The distribution and abundance of Great Basin redband trout: an application of variable probability sampling in a 1999 status review

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Table of Contents

List of Tables

List of Figures

Abstract

Using a variable probability sampling design, streams throughout the entire range of Great Basin redband trout (*Oncorhynchus mykiss* ssp.) were randomly sampled use the EMAP sampling protocol, such that 35 sample sites were apportioned to each of six subbasins (Silver Lake, Lake Abert, Goose Lake, Warner Valley, Catlow Valley, and Malheur Lakes). A total of 185 sites (out of a target of 210) were visited by three-person crews that conducted habitat surveys and population estimates in sample reaches whose length were nearly 20 times their channel width. A minimal sampling intensity was based on previously encountered levels of between site variance in abundance estimates for the species. The population estimate for age 1+ redband trout was 948,852 fish (+/– 21%), with confidence limits ranging from 26% to 43% of individual subbasin estimates. Age 1+ fish abundance in terms of density (fish m^{-2}) showed no significant differences between any subbasin, while there were significant differences in biomass (g m^{-2}), where one subbasin had significantly higher (Catlow Valley) biomasses, and one significantly lower (Goose Lake). These comparisons were supported by like differences in mean weight (g $fish^{-2}$). Analysis of stream habitat characteristics and fish abundance revealed no relationship, or model, that was generally consistent throughout the Great Basin, though interpretable patterns were evident within some stream systems where sampling intensity happened to be sufficiently high. Thus while a landscape level sampling design was well suited to address a regional estimate of abundance, useful interpretation of fish and habitat relationships appeared to be embedded within the stream level of organization, and could not be addressed by the variable probability sampling design set for a minimal sampling intensity.

Introduction

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

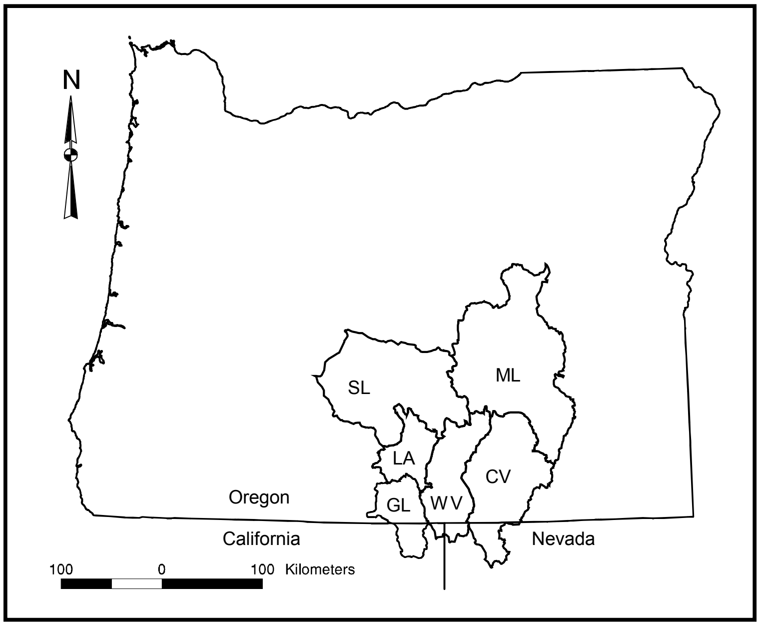

Figure 1. Six subbasins with Great Basin redband trout; SL: Silver Lake, LA: Lake Abert, GL: Goose Lake, WV: Warner Valley, CV: Catlow Valley, and ML: Malheur Lakes.

Great Basin populations of redband trout are in arid forest and desert environments characterized by extreme fluctuations in stream flow and temperature. Information collected after droughts in 1992 and 1994 suggested that some populations had depressed abundance. A 1997 petition to list Great Basin redband trout as a threatened or endangered species prompted a population status review by the US Fish and Wildlife Service 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, have not been well researched, nor has their status been sufficiently documented compared to other salmonids in the Pacific Northwest. And while the distribution of Great Basin redband trout was generally known (Flitcroft and Dambacher 1999), particularly lacking were 1) reliable estimates of population abundance, and 2) an understanding of critical habitat. The objective of this study was to help fill these information gaps.

While population estimates of fishes throughout entire stream systems have effectively been carried out 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. Where this is impractical, as in landscape level survey across many basins, a variable probability sample design (Horvitz and Thompson 1952, Stehman and Overton 1994) can be used, provided sample sites are randomly selected. If sample sites are also spatially dispersed then surveys and analyses can yield additional benefits, such as variable sampling intensity and a posteriori stratification (personal communication, Don Stevens, Dynamac Corporation, Corvallis, Oreg.). Such surveys are currently being conducted by the U.S. Environmental Protection Agency, under the so-called Environmental Monitoring and Assessment Program (EMAP) (Stehman and Overton 1994). Stream population estimates from both the Hankin and Reeves and EMAP surveys can be based upon a two-stage sample design, from which arise two sources of variance. First stage variance comes from extrapolating the subsample into the entire strata, and is minimized when individuals in a population are evenly distributed with respect to sampled units. Second stage variance is derived from the relative precision of the sampling method (here electroshocking). It is typically a minor component of the total variance in salmonid population estimates.

Models that predict fish abundance and production based on habitat parameters implicitly assume a deterministic relationship between fish and their physical environment. Such models are typically based on either regression analyses, or a limiting factors approach. While some regression-based models have been highly predictive (R^2 = 50 – 96 %) in the areas from which they were developed, their generality appears limited (R^2 < 30 %) when applied elsewhere without recalibration (Shirvell 1989). Limiting factor type models are applied with the implicit assumption that included variables are of general importance. Where the status of a particular population is poorly predicted, it is implied that the population is limited by variables not included in the model.

Methods

Sample Design and Access.—Stream sample sites were selected according to the EMAP sample design, which uses GIS to partition stream networks into discrete reaches with a hexagon grid (Stehman and Overton 1994). Stream reaches are then arranged along a single line in a hierarchically randomized order that is systematically sampled in a recursive-partition-based manner. A single reference point is then placed within each selected reach to designate, by latitude and longitude, a specific sample site location. Consequently, all sample sites are spatially dispersed within the sample strata. This spatial dispersion is convenient for a number of reasons, including a posteriori stratification and application of hierarchically nested sets of sample draws. Sample draws can be both temporally and spatially nested to create a rotating monitoring schedule that incorporates both repeat and novel sample sites, or to create a survey that addresses objectives at multiple spatial scales. The objective of this study, however, was quite simple and involved only a one-time estimate of redband trout in the Great Basin, though it designed and anticipated that it will serve as a baseline for future monitoring.

