimates, in part to highlight the benefit of the GRTS design and NBH analytical procedures. Both methods are available as part of the R package, spsurvey (available: www.epa.gov/nheer/arm).

Bartlett's test (Snedecor and Cochran 1989) was used to test for homogeneity of variance in measures of fish abundance. Log-transformed abundance measures of redband trout were compared among subbasins using both parametric analysis of means (Ott 1983; Ramig 1983) and a Kruskal–Wallis test (Zar 1996) for a nonparametric analysis of ranked medians. Habitat variables for each site were standardized by division of each site datum by the sum of all sites (Milligan and Cooper 1988).

Habitat and abundance relationships were analyzed by multiple linear regression using both raw and standardized data. For linear regression analysis, we first conducted a principal components analysis (PCA) to reduce the suite of habitat variables (Table A.1) to a few that represented the major sources of variation at the basin, reach, and habitat-unit levels and to reduce the number of variables in the regression analysis. The first three principal component axes explained 57% to 67% of the variation in habitat. In the regression models, the number of potential explanatory variables was limited to a ratio of no more than 1 variable : 10 sample sites. Thus, in the six subbasins, we selected the most heavily weighted variable from each of the first three component axes (i.e., 3 variables/subbasin). In this selection process, we desired to include both macro- and meso-scale variables in each subbasin model. This was achieved by the three most heavily weighted variables in all subbasin models except that for Silver Lake, which lacked a meso-scale variable. For this subbasin model, gradient was included as an additional fourth variable, as it was a meso-scale variable and had the next highest weighting. For the Great Basin model, seven habitat variables were selected from the first five principal component axes. Log(density, g/m^2) of age-1+ fish had the highest correlation to habitat variables of any abundance measure and was used as the dependent variable for all regression analyses.

Results

Access, Map Accuracy, and Potential for Sample Bias

Fish population and stream habitat data were collected by survey crews that visited 185 sample sites out of an adjusted total of 205 target sites (Table 1; Figure 2). In the Malheur Lakes subbasin, main-stem habitat that was misidentified as being within the year-round distribution of redband trout was reclassified as migration corridor. This resulted in five sites being dropped from the initial target of 210 sites and an adjustment to the distribution distance within the Malheur Lakes subbasin.

Forty-one sites were selected from the oversample as replacements for lack of access or errors in the distribution map. Access was denied to about half of the 90 private land sites in the base sample. Ten headwater sites were either dry or outside of the distribution of redband trout. These sites were dropped from the survey and replaced with sites from the oversample. We presumed that the likelihood of errors around the headwater distribution limit would vary equally both upstream and downstream, and therefore we did not adjust the map distribution distance of redband trout in subbasins where these sites occurred.

We used a ratio of sites visited from the base sample relative to the target sample to describe our ability to sample the target sites in a spatially balanced fashion (Table 1). We did not assume that the sites were "missing at random" because most of the denied sites were on private land. Access to private lands was particularly difficult to obtain in the Warner Valley subbasin, and there were insufficient replacement sites available such that sampling was done in only 24 of 35 target sites (Table 1). The sampling denial was most severe in this subbasin (0.60) because access to sites was refused over large contiguous blocks of land in the lower portions of the subbasin (Figure 2b). In contrast, Catlow Valley had few access issues (0.06). Since the Malheur Lakes subbasin had both the majority (52%) of stream habitat and a high denial rate (0.36), lack of access could have influenced the final abundance measures for this subbasin and for the Great Basin. To account for the differences in site visitation rates and average fish densities on private and public lands, we poststratified the basins by land ownership and adjusted the site weights to represent land management (public or private) according to prevalence within each basin. Because of refused access, we generally sampled proportionately fewer sites on private lands, which tended to have lower densities of redband trout. Uncertainty would be higher in the private lands

TABLE 1.—Distance (km) of known Great Basin redband trout stream distribution, as calculated from a 1:100,000-scale digital line graph map; sample draws (first, second, and total) of 205 sites visited by field crews for sampling in summer 1999; average sample site length and width; and percentage of total stream length sampled in fish population estimates. There were 35 sites targeted in each subbasin, except as noted for the Malheur Lakes basin.

Subbasin	Distribution		Sites visited from sample draws				Mean sample site		Percent of stream distance sampled
	Distance (km)	Percent of total	First	Second	Total	$B{:}T$[a]	Length (m)	Width (m)	
Silver Lake	97	4	25	5	30	0.28	82	4.3	3.0
Lake Abert	314	15	26	9	35	0.26	72	4.2	0.8
Goose Lake	303	14	28	7	35	0.20	71	2.8	0.8
Warner Valley	269	12	14	10	24	0.60	92	4.1	0.8
Catlow Valley	69	3	33	0	33	0.06	78	2.7	4.0
Malheur Lakes	1,115	52	18	10	28[b]	0.40	92	3.7	0.2
Total	2,167		144	41	185	0.36[c]	80	3.6	0.7

[a] $B{:}T$ is the ratio of base sample to target sample = 1 − (number of first-draw sites visited/number targeted).
[b] Main-stem habitat withdrawn from known distribution map resulted in the exclusion of five sample sites, leaving an adjusted target of 30 sites for the Malheur Lakes subbasin.
[c] Weighted to percent of total stream distance within each subbasin.

because of the lower sample size, but the actual estimates in each subbasin and the Great Basin are probably accurate.

