

Local and Geographic Variability in the Distribution of Stream-Living Lahontan Cutthroat Trout

J. B. DUNHAM*¹

Biological Resources Research Center and Department of Biology,
University of Nevada, Reno, Nevada 89557, USA

M. M. PEACOCK

Biological Resources Research Center, University of Nevada, Reno, Nevada 89557, USA

B. E. RIEMAN

U.S. Forest Service, Rocky Mountain Research Station,
316 East Myrtle Boise, Idaho 83702, USA

R. E. SCHROETER

Department of Biology, University of Nevada, Reno, Nevada 89557, USA

G. L. VINYARD²

Biological Resources Research Center and Department of Biology,
University of Nevada, Reno, Nevada 89557, USA

Abstract.—We investigated local and geographic variability in the up- and downstream distribution limits of threatened Lahontan cutthroat trout (*Oncorhynchus clarki henshawi*) in stream habitats of the eastern Lahontan basin in northern Nevada and southeastern Oregon. At a geographic scale, elevations of upstream distribution limits were significantly correlated with latitude and longitude, suggesting a potential influence of climatic gradients. Elevations of upstream distribution limits also were positively correlated with maximum basin elevation, which suggested topographic, rather than climatic constraints may be important. Upstream distribution limits were not significantly affected by local variation in stream size or presumptive dispersal barriers. Stream gradient was related to upstream distribution limits, but this was again confounded by maximum basin elevation. Stream gradients used by Lahontan cutthroat trout at upstream limits were considerably steeper than those observed for other subspecies of cutthroat trout in other areas. Geographic variation in elevations of downstream distribution limits was also apparent, paralleling variability in summer air temperatures and presumed restriction of Lahontan cutthroat trout from lower elevation habitats by unsuitably warm temperatures in summer. Previous regional models assumed downstream distribution limits for salmonids correspond to isotherms of 22–24°C (mean July air temperature), but we found the distribution of Lahontan cutthroat trout to be considerably more restricted, most closely corresponding to a mean July air temperature of 18°C. Occurrence of nonnative brook trout *Salvelinus fontinalis* was associated with a significant upstream shift of the downstream distribution of Lahontan cutthroat trout, suggesting a highly variable, but negative interaction between these species.

Lahontan cutthroat trout *Oncorhynchus clarki henshawi* is a threatened subspecies (Office of the Federal Register 40:29864) endemic to the Lahontan basin of northeastern California, southeastern Oregon and northern Nevada (Coffin and Cowan 1995; Figure 1). It is estimated that Lahontan cutthroat trout occupy less than 3% of the

species' historical habitat in the Walker, Carson and Truckee River basins of northeastern California and western Nevada, and about 14–15% of historical habitat in the eastern Lahontan basin, which includes the Quinn and Humboldt river and Coyote Lake basins (Coffin and Cowan 1995). Like other subspecies of cutthroat trout (e.g., Gresswell 1988; Young 1995; Duff 1996; Hall et al. 1997), the presently contracted distribution of Lahontan cutthroat trout has been attributed primarily to interactions with hatchery and nonnative salmonids, and habitat degradation (Coffin and Cowan 1995).

* Corresponding author: jdunham@proaxis.com

¹ Order of last four authors is alphabetical.

² Deceased.