The sampling universe for this study was based upon 1:100,000 scale digital line graphs of the known distribution of redband trout in Great Basin streams of Oregon, Nevada, and California (Flitcroft and Dambacher 1999, Figure 2). The goal of sampling was to obtain 95% confidence intervals that were less than +/- 50% of population estimates for age 1+ redband trout in each of six subbasins (Silver Lake, Abert Lake, Goose Lake, Warner Valley, Catlow Valley, and Malheur Lakes). A minimal sampling intensity of 35 sites per subbasin was chosen, hence 210 for the entire Great Basin, based on previously encountered levels of between-site variance in abundance estimates of age 1+ Great Basin redband trout (*CV* as high as 150%, unpublished data JMD). Two independent sample draws were taken in anticipation of a need for replacement sites in the event of access refusal by private landowners. To encourage the granting 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 signatured endorsement was included in access request letters that were mailed to all owners of private lands selected in the two sample draws.

Deviations from Protocol and Sample Bias.—Two EMAP sampling protocols were not followed in this study. Normally, EMAP protocol calls for factoring into the selection of samples an anticipated proportion of sites that are either inaccessible sites, or outside the distribution of a target. This protocol create an intentional 'over sampling' of sites, from which the effort is made to access all sites equally. After sampling, the fraction of sites occupied by a species is then used to calculate its distribution (aerially or linear as the case may be). If inaccessible sites occur randomly throughout the spread of sampled sites, then sample bias is minimized. We did not, however, follow either of these protocols since we could not commit to an over sampling of sites due to labor limitations. In addition, while we knew general proportions of ownership categories in the Great Basin, we could not anticipate the varying degree of accessibility within each subbasin. However, we had a relatively precise and up-to-date map of the stream distribution of redband trout from which to work (Flitcroft and Dambacher 1999, Figure 2).

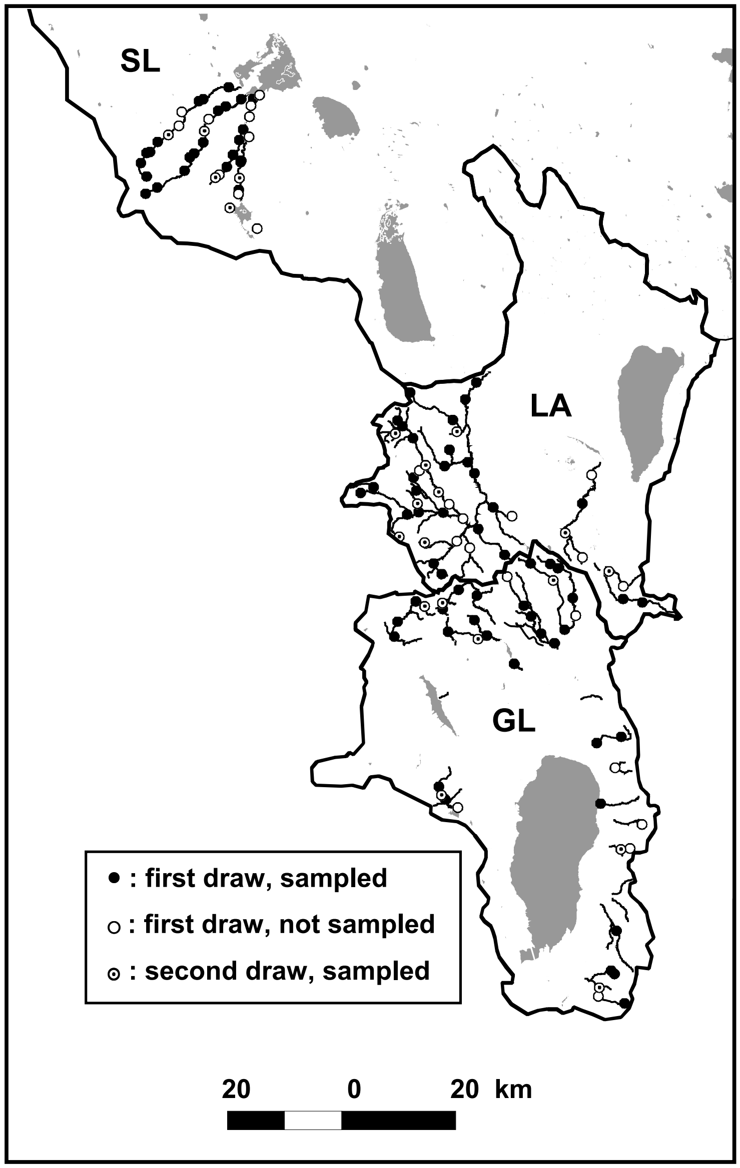

Figure 2a. Sites selected and sampled, from first and second sample draws within the documented distribution of Great Basin redband trout in streams of the Silver Lake (SL), Lake Abert (LA), and Goose Lake (GL) basins. Lakes and wetlands denoted by shaded regions.