Relative Sampling Intensity

The length of stream sampled for fish population estimates at each site averaged 80 m, which was roughly 20 times the wetted channel width (Table 1). Initial survey protocol called for a stream sample length that was 30 times the active channel width. This was relaxed at the discretion of field crews so that on average, two sites could be visited per day; this decision, however, was bounded by the criterion that there be at least two pool–riffle sequences within each sampled site. Overall, 0.7% of the total stream distribution of Great Basin redband trout was sampled in this study (Table 1). The greatest sampling intensity occurred in the Silver Lake and Catlow Valley subbasins, where 2% and 4% of the stream length, respectively, were sampled.

Population Estimates and Associated Error

The population estimate for age-1+ Great Basin redband trout was about 970,000 fish, with a 95% CI that was ±15% of the estimate (using the NBH variance estimator; Table 2). Population estimates for age-1+ fish in individual subbasins ranged from about 57,000 fish (95% CI = ±13%) in the Silver Lake subbasin to 435,000 fish (95% CI = ±29%) in the Malheur Lakes subbasin. The population of age-0 fish was roughly two-thirds that of the age-1+ population, with confidence limits (CLs) that were consistently greater (up to four times greater in some subbasins).

Compared with the IRS variance estimator, the use of the GRTS design with the NBH variance estimator yielded substantially lower variance estimates for both age-0 and age-1+ fish populations (Tables 2, 3). Comparing 95% CLs derived from each variance estimator and expressed as a percentage of the population estimate, there was a relatively large difference for age-1+ fish but less of a difference for

TABLE 2.—Population estimate for age-1 and older (age-1+) Great Basin redband trout, with 95% confidence limits (CLs; expressed as percent of estimate), coefficient of variation (CV, %) for density estimates among sample sites, field sampling error (expressed as percent of total variance), and average catchability p (with CV) from electroshocking removal-depletion estimates. Confidence limits were calculated from independent random sampling (IRS) and neighborhood (NBH) based estimates of variance.

Subbasin	Age-1+ population estimate	95% CL		CV (%) of density (fish/m)	Field sampling error (% of total IRS variance)	Average p (CV, %)
		IRS (%)	NBH (%)			
Silver Lake	57,270	27	13	73	1.0	0.76 (17)
Lake Abert	149,103	42	30	124	0.3	0.84 (15)
Goose Lake	98,409	31	26	93	6.0	0.81 (20)
Warner Valley	171,715	36	28	76	1.0	0.80 (19)
Catlow Valley	59,771	34	14	95	0.1	0.85 (14)
Malheur Lakes	435,045	44	29	115	0.3	0.81 (21)
Total	971,313	22	15	92	0.6	0.81 (17)

TABLE 3.—Population estimate for age-0 Great Basin redband trout, with 95% confidence limits (CLs; expressed as percent of estimate), coefficient of variation (CV, %) for density estimates among sample sites, field sampling error (expressed as percent of total variance), and average catchability *p* (with CV) from electroshocking removal-depletion estimates. Confidence limits were calculated from independent random sampling (IRS) and neighborhood (NBH) based estimates of variance.

Subbasin	Age-0 population estimate	95% CL		CV (%) of density (fish/m)	Field sampling error (% of IRS variance)	Average *p* (CV, %)
		IRS (%)	NBH (%)			
Silver Lake	26,075	69	56	203	0.7	0.73 (34)
Lake Abert	27,508	63	54	212	0.05	0.90 (20)
Goose Lake	48,867	66	55	202	0.08	0.78 (31)
Warner Valley	51,406	71	53	141	2.0	0.75 (36)
Catlow Valley	25,431	60	40	169	0.05	0.85 (20)
Malheur Lakes	440,002	58	49	140	0.003	0.79 (19)
Total	619,286	42	35	190	0.03	0.81 (25)

age-0 fish. The 95% CLs for age-1+ fish in Catlow Valley had the greatest difference of any subbasin (IRS-based CL = 34%; NBH-based CL = 14%; proportional difference between CLs = 0.59); the next-largest difference was for Silver Lake (IRS-based CL = 27%; NBH-based CL = 13%; proportional difference = 0.52). Goose Lake had the least difference in 95% CLs for age-1+ fish (proportional difference = 0.16). The 95% CLs for the total Great Basin estimate of age-1+ fish were 22% for the IRS estimator and 15% for the NBH estimator (proportional difference = 0.32). By comparison, the 95% CLs for age-0 fish were much less affected by the NBH estimator, with proportional differences for the two estimators ranging from 0.33 (Catlow Valley) to 0.14 (Lake Abert) in the subbasins and an overall proportional difference of 0.17. The differences in 95% CLs generated by the IRS- and NBH-based variance estimators represent the degree of spatial pattern in the data (Stevens and Olsen 2003). Thus, the larger differences in 95% CLs for age-1+ fish than for age-0 fish indicate that the younger age-class was more evenly distributed.

Redband trout population estimates for each subbasin were inferred from the fish densities estimated at each of the surveyed sites. The coefficient of variation for densities of age-1+ fish among sites in each subbasin ranged between 73% and 124% and averaged 92% among all subbasins combined (Table 2). The coefficient of variation for age-0 densities was roughly twice that of age-1+ fish density (Table 3). Stemming from this variation, the greatest source of uncertainty in population estimates came from the site-to-site variance. Field sampling error from removal-depletion estimates constituted, on average, less than 1% and was at most 6% (Tables 2, 3). The catchability (*p*) of both age-classes of redband trout averaged 0.81 but was generally more variable for age-0 fish than for age-1+ fish (as measured in terms of the coefficient of variation of *p*; Tables 2, 3).

Potential and Observed Impact of Sampling

Approximately 6,900 age-1+ redband trout and 2,700 age-0 redband trout were captured and handled in this study (Table 4), corresponding to less than 1% of the total estimate for the Great Basin. The percentage of fish captured and handled were on average 92% of the age-0 fish and 97% of the age-1+ fish estimated at each sample site. In terms of the total

TABLE 4.—Potential and observed effects of sampling on age-0 and age-1 and older (age-1+) Great Basin redband trout from the summer 1999 population survey.

Subbasin	Number of fish handled (% of population estimate[a])		Observed sampling mortality (% of estimate)	
	Age 0	Age 1+	Age 0	Age 1+
Silver Lake	454 (2.0)	1,280 (2.0)	38 (0.1)	22 (0.04)
Lake Abert	234 (0.9)	1,031 (0.7)	3 (0.01)	5 (0.003)
Goose Lake	318 (0.7)	771 (0.8)	5 (0.01)	12 (0.01)
Warner Valley	298 (0.6)	1,328 (0.8)	30 (0.06)	30 (0.02)
Catlow Valley	657 (3.0)	1,624 (3.0)	37 (0.1)	69 (0.1)
Malheur Lakes	817 (0.2)	927 (0.2)	4 (0.001)	3 (0.001)
Total	2,778 (0.4)	6,961 (0.7)	117 (0.02)	141 (0.02)

[a] Fish captured and handled constituted, on average, 92% of the age-0 fish and 97% of the age-1+ fish estimated at each sample site.

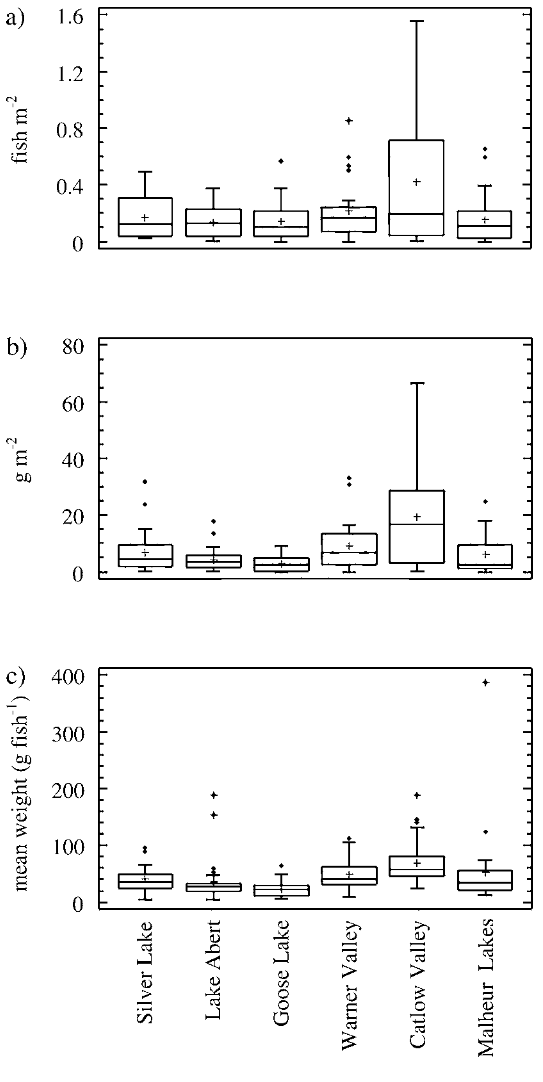

FIGURE 3.—Box-and-whisker plots describing age-1 and older Great Basin redband trout in each of six subbasins in terms of log-transformed **(a)** numerical density (fish/m^2), **(b)** biomass (g/m^2), and **(c)** average weight (g/fish). Each box encloses the middle 50% of data, the horizontal line represents the median, and the plus symbol inside the box represents the subbasin mean. Upper and lower whiskers extend 1.5 interquartile ranges from each edge of the box. Points beyond whiskers and within 3.0 interquartile ranges are denoted by diamond symbols; those beyond 3.0 interquartile ranges are represented by plus symbols.

population in individual subbasins, however, handled fish were an exceedingly small proportion and ranged between 0.2% in the largest subbasin (Malheur Lakes) and 3.0% in the smallest subbasin (Catlow Valley). During the course of sampling, 177 age-0 fish and 141 age-1+ fish (0.02% of the total population) were observed as mortalities (Table 4), and their deaths were attributed to stress or injury from capture and handling.