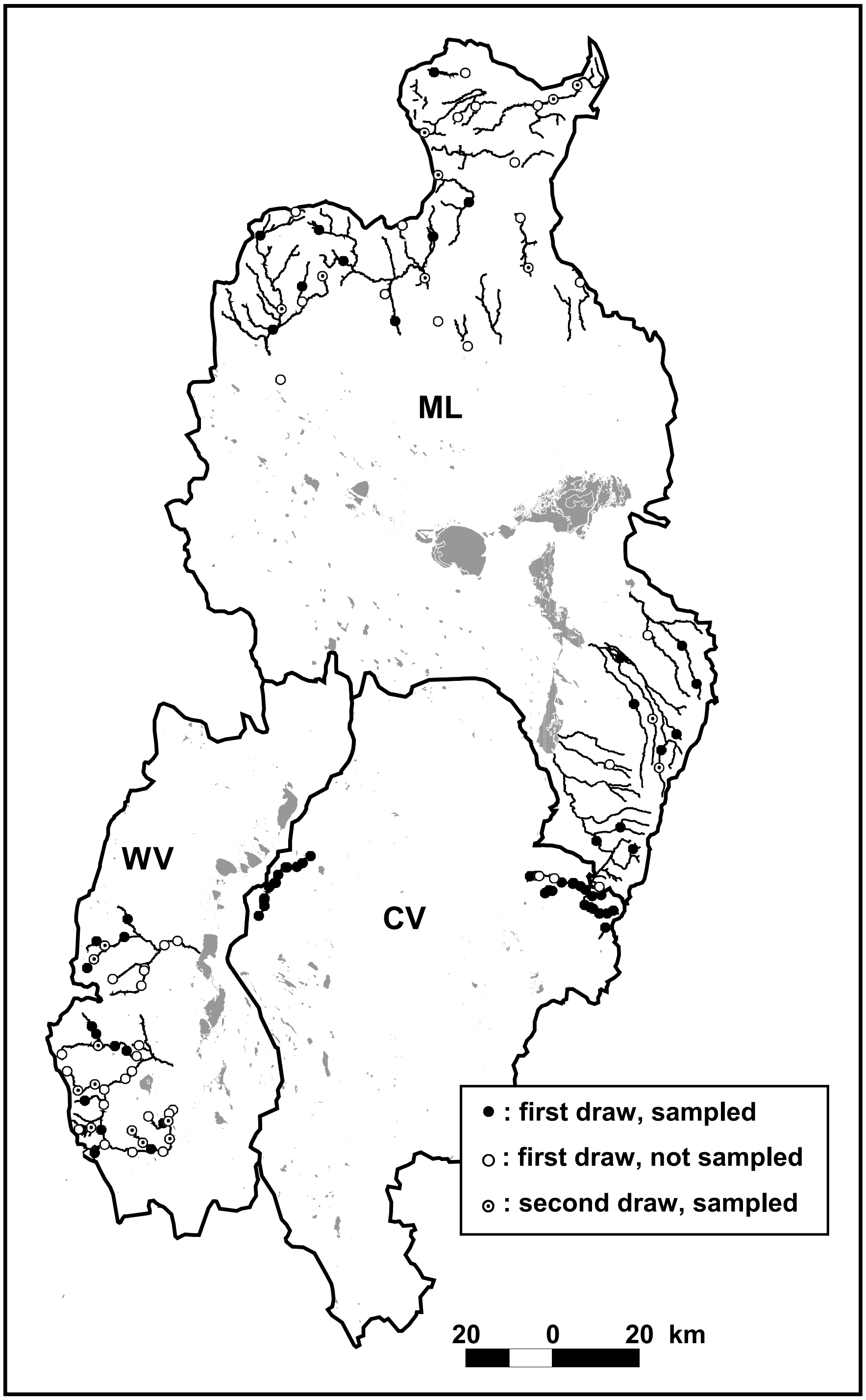

Figure 2b. Sites selected and sampled, from first and second sample draws within the documented distribution of Great Basin redband trout in streams of the Warner Valley (WV), Catlow Valley (CV), and Malheur Lakes (ML) basins. Lakes and wetlands denoted by shaded regions.

By use of replacement sites from a second sample draw, we introduced an element of bias into the sample, the magnitude of which is unknowable. We sought to minimize this bias by selecting replacement sites that were judged to be of similar location, land use, stream size, and elevation (Figure 2). To identify the potential for bias in our data, we developed an index based upon the proportion of target sites from the first sample draw that were not sampled, where

$$\text{potential bias} = 1 - (\text{number of } 1^{st} \text{ sample draw sites visited / number of target sites}) \ . \quad (1)$$

Site Location.—Sample site reference points were located in the field by use of handheld 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 a stream channel, and therefore the nearest portion of stream channel was chosen as an adjusted reference point for each sample site. Stream sample sites were 30 times the active channel width, and were enclosed by blocknets (6 mm mesh) set in fast-water habitat units. Care was taken not to scare or herd fish in or out of the sample area during site selection and placement of blocknets.

Fish Population Estimates.–Depletion-removal estimates (Zippin 1958) were made using backpack electroshockers in wadable streams, and a raft mounted electroshocker in channels too deep to wade. After two removal passes, the decision to cease or proceed with an additional sampling pass was made by 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 as well. Each sampling pass started at the downstream blocknet, and proceeded systematically upstream. Anode probes where 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 ¼ of upstream effort, but this time by pushing the activated probe downstream so as to herd fish to the lower block net. These two separate efforts constituted a single 'pass'. Captured fish were identified by species and apparent age-class, and their lengths measured to the nearest mm, and weights to the nearest 0.1 g. Length-frequency analysis was later used to categorize redband trout as either age 0 and age 1+ (i.e. ≥ age 1) fish. Separate age-class designations were made in each of the six subbasins.

These designations were putative, and uncorroborated 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 reach and habitat unit level (Appendix Table A). In general, descriptions were recorded for channel dimension, streambed composition, amount of large woody debris, and riparian characteristics, according to ODFW stream survey protocol (Moore et al. 2000). Stream habitat was surveyed within the sample site, and upstream to a distance that included 30 habitat units, which from analyses of previous surveys has been shown to provide a robust characterization of habitat at a reach level. Habitat data was separately summarized for the sample site, and for the 30 units combined. Additional reach and watershed level variables (Appendix Table A) were obtained from GIS analyses of digital line graphs and elevation models.

Data Analysis.—Fish population estimates were made by extrapolating average fish m^{-1} in sample sites to total length of stream channel occupied in each subbasin. This was done through a weighting factor that scaled the relative contribution of each sample site to the total subbasin estimate. Total stream distance in each basin was based on analysis of 1:100,000 scale digital line graphs of their known distribution (Flitcroft and Dambacher 1999).

Log transformed abundance measures of redband trout was compared among subbasins using both parametric analysis of means, and nonparametric analysis of ranked medians. Habitat data was transformed, or relativized, by division of each x_{ij} datum by the sum of each x_j data column, whereby

$$x_{ij}^{relativized} = x_{ij} \,/\, \Sigma\, x_j \,. \quad (2)$$

Habitat and abundance relationships were analyzed by various multivariate techniques, including multiple linear regression, regression tree analysis, nonmetric multidimensional scaling, and discriminant function analysis, using both raw and relativized data.

Results

Access, Map Accuracy, and Potential for Sample Bias.–There were 185 sites, out of the adjusted total of 205 target sites, that were visited by survey crews, in which fish population and stream habitat data was collected (Table 1, Figure 2). In the Malheur Lakes subbasin, mainstem 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 (Figure 2b, see sites labeled as 'first draw, not sampled' which do not overlay redband trout stream segments in north half of Malheur Lakes subbasin).

Table 1. Distance of known stream distribution of Great Basin redband trout, as calculated from 1:100,000 scale digital line graph map, with sample draws of 205 sites visited by field crews for sampling in summer 1999, average sample site dimension, and proportion of total stream length sampled (for fish population estimates). There were 35 sites targeted in each of the subbasins, except as noted†. Potential (pot.) bias of sample calculated as proportion of target sites in 1st sample draw that were not visited (Eq. 1).

Subbasin	Redband trout distribution distance (km) and percent of total		Sites visited from sample draws:				(m) Mean sample:		Percent stream distance sampled
			1st	2nd	total	pot. bias	length	width	
Silver Lake	97	4.5%	25	5	30	0.28	82	4.3	2.5%
Lake Abert	314	15%	26	9	35	0.26	72	4.2	0.80%
Goose Lake	303	14%	28	7	35	0.20	71	2.8	0.81%
Warner Valley	269	12%	14	10	24	0.60	92	4.1	0.82%
Catlow Valley	69	3.2%	33	0	33	0.06	78	2.7	3.7%
Malheur Lakes	1,115	52%	18	10	28†	0.40	92	3.7	0.23%
Total	2,167		144	41	185	0.36‡	80	3.6	0.68%

†: Mainstem habitat withdrawn from 'known' distribution map resulted in dropping 5 sample sites, leaving an adjusted target of 30 sites for Malheur Lakes subbasin.
‡: Weighted to percent of total stream distance within each subbasin.