Typically, there were few or no mortalities recorded at a sample site, but on a number of occasions—in Silver Lake, Warner Valley, and Catlow Valley specifically—a large number of fish deaths occurred at single sample sites. These instances were caused by the capture of large numbers of fish that exceeded the capacity for safe storage in buckets. In retrospect, this could easily have been avoided by dividing the sample unit into smaller subsections so that smaller lots of fish were handled—this was done elsewhere when it was suspected that large-sized sites might also have high fish abundance. A large number of mortalities that occurred at a single site in Catlow Valley represented the worst case as this subbasin had the smallest of any estimated population. However, the total observed mortality in proportion to the total Catlow Valley population estimate was less than 0.2%. In the context of the stream system in which it happened (Home Creek), it constituted less than 0.5% of the total stream population.

Relative Abundance and Weight of Age-1 and Older Redband Trout

Examination of box-and-whisker plots of raw data for abundance and weight of age-1+ redband trout (Figure 3) show that in general, most of the six subbasins had similar mean, median, and lower quartile values for numerical density (fish/m^2) and biomass (g/m^2). Catlow Valley, however, stood out as having a relatively high abundance of age-1+ fish. Moreover, Catlow Valley sites had a high average weight per fish, although a few sites in the Lake Abert and Malheur Lakes subbasins exceeded the upper range from Catlow Valley.

Variances deviated significantly ($P \ll 0.001$) from homogeneity for all measures of abundance and average weight of age-1+ fish across the six subbasins. Raw measures of abundance and weight in all subbasins were skewed towards higher values (Figure 3), and data were log transformed for the analysis-of-means tests (Figure 4). This was only partially successful in achieving normal distributions because for each measure of abundance or weight, there were still two or three subbasin groups that remained skewed. In addition, there were unequal variances in the log-transformed data for numerical density (fish/m^2). Neither of these departures from analysis of variance (ANOVA) assumptions are thought to be severe when sample numbers are as large and as even as those used herein (Sokal and Rohlf 1995); we nevertheless chose to complement the analysis-of-

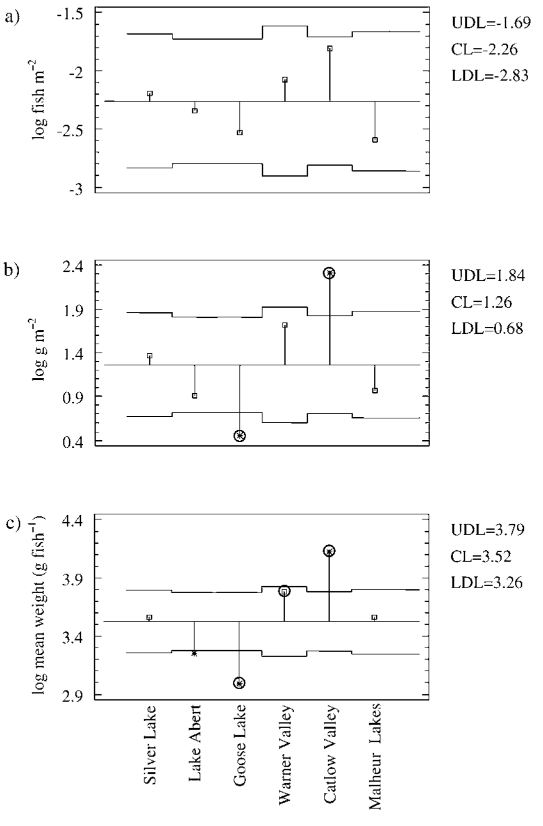

FIGURE 4.—Parametric analysis-of-means plots comparing subbasin values of log-transformed **(a)** numerical density (fish/m^2), **(b)** biomass (g/m^2), and **(c)** average weight (g/fish) of age-1 and older Great Basin redband trout. Subbasin means are represented by open squares unless significantly different ($\alpha = 0.05$) from the grand mean (denoted by the centerline [CL]), in which case they are represented by asterisks falling outside of the upper decision limit (UDL) and lower decision limit (LDL). Group differences supported by corresponding nonparametric tests (nonoverlapping 95% confidence interval of group medians) are circled.

means comparisons with a nonparametric test for differences among group medians.

Analysis-of-means plots (Figure 4) depicting log-transformed numeric density of age-1+ redband trout show that none of the subbasin values were significantly different ($\alpha = 0.05$) from the mean of the entire Great Basin. This result is supported by a Kruskal–Wallis test that found no significant ($P = 0.24$) difference among any of the group medians. There were, however, significant differences in average biomass of redband trout. Biomass in the Catlow Valley was significantly higher than the Great Basin mean, and biomass in Goose Lake was significantly lower than the basinwide mean; these differences were supported by both parametric and nonparametric tests (Figure 4). Similarly, the weight of age-1+ fish was significantly higher in Catlow Valley and lower in Goose Lake, with the significance of these differences also being supported by both parametric and nonparametric tests. Conversely, the significance of the difference in age-1+ fish weights was supported only by the parametric test for Lake Abert and only by the nonparametric test for Warner Valley (Figure 4).

Interquartile and median values for redband trout abundance measures were separately developed for age-1+ fish (Table 5) and age-0 fish (Table 6). Each measure was adjusted by the relative sample weight of each subbasin to be representative of the entire Great Basin.

TABLE 5.—Interquartile (25% and 75%) and median (50%) values of age-1 and older (age-1+) Great Basin redband trout density, biomass, and average weight from summer 1999 stream population surveys. Values were adjusted by relative sample weights between each of six subbasins (Figure 1).

Variable	25%	50%	75%
Density (fish/m)	0.11	0.27	0.71
Density (fish/m^2)	0.036	0.12	0.22
Biomass (g/m)	2.4	7.5	21.4
Biomass (g/m^2)	1.3	3.0	8.7
Mean weight (g/fish)	21.6	31.3	54.7

Multivariate Analysis of Abundance and Habitat Relationships

Although we sought a general habitat-based model that could account for the observed variation in the abundance of redband trout throughout the entire Great Basin, no convincing relationships were forthcoming from our analysis. We used PCA to select 12 variables for regression modeling at the Great Basin scale. The first five principal component axes accounted for 54% of the habitat variation. Variables representing each of the first five axes were regressed against log(biomass) of age-1+ redband trout, and even though the model produced a significant relationship ($P < 0.03$) it

TABLE 6.—Interquartile (25% and 75%) and median (50%) values of age-0 Great Basin redband trout density, biomass, and average weight from summer 1999 stream population surveys. Values were adjusted by relative sample weights between each of six subbasins (Figure 1).

Variable	25%	50%	75%
Density (fish/m)	0.0	0.05	0.35
Density (fish/m^2)	0.0	0.02	0.14
Biomass (g/m)	0.0	0.2	0.8
Biomass (g/m^2)	0.0	0.1	0.3
Mean weight (g/fish)	1.5	2.1	3.1

TABLE 7.—Multiple linear regression models (β_0 = intercept constant; β_i = partial regression coefficient) of stream habitat variables associated with log(biomass, g/m^2) of age-1 and older redband trout in the entire Great Basin and in each of six subbasins. All coefficients (habitat variables) listed below were significant ($P < 0.05$) within the linear models. Entries of "ns" indicate variables that were entered in the regression but were not significant ($P > 0.05$), with the exception of two Great Basin variables marked with asterisks (gradient: positive and significant at $P = 0.08$; riparian width: positive and significant at $P = 0.06$).

Variable	Great Basin	Silver Lake	Lake Abert	Goose Lake	Warner Valley	Catlow Valley	Malheur Lakes
Model *P*-value	0.03	0.23	0.06	0.019	0.86	0.019	0.004
Adjusted R^2	8.3	20.1	21.3	33.3	3.6	28.6	40.1
Model parameters							
β_0	0.74	0.36	0.41	0.35	0.84	0.81	ns
β_i							
Distance from divide						ns	
Gradient	ns*	ns	ns	0.18	ns		
Wetted width	ns			ns	ns		
Riparian width	ns*		ns				
Shade						ns	
Scour pool depth		ns					
Large wood pieces	ns						
Percent fines		ns					0.011
Percent gravel	ns						
Percent boulder		ns	ns				0.016
Percent undercut	ns			ns	ns	0.014	ns
Percent erosion	ns						

explained only 8% of between-site variation (Table 7). No individual variables were significant ($P < 0.05$) at the scale of the Great Basin, although higher levels of biomass were associated with increasing gradient ($P = 0.08$) and riparian width ($P = 0.06$). We also conducted PCA at the subbasin scale. The first three principal components accounted for 58–67% of the habitat variation in the six subbasins. Separate regression models for individual subbasins were significant for three of the six subbasins and explained limited variation in biomass (4–40%). Variables that were significant were boulders, fines, percent undercut, and gradient, and these were correlated with other variables of similar PCA loadings.

Spatial Patterns of Abundance

While we found no general model to describe variation in abundance among the Great Basin sites based on physical habitat variables, spatial patterns of abundance were evident within individual stream systems and subbasins (Figure 5). In the Silver Lake basin, the biomass of age-1+ redband trout generally increased in a downstream direction. In the Catlow Valley subbasin, Rock Creek (the only stream on the west side of the basin) had the highest biomass values recorded for any of the sample sites visited, while streams on the east side of the basin (Home, Three Mile, and Skull creeks) generally had low to moderate biomass of age-1+ redband trout. The strong spatial patterns of abundance for Catlow Valley and Silver Lake are also evident in the relatively large reduction in 95% CIs for these subbasins, as reported above. All streams in the Catlow Valley subbasin are dominated by spring flow, but Rock Creek in particular has significant contributions from thermal springs and consequently has high conductivity (TDS = 151 ppm in sites below springs, as opposed to TDS < 73 ppm in sites upstream or in other Catlow Valley streams). Higher biomass in Catlow Valley streams was positively and significantly associated with undercut banks and riparian width. The regression analysis showed a significant positive association with undercut banks ($P = 0.0022$). The PCA showed that riparian width and undercut were equally highly weighted on the same PCA axis. We choose to use undercut from that axis in the regression analysis.