There were 41 sites included in the sample that were selected from the second sample draw as replacements for lack of access or errors in the distribution map. Access was granted to about half of the 90 private land sites in the first sample draw. Ten headwater sites were either dry or outside of the distribution of redband trout. These sites were omitted from the survey and replaced with sites from the second sample draw. We considered the likelihood of errors around the headwater distribution limit to 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.

Access to private lands was particularly difficult to obtain in the Warner Valley basin, and there were insufficient replacement sites available, such that sampling was done in only 24 (68%) of the 35 target sites (Table 1). The potential for bias was most severe in this basin (0.60), as access was refused over large contiguous blocks of land in the lower portions of the basin (Figure 2b). Catlow Valley had the least potential for bias (0.06). The potential for bias for the entire sample of all subbasins combined is weighted towards subbasins with greater stream distance. Since the Malheur Lakes subbasin had the majority (52%) of stream habitat, it had the largest proportional influence on the total potential bias of the entire data set (0.36).

Relative Sampling Intensity.—The length of stream sampled for fish population estimates at each site was on average 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 criteria that there be at least two pool-riffle sequences within each sampled site. Overall, 0.68% of the 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 2.5% and 3.7% of the stream length was sampled, respectively.

Population Estimates and Associated Error.— The population estimate for age 1+ Great Basin redband trout was about 946,000 fish, with a 95% confidence interval that was +/- 21% of the estimate (Table 1). Population estimates for age 1+ fish in individual subbasins ranged from 55,000 (+/- 26%) in Catlow Valley subbasin, to 414,000 (+/- 46%) in the Malheur Lakes subbasin. The population of age 0 fish was roughly two-thirds that of the age 1+ population, with confidence intervals that were consistently greater (up to 3 times greater in some subbasins) than those were for age 1+ fish.

Redband trout population estimates for each subbasin were extrapolated from estimates of fish density (fish m^{-1}) at each sample site. 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 (Table 3). Stemming from this variation, the greatest source of error in population estimates came from extrapolation error (first stage variance). Sampling error (second stage variance) from removal depletion estimates constituted, on average, less than 1%, and at most was 6.2%, of the total variance in population estimates for both age 1+ and 0+ fish

(Tables 2 and 3). The catchability (*p*) of both age classes of redband trout averaged 0.81, though was somewhat more variable, in terms of the coefficient of variation (*CV*), for age 0 fish (Tables 2 and 3).

Table 2. Age 1+ Great Basin redband trout population estimates with 95% confidence limits (*CL*) expressed as percent of estimate, coefficient of variation (*CV*) for density estimates among sample sites, sampling error expressed as second stage variance percent of total variance, and average catchability from electroshocking removal depletion.

Subbasin	Age 1+ redband trout population estimate (+/– 95% *CL* % of estimate)	*CV* of density (fish m^{-1}) estimates	Sampling error as second stage variance % of total variance	Average catchability *p* (*CV*)
Silver Lake	56,964 (26%)	73%	1.4%	0.76 (17%)
Lake Abert	147,878 (41%)	124%	0.33%	0.84 (15%)
Goose Lake	102,352 (32%)	93%	6.2%	0.81 (20%)
Warner Valley	172,240 (31%)	76%	1.1%	0.80 (19%)
Catlow Valley	54,866 (33%)	95%	0.13%	0.85 (14%)
Malheur Lakes	414,551 (43%)	115%	0.35%	0.81 (21%)
Total	948,852 (21%)	92%	0.56%	0.81 (17%)

Table 3. Age 0 Great Basin redband trout population estimates, with 95% confidence limits (*CL*) expressed as percent of estimate, coefficient of variation (*CV*) for density estimates among sample sites, sampling error expressed as second stage variance percent of total variance, and average catchability from electroshocking removal depletion.

Subbasin	Age 0 redband trout population estimate (+/– 95% *CL* % of estimate)	*CV* of density (fish m^{-1}) estimates	Sampling error as second stage variance % of total variance	Average catchability *p* (*CV*)
Silver Lake	27,550 (73%)	203%	0.71%	0.73 (34%)
Lake Abert	28,725 (70%)	212%	0.046%	0.90 (20%)
Goose Lake	49,880 (67%)	202%	0.083%	0.78 (31%)
Warner Valley	41,931 (57%)	141%	1.6%	0.75 (36%)
Catlow Valley	23,012 (58%)	169%	0.045%	0.85 (20%)
Malheur Lakes	394,492 (52%)	140%	0.0028%	0.79 (19%)
Total	565,590 (37%)	190%	0.032%	0.81 (25%)

Potential and Observed Impact of Sampling.—Approximately 10,000 redband trout, about 1% of the total Great Basin population, were captured and handled in this study (Table 4). In the smaller subbasins of Catlow Valley and Silver Lake, the proportion handled approached 3% of the total population estimate. A total of 258 mortalities (0.017% of total population estimate) of redband trout (117 age 0 and 141 age 1+) were observed during the course of sampling (Table 4), and these can be attributed to stress or injury from capture and handling.

Table 4. Potential and observed impact of sampling on Great Basin redband trout from summer 1999 population survey.

	Number of fish handled (percent of population estimate†)		Observed sampling mortality (percent of estimate)	
Subbasin	age 0	age 1+	age 0	age 1+
Silver Lake	454 (1.6%)	1,280 (2.2%)	38 (0.14%)	22 (0.039%)
Lake Abert	234 (0.81%)	1,031 (0.70%)	3 (0.010%)	5 (0.0034%)
Goose Lake	318 (0.64%)	771 (0.75%)	5 (0.010%)	12 (0.012%)
Warner Valley	298 (0.71%)	1,328 (0.77%)	30 (0.072%)	30 (0.017%)
Catlow Valley	657 (2.8%)	1,624 (2.9%)	37 (0.16%)	69 (0.13%)
Malheur Lakes	817 (0.21%)	927 (0.22%)	4 (0.0010%)	3 (0.00072%)
Total	2,778 (0.49%)	6,961 (0.73%)	117 (0.021%)	141 (0.015%)

†: 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.

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, there were a large number of fish deaths that occurred at a single sample site. These deaths were caused by 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 had high fish abundance.

A high number of mortalities that occurred at a single site in Catlow Valley represent a worst-case scenario, as this subbasin had the smallest of any estimated population. The total observed mortality, in proportion to the total Catlow Valley population estimate however, was less than two tenths of one percent. In the context of the stream system in which it happened (Home Creek), it constituted less than one-half of one percent of the total stream population.

Abundance and Weight of Age 1+ Redband Trout.—Examination of box-and-whisker plots of raw data for abundance and weight of age 1+ redband trout (Figure 2), show, in general, that 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.

Raw measures of abundance and weight in all subbasins were skewed towards higher values (Figure 3), and data were log transformed for the purpose of analysis of means (ANOM) tests (Figure 4). This was only partially successful in achieving normal distributions, as for each measure of abundance or weight, there were still two or three subbasin groups that remained considerably skewed or kurtotic. In addition, there was unequal variance in the log-transformed data for numerical density (fish m^{-2}). Neither of these departures from analysis of variance assumptions are thought to be severe when sample numbers are as large and as even as herein (Sokal and Rohlf 1995); we nevertheless chose to supplement the analysis of means comparisons with nonparametric tests for differences amongst group medians.

Analysis of means plots (Figure 4) of log transformed density (log fish m^{-2}) of age 1+ redband trout, show none of the subbasins to be significantly different ($\alpha = 0.05$) from the grand mean of the entire Great Basin. This result is supported by a Kruskil-Wallis test that found no significant ($p = 0.24$) difference amongst any of the group medians. Catlow Valley had a significantly higher biomass, and Goose Lake a significantly lower biomass, and 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 difference in weights of fish in Lake Abert and Warner Valley, were oppositely supported by parametric and nonparametric tests (Figure 4).

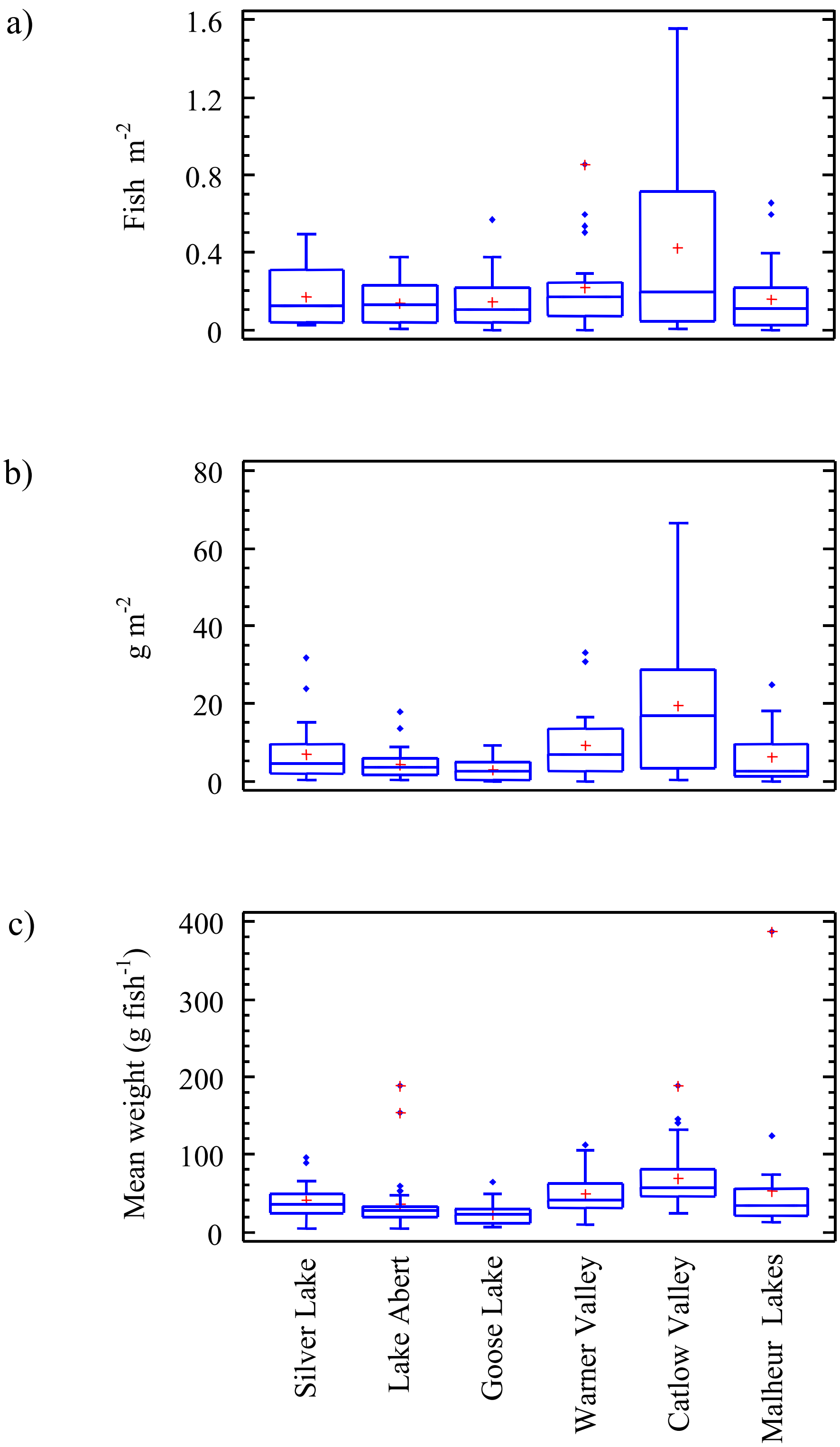

Figure 3. Box-and-whisker plots for age 1+ Great Basin redband trout in terms of a) numerical density, b) biomass, and c) average weight in each of six subbasins. Boxes enclose middle 50 percent of data, median vertical line, and subbasin mean (+). Upper and lower whiskers extend 1.5 interquartile ranges from edge of box. Points beyond whiskers and within 3 interquartile ranges are denoted by '⬩', those beyond are marked by '+'.