Spatial patterns in the abundance of age-1+ redband trout were evident within streams and between adjacent streams in the Catlow Valley and Silver Lake subbasins, but these interpretations were made possible by relatively high sampling intensities (i.e., >2% of stream length sampled; Table 1). In the other four basins, sampling intensity was comparatively low (<1% of stream length), but patterns emerged in the Goose Lake and Malheur Lakes subbasins. In the Goose Lake subbasin, the regression model accounted for 33% of the variation. Gradient had a significant and positive association with age-1+ fish biomass (Table 7); shade, boulders, and large wood were weighted positively on the same component axis, suggesting that forested streams with large wood and boulders higher in the watershed supported higher biomass. Spatial patterns at the subbasin level, however, were evident in the Malheur Lakes subbasin, which had the lowest sampling intensity of any subbasin in this study (0.23% of stream length). Higher abundances in the Malheur

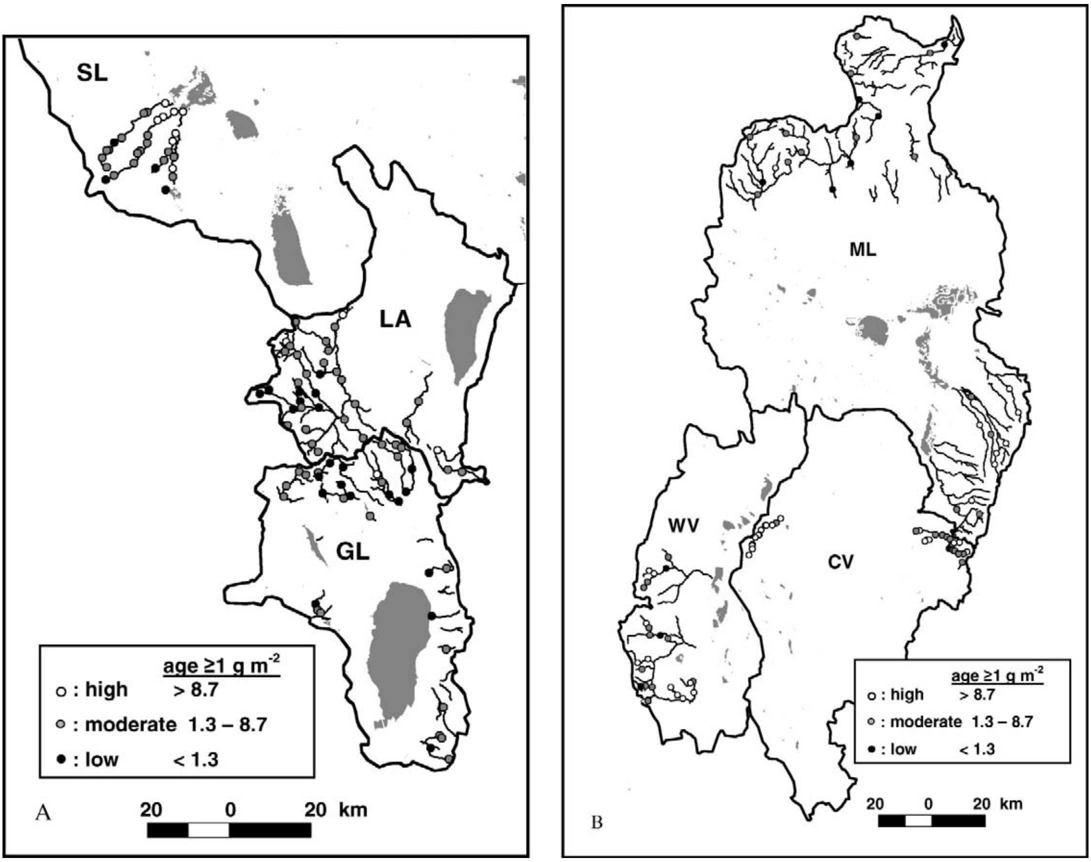

FIGURE 5.—Biomass (g/m^2) of age-1 and older Great Basin redband trout during summer 1999 sampling at sites in the **(a)** Silver Lake (SL), Lake Abert (LA), and Goose Lake (GL) subbasins; and **(b)** Warner Valley (WV), Catlow Valley (CV), and Malheur Lakes (ML) subbasins. Lakes and wetlands are denoted by shaded regions.

Lakes subbasin were associated with low-gradient sites with fine sediments and boulders, reflecting patterns from north to south. Sites in the northern half of the Malheur Lakes subbasin generally had a lower biomass of age-1+ fish than sites in the southern half. These differences can be reasonably associated with regional differences in geology. Streams in the southern half of the subbasin originate in the Steens Mountains, which drain high-elevation slopes composed of parent material (principally basalt and andesite) that is less friable (thus, produces more boulders) than that in the lower-lying northern half of the subbasin (parent material is principally silicic ash-flow tuff). The PCA axis with boulders also was positively associated with width (i.e., wide, boulder-strewn sites). The axis associated with fines was negatively associated with gradient and positively associated with distance to the watershed divide (i.e., lower-gradient, lower-basin sites with higher fines).