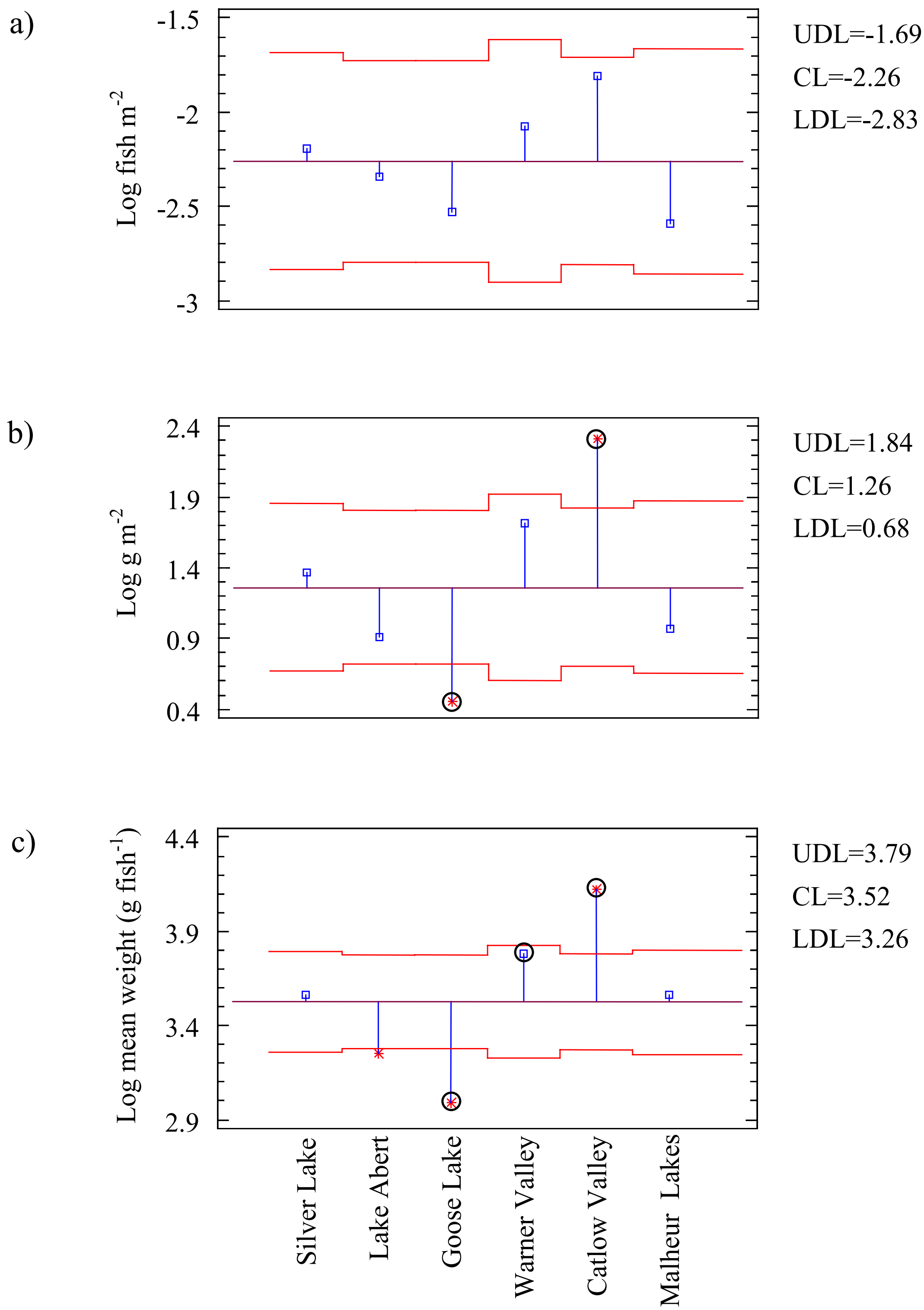

Figure 4. Parametric analysis of means plots for comparison of subbasins for age 1+ Great Basin redband trout in terms of a) numerical density, b) biomass, and c) average weight, with log transformed data. Subbasin means (□) significantly different (α = 0.05) from grand mean, denoted by centerline (CL), are shown by asterices (∗) falling outside of the upper (UDL) and lower (LDL) decision limits. Group differences supported by corresponding nonparametric test (non-overlapping 95% confidence interval of group medians) are circled (⊛ or ⊡).

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

Multivariate Analysis of Abundance and Habitat Relationships.—While 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. A multiple linear regression model for log of biomass of age 1+ redband trout, produced a highly significant relationship ($p < 0.001$) with five habitat variables, however, it explained only 14% of between site variation (Table 7). Separate regression models for individual subbasins were also highly significant, and explained substantial portions of variation in biomass (up to 68%), yet there was little correspondence among 12 variables included in the models, either between subbasins, or in relation to the overall Great Basin model. Moreover, four of the included variables (1/3rd) had opposite effects (signs) within different models (Table 7).

Discriminant function analysis produced two highly significant functions that discriminated between sites with low, medium, or high biomass (Table 5), based on riparian and valley width. While both functions were significant ($p < 0.002$), they correctly classified only 56% of the sites. Analysis at the subbasin level was less successful, in that significant functions were found in only three of the six subbasins. Moreover, while these functions correctly classified 50% to 75% of the sites, there was minimal correspondence between variables included in the functions. Only one variable (valley width) was common between any of the models (total Great Basin model and Goose Lake subbasin model), and it had an opposite effect upon biomass in the functions that included it.

Nonmetric multidimensional scaling developed three axes based on habitat variables, though correlations with any measures of fish abundance were vanishing small (i.e. $R^2 < 1\%$ in all axes for all abundance measures). Use of regression tree analysis also gave significant models at the subbasin level, though a general model for the entire Great Basin remained elusive.

Spatial Patterns of Abundance.—While we found no general model to describe differences in abundance among Great Basin sites based on physical habitat variables, there were spatial patterns of abundance that were interpretable within individual stream systems and subbasins (Figure 5). In the Silver Lake basin, the biomass of age 1+ redband trout

Table 5. Interquartile, and mean values of age 1+ Great Basin redband trout density, biomass, and average weight, from summer 1999 stream population surveys, adjusted by relative sample weights between each of six subbasins.

Age 1+	25%	50%	75%
fish m^{-1}	0.11	0.27	0.71
fish m^{-2}	0.036	0.12	0.22
g m^{-1}	2.4	7.5	21.4
g m^{-2}	1.3	3.0	8.7
mean weight (g)	21.6	31.3	54.7

Table 6. Interquartile, and mean values of age 0 Great Basin redband trout density, biomass, and average weight, from summer 1999 stream population surveys, adjusted by relative sample weights between each of six subbasins.

Age 0	25%	50%	75%
fish m^{-1}	0	0.05	0.35
fish m^{-2}	0	0.02	0.14
g m^{-1}	0	0.2	0.8
g m^{-2}	0	0.1	0.3
mean weight (g)	1.5	2.1	3.1

Table 7. Multiple linear regression models of relativized stream habitat variables (Eq. 2) associated with biomass (log g m^{-2}) of age 1+ redband trout, for the entire Great Basin, and each of six subbasins. All parameters (habitat variables) listed below were significant ($p < 0.05$) within the linear models, and are arranged in descending frequency.

	Great Basin	Silver Lake	Lake Abert	Goose Lake	Warner Valley	Catlow Valley	Malheur Lakes
Model *p*-value	<0.001	<0.001	<0.001	<0.001	<0.001	<0.007	<0.006
Adjusted R^2	13.8	60.5	48.2	26.8	68.3	18.6	28.6
Model parameters (β)							
β_0: intercept constant	1.94	5.73	–5.32	1.28	–0.831	13.0	–4.96
β_i: conductivity			161		341	298	
riffle gravel	–71.0	–169					
residual pool depth†	–65.6	295					
distance from divide†	55.2				–284		
riffle fines	–87.6						–96.2
riparian width†	41.8				–29.2		
elevation†		–818					1290
wetted width		–145					
substrate diversity			759				
percent undercut			180				
valley width index				–140			
riffle depth					216		

†: Model parameter (β_i) with opposite sign or effect within different models.

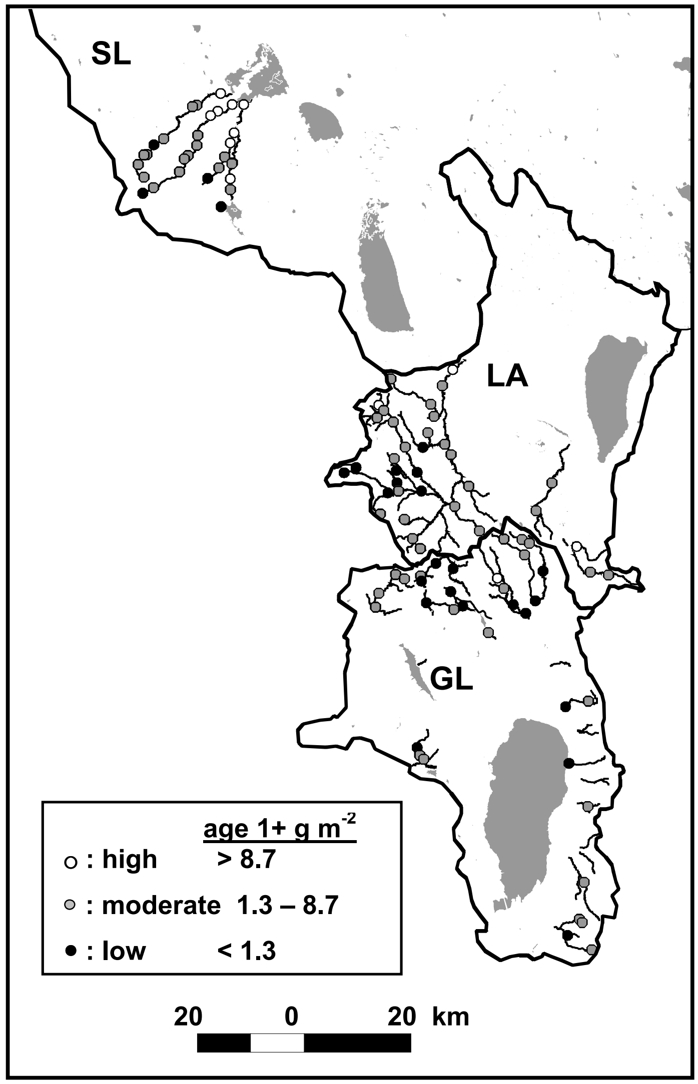

Figure 5a. Biomass of age 1+ Great Basin redband trout in sample sites from Silver Lake (SL), Lake Abert (LA), and Goose Lake (GL) subbasins, from summer 1999 sampling. Lakes and wetlands denoted by shaded regions.

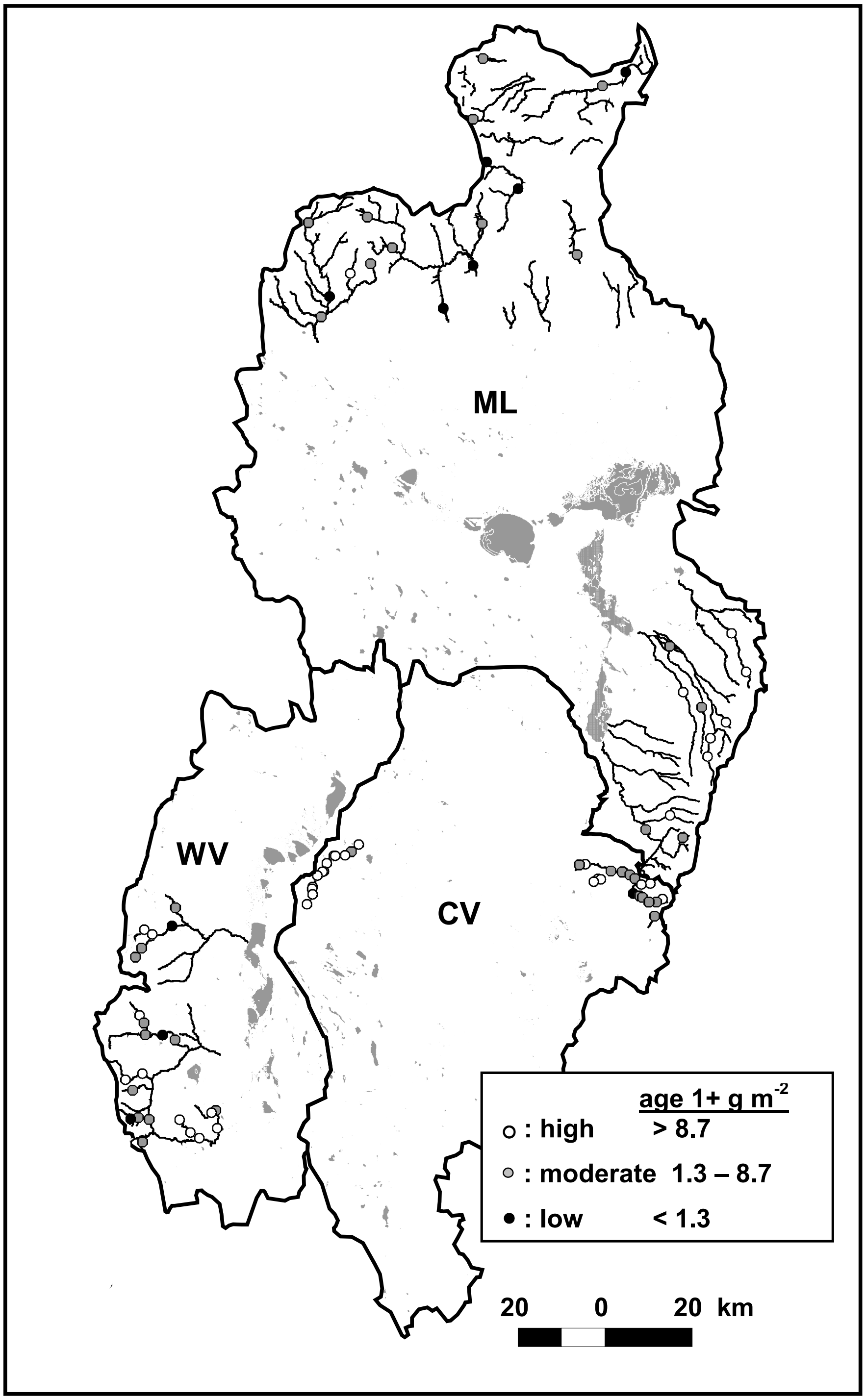

Figure 5b (continued). Biomass of age 1+ Great Basin redband trout in sample sites from Warner Valley (WV), Catlow Valley (CV), and Malheur Lakes (ML) subbasins, from summer 1999 sampling. Lakes and wetlands denoted by shaded regions.

appeared to increase in a downstream direction. This spatial pattern was supported by multivariate analysis; two variables with the greatest effect, elevation (β = –818) and pool depth (β = 295), have obvious spatial correlations along streams. In the Catlow Valley subbasin, Rock Creek (the only stream on the west side of the basin) had some of the highest recorded biomass among 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. All streams in the Catlow Valley subbasin dominated by spring-flow, but Rock Creek in particular has significant contributions from thermal springs, and consequently high conductivity. Here the pattern is supported by multivariate analysis, where the only variable of importance was conductivity (β = 298). Surveys of the three east-side streams in 1995 identified reaches receiving spring flow, and canyon reaches as having the highest abundance of age 1+ redband trout (Dambacher and Jones *In Press*). Our 1999 sampling repeated this pattern, which can be seen in the high versus moderate and low biomass sites in Figure 5b.