Discussion

Relatively precise estimates of population size for Great Basin redband trout were obtained in each of the six subbasins (Tables 2, 3), with minimal impact either to local populations or to the total population (Table 4). This precision was obtained because we (1) accurately anticipated the average between-site variation in densities of redband trout; (2) set a minimal, yet sufficient, sampling intensity that was within the means of limited labor resources; and (3) used a survey design that maximized the value of each site. This study demonstrates the usefulness and effectiveness of the GRTS sampling design for population estimates of stream fishes at the basin and landscape scales. Employing the GRTS algorithm with the NBH variance estimator reduced the variance, sometimes significantly, over that obtained by using the IRS estimation method. This reduction was possible by virtue of the GRTS and NBH methods being able to take advantage of spatial patterns in fish abundance wherever they occurred across Great Basin streams. This lowered our sampling effort and allowed us to meet goals for relatively precise abundance estimates in all six subbasins.

The variable probability sampling design proved to be ideally suited to meet the needs of a rapid status review for an ESA listing decision. The USFWS 12-month petition finding of "not warranted" was based primarily on the results of this study (USFWS 2000; A. Bentivoglio and R. Rhew, USFWS, Portland, Oregon, personal communication). Moreover, a decision by the main petitioner to not appeal this finding was based directly on the perceived credibility of this study's results (A. J. Belsky, Oregon Natural Desert Association, Bend, personal communication).

A common concern with electrofishing sampling in streams is its harmful effects on fish through injury and mortality (Snyder 2004), especially for small or remnant populations that are endangered (Nielsen 1998). Where the status of a species is uncertain and of concern, there is a tradeoff between the need to determine its status, which indirectly might lead to improved protection and rehabilitation, and the need to avoid directly diminishing the species' viability through sampling-induced injuries and mortalities. When applying a sampling design where the distribution of a species is relatively well known, it is possible to determine the potential impact of sampling a priori. In this study, we were able to justify electrofishing sampling in terms of a likely minimal effect, which was subsequently supported by the results presented in Table 4.

Although this study presents a one-time estimate of Great Basin redband trout abundance, it is intended for use as a baseline in future monitoring. The GRTS design is easy to repeat in a consistent manner, and future comparisons can be rigorously evaluated. Similarly, the abundance benchmarks (Tables 5, 6) complement historical summaries (Dambacher and Jones 2007) and will also serve as a useful means of comparison for smaller-scale population estimates of redband trout both within and outside of the Great Basin.

The decision to depart from standard GRTS protocol in our use of replacement sites from an oversample introduced the potential for bias in estimates of population density and size. In doing so, however, a critical level of efficiency was gained that allowed us to more fully complete our planned sampling schedule. Use of the standard GRTS protocol might have reduced the potential for bias to some extent, but results might still have been tainted by the nonrandom distribution of inaccessible site locations, namely on private land. Fortunately, the GRTS design allowed for poststratification and the adjustment of site weights to compensate for our inability to access sites in exact proportion to the base sample. Even with this adjustment, however, the potential remains for an unknown, but probably small, amount of leftover bias in the abundance estimates. This potential was greatest in the Warner Valley subbasin, where access to 60% of the subbasin sites was denied. Population estimates from this subbasin will need to be judged with an equivalent proportion of caution.

While our use of a distribution map that was presumed to be accurate decreased the need for oversampling, it also introduced an additional element of potential bias in the representation of the distribution at headwater fringes. Headwater sites that lacked redband trout were not used to adjust the distribution distance of the species, as is standard to GRTS protocol when using an oversample. These mapping errors can become cumulatively important if they significantly overestimate the true distribution of the species, the distance of which is used to extrapolate to an estimate of total population size. While we presumed that the distribution of redband trout extended beyond mapped limits as often as it fell short, this was not verified by field inspection. The potential for bias appeared to be relatively small, however, as headwater map errors accounted for only 10 (5.4%) of the 185 sites visited.

A final source of potential bias in this study was our use of the removal-depletion method, which underestimates the true population size when capture efficiencies decline between successive passes (Zippin 1958). In stream fish sampling, the instability of capture efficiencies has been shown to be influenced by variation in habitat characteristics, such as stream size, substrate, instream wood, and undercut bank (Peterson et al. 2004; Rosenberger and Dunham 2005). While mark–recapture techniques have been shown to be unbiased, they require a prolonged recovery period for marked fish, which was impractical within the constraints of the field crew's sampling schedule of 2 sites/d. The bias of removal-depletion methods, however, is minimized when capture efficiencies are high (Zippin 1958; Peterson et al. 2004; Rosenberger and Dunham 2005). Our electrofishing technique applied additional effort within each pass (i.e., downstream sweep of activated probe; see *Fish Population Estimates*) and achieved consistently high levels of p across all subbasins (average $p = 0.81$; Tables 2, 3), and thus any negative bias in the electrofishing estimates is probably small.

The objective of obtaining a general understanding of habitat requirements for Great Basin redband trout was not well met in this study. For example, the general model only accounted for 8% of the variation and five individual subbasin models accounted for 20–40%. The model in Warner Valley only accounted for 4%, but sampling was concentrated on public lands higher in the drainage. Although the explanatory variation was similar to that in a study conducted in southwestern Idaho (36%; Zoellick and Cade 2006), in the present study patterns of habitat relationships varied by subbasin. Findings in the Goose Lake subbasin suggested higher biomass in higher-gradient streams with shade, large wood, and boulders. In the Catlow Valley subbasin, high biomass densities were positively associated with undercut banks and riparian width. In the Malheur Lakes subbasin, geology may play a large role at the subbasin scale; in the Silver Lake subbasin, biomass increased in a downstream direction. While the habitat-based linear models did augment interpretation to some spatial patterns of abundance, we do not see these models as being useful in developing a general understanding of redband trout ecology in the Great Basin since there was no correspondence among subbasin models.

The analysis of stream habitat and fish abundance in this study could probably be improved by including comprehensive measurements of stream water temperature and flow and perhaps other variables, such as conductivity. Moreover, by confining sampling to a known distribution, an opportunity was missed to evaluate habitat conditions that did not support redband trout. Dambacher and Jones (1997), using an array of habitat variables similar to those measured in this study, described significant habitat associations for stream populations of juvenile bull trout *Salvelinus confluentus* in Oregon based on presence–absence sampling. This may well approach a best-case scenario for detecting significant fish–habitat associations, as the juvenile life stage of bull trout is generally confined to relatively short reaches of pristine, high-elevation, forested streams and these fish can be considered as specialists in their use of stream habitat. Great Basin redband trout, by comparison, are generalists in their use of stream habitat across a broad range of conditions. This raises the perspective that in using a broad range of habitat conditions, Great Basin redband trout resolve various tradeoffs within contexts that are sometimes unique to individual streams. Dunham and Vinyard (1997) found strong stream-level effects for populations of Lahontan cutthroat trout *O. clarkii henshawi* and cautioned that these effects should be considered in studies of stream fish and habitat associations. In this study, the GRTS sample design was applied with the primary objective of a minimal level of sampling for the needs of a rapid status review, which led to a varied sampling intensity across subbasins. Thus, in relatively small subbasins, the sampling intensity was sufficiently high so as to suggest the existence of redband trout abundance patterns at the stream level, while in larger subbasins a relatively low sampling intensity precluded observation of stream-level patterns, although possible patterns emerged at the subbasin level. While a uniformly high level of sampling would have been the obvious remedy, it was beyond available resources.

Our results strongly demonstrate the utility of the GRTS sample design for a landscape-level status review. The utility of the GRTS method for detecting associations of fish and stream habitat, however, is not limited by its intrinsic design per se but rather by whether or not applied sampling intensities are sufficient to detect the spatial scales of the association.

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Appendix: Variables Measured at Great Basin Sites

TABLE A.1.—Dependent and independent variables collected at Great Basin stream sites used for a survey of redband trout abundance. Stream channel typing and habitat variables are detailed in Moore et al. (1997); variables that describe fish habitat capacity (e.g., area, volume, and cover) were summarized only within channel units that were sampled for fish abundance (F), while variables describing reach-level habitat attributes (R) were summarized over a longer channel section that included 30 channel units.

Variable type	Variable	Description
Dependent	Redband trout density	fish/m, fish/m^2
	Redband trout biomass	g/m, g/m^2
	Average redband trout weight	g/fish
Independent		
Biological		
R	Riparian width	Total riparian zone width (m), left and right bank
R	Percent macrophytes	Percent surface covered by stream macrophytes

TABLE A.1.—Continued.

Variable type	Variable	Description
Physical		
Macro	Maximum elevation	Maximum elevation of basin (m)
R	Elevation	Elevation at sample site (m)
	Distance from divide	Distance (km) of site from watershed divide
	Basin area	Basin area (km^2) upslope of sample site
R	Channel gradient	Gradient measured with a clinometer
R	Valley width index	Valley floor divided by active channel width
Meso		
R	Percent shade	Measured with a clinometer, percent of 180° for which topography or vegetation occludes the sky
R	Active channel width	Width (m) of exposed substrate (~1.5-year flood)
F	Wetted width	Width (m) of wetted channel
F	Percent pool	Percent of wetted area composed of pool habitat
F	Riffle depth	Modal depth of riffles (m)
R	Percent bank erosion	Percent distance, average for left and right banks
F	Percent undercut bank	Percent distance, average for left and right banks
F	LWD pieces	Large woody debris pieces per 100 m
F	LWD volume	Large woody debris volume (m^3/100 m)
F	Residual pool depth	Mean pool depth minus riffle depth (m)
F	Scour pool depth	Average depth of scour pools (m)
F	Riffle width : depth ratio	Mean width divided by depth of riffles
F	Large boulders/100 m	Roughness index, for boulders > 0.5 m in diameter
R	Percent fines	Percent of wetted substrate surface area composed of fines
R	Percent gravel	Percent of wetted substrate surface area composed of gravel
R	Percent cobble	Percent of wetted substrate surface area composed of cobble
R	Percent boulder	Percent of wetted substrate surface area composed of boulder
R	Percent bedrock	Percent of wetted substrate surface area composed of bedrock
R	Percent riffle gravel	Percent gravel in riffle substrate
R	Percent riffle fines	Percent fines in riffle substrate