While spatial patterns in the abundance of age 1+ redband trout were interpretable *within* stream systems of east side of the Catlow Valley and the Silver Lake subbasins, and also *between* streams of the east and west side of Catlow Valley subbasin, these interpretations were supported by relatively high sampling intensities (i.e. at least 2.5% of stream length sampled, Table 1). In the other four basins, sampling intensity appeared to be too low (< 1% stream length) to afford a useful interpretation at the stream level of organization. Spatial patterns at the subbasin level of organization, however, were evident in the Malheur Lakes subbasin, which had the lowest sampling intensity of any subbasin in this study (0.23% stream length). Sites in the north half of the Malheur Lakes subbasin generally had lower biomass of age 1+ fish than sites in the south half. Here multivariate analysis indicates only two significant correlating variables: elevation (β = 1290), and the amount of fine sediments in riffles (β = –96.2). These correlates can be reasonably associated with regional differences in geology. Streams in the south-half of the basin originate in the Steens Mountains, which are composed of less friable parent material (principally basalt and andesite), than the lower laying north-half of the basin (parent material principally silicic ash-flow tuff).

Discussion

This study demonstrates the usefulness and effectiveness of the EMAP sampling design for population estimates of stream fishes at the basin and landscape scale. The variable probability sampling design proved to be ideally suited to meet the needs of a rapid status review for an Endangered Species Act listing decision. The U.S. Fish and Wildlife Service's March 2000 finding of "not warranted" was based primarily upon the results of this study (personal communication; Antonio Bentivoglio and Ronald Rhew, U.S. Fish and Wildlife Service, Portland, Oreg.). Relatively precise estimates of population size for Great Basin redband trout were obtained in each of the six subbasins (Tables 2 and 3), with a minimal impact to either local populations or to the total population (Table 4). This precision was obtained because we accurately anticipated the average between-site variation in densities of redband trout, and set a minimal, yet sufficient, sampling intensity that was within the means of limited labor resources.

Our study objective of obtaining reliable estimates of population abundance were well served by the variable probability survey design, however, the objective of obtaining a general understanding of critical habitat requirements was not met by a survey design set for a minimal sampling intensity. While this study presents a one-time census of Great Basin redband trout, it is intended that is will be useful as a baseline for future monitoring. The EMAP method is easy to repeat in a consistent manner, and future comparisons can be rigorously evaluated. Similarly, the abundance benchmarks (Tables 5 and 6) 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 departure from standard EMAP protocol in our use of replacement sites from a second sample draw, introduced potential bias to 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 EMAP protocol might have reduced the potential for bias to some extent, but results would still have been tainted by the nonrandomness of where inaccessible sites occurred, namely private land. This was especially critical in the Warner Valley subbasin, where access was denied to roughly 60% of the basin. 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 EMAP protocol. 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. This potential for bias, however, appears to be relatively small as headwater map errors accounted for only 10 (5.4%) of the 185 sites visited. Moreover, these errors were likely cancelled by a similar degree of error where the actual distribution of redband trout extended beyond mapped limits.

The March 20, 2000 listing decision of “not warranted” by the USFWS was based upon early interpretation of results of this study, which showed Great Basin redband trout densities (fish m^{-2}) to be “moderate to high” in each of the six subbasins. Further analyses, reported herein, substantiate that finding but also raise specific concerns and questions. While 60% of sites in the Goose Lake subbasin had moderate or high biomass of age 1+ redband trout (Figure 5a), the biomass and average weight of age 1+ fish was significantly lower there than in any other subbasin, by both parametric and nonparametric comparisons (Figure 4). Despite perceptions that stream habitat conditions for redband trout appear highly degraded by cattle grazing in a large portion of the Goose Lake subbasin, the only habitat parameter with a significant (negative) association with age 1+ biomass was valley width (Table 7). And while this finding agrees with a general intuition that broad meadow reaches are most sensitive to, and impacted from the effects of intensive grazing, we would have expected additional in-channel parameters, such as bank erosion, levels of fine sediments, etc., to also have been included in the linear model, or for valley width to have been included in other subbasin models, which it was not.

This limitation in the results from the Goose Lake subbasin illustrates a cautionary point in our work. From analysis of our data, it was evident that one could easily put forward various plausible interpretations of fish and habitat associations in a given subbasin, by merely picking and choosing from various multivariate techniques (the results for all of which are not presented herein). While the habitat based linear models added useful 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 amongst subbasin models. Coinciding with this perspective however, is a more obvious interpretation that redband trout are generalists in their use of stream habitat, and various countervailing tradeoffs are being resolved within contexts unique to individual streams. If this is the case, then our understanding of habitat use of stream populations of Great Basin redband trout will depend largely upon the story presented by each stream, or group of similar streams. Moreover, our results suggest that understanding will likely be gained at various spatial scales (i.e. reach, stream, and beyond).

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Appendix

Appendix Table A. Dependent and independent variables derived from data collected at stream sample sites. Habitat variables detailed in Moore et al. 2000.

Variable Type	Variable	Description
Dependent	redband trout density	fish m^{-2}
	redband trout biomass	g m^{-2}
	average weight	g $fish^{-1}$
Independent		
Biological	riparian width	total riparian zone width (m) left and right bank
	percent macrophytes	percent surface covered by stream macrophytes
Physical		
Macro	maximum elevation	maximum elevation of basin (m)
	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
	channel gradient	gradient measured with clinometer
	valley width index	valley floor divided by active channel width
Meso	percent shade	measured with clinometer, percent of 180^o that topography or vegetation occludes the sky
	active channel width	width (m) of exposed substrate
	wetted width	width (m) of wetted channel
	percent pool	percent of wetted area
	riffle depth	modal depth of riffles (m)
	percent bank erosion	percent distance, left and right bank average
	percent undercut bank	percent distance, left and right bank average
	Lwd pieces	large woody debris pieces 100 m^{-1}
	Lwd volume	large woody debris volume (m^3 100 m^{-1})
	residual pool depth	mean pool depth minus riffle depth (m)
	riffle width-depth ratio	mean width divided by depth of riffles
	large boulders 100 m^{-1}	roughness index, for boulders >0.5m diameter
	percent fines	percent of wetted substrate surface area
	percent gravel	percent of wetted substrate surface area
	percent cobble	percent of wetted substrate surface area
	percent boulder	percent of wetted substrate surface area
	percent bedrock	percent of wetted substrate surface area
	percent riffle gravel	percent gravel in riffle substrate
	percent riffle fines	percent fines in riffle substrate