Received March 23, 1998; accepted November 30, 1998

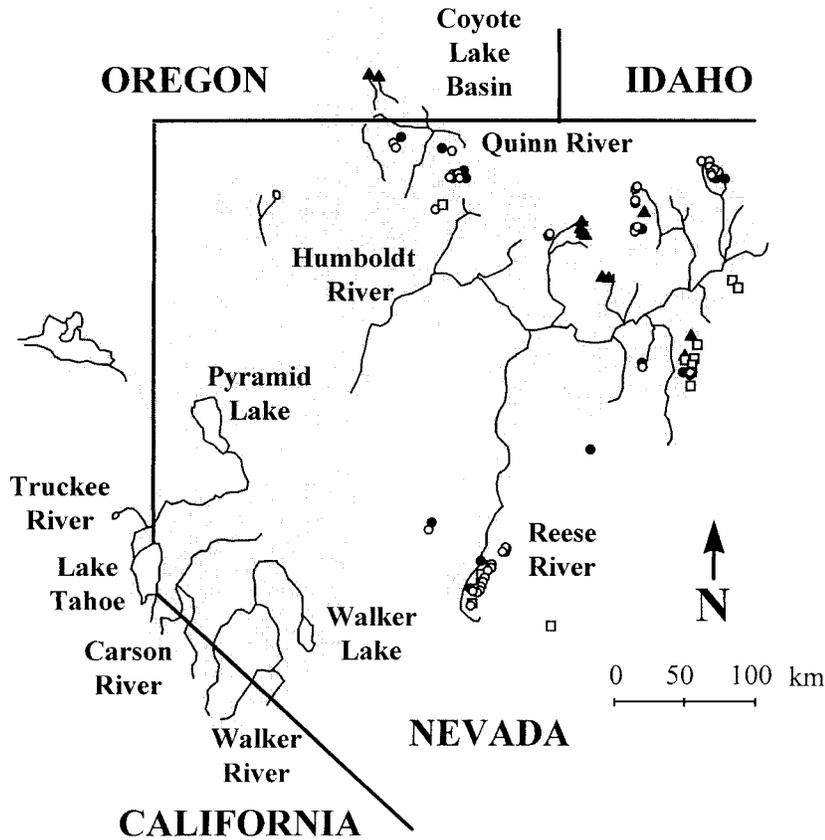


FIGURE 1.—Map of Lahontan basin (shaded) with locations of streams sampled for up- and downstream distribution limits of Lahontan cutthroat trout. Sampled streams outside the basin have translocated populations. Symbols represent the following samples: ● = downstream distribution limits for streams with Lahontan cutthroat trout only; ▲ = downstream distribution limits for streams with Lahontan cutthroat trout and brook trout; □ = upstream distribution limits for streams with Lahontan cutthroat trout only (agency data); ○ = upstream distribution limits for streams with Lahontan cutthroat trout and brook trout.

Most remaining populations of Lahontan cutthroat trout in the eastern Lahontan basin occupy higher-elevation, low-order headwater stream habitats. The distribution of Lahontan cutthroat trout in these habitats is highly fragmented, and as a result, many populations may be at risk of extinction (Dunham et al. 1997). While it is clear that fragmentation poses a significant threat, factors affecting the distribution of Lahontan cutthroat trout in streams have been quantitatively analyzed only within a limited portion of the basin (Nelson et al. 1992).

Previous work on Lahontan cutthroat trout attempted to explain trout distributions in terms of geologic and geomorphic landscape characteristics. Nelson et al. (1992) found trout (both La-

hontan cutthroat trout and nonnative brook trout *Salvelinus fontinalis*) occurred primarily in sites within sedimentary land type associations and hypothesized a connection between land type associations and habitat characteristics that may be limiting trout distributions. Although geology and geomorphology may play an important role, several aspects of the study by Nelson et al. (1992) warrant concern. Most importantly, Nelson et al. (1992) suggested that “neither temperature nor dissolved oxygen currently limit cutthroat trout distributions.” This statement was based on limited evidence from point samples of water temperature and dissolved oxygen, and anecdotal reports and evidence suggesting Lahontan cutthroat trout may tolerate higher temperatures than other

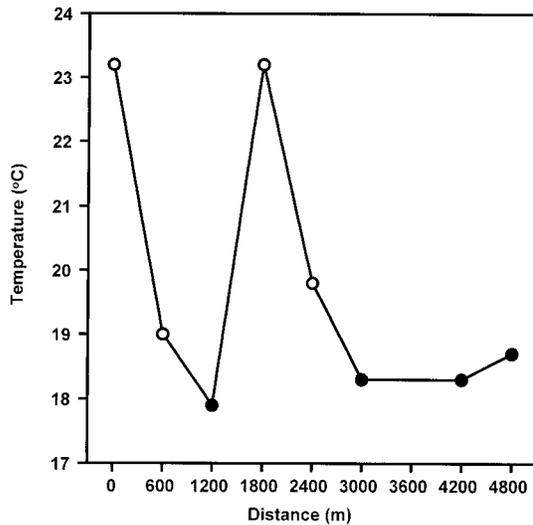


FIGURE 2.—Longitudinal profile of maximum stream temperatures recorded (16 July–15 September 1998) from Edwards Creek, Nevada. Filled and unfilled circles represent sites with and without Lahontan cutthroat trout, respectively. Distance is an arbitrary measure of relative distance (meters) between sample sites, beginning with zero at the most-downstream site. The drop in maximum temperature at 1,200 m corresponds to the influence of discharge from a large, cold spring.

closely related salmonids. A more fundamental issue is that temperature, elevation, and land type associations defined by Nelson et al. (1992) are inextricably interrelated, and therefore temperature cannot be rejected as an important factor.

Several lines of evidence available since the work of Nelson et al. (1992) suggest temperature may indeed be an important factor affecting the distribution of Lahontan cutthroat trout. In the laboratory, Dickerson and Vinyard (1999) found that juvenile Lahontan cutthroat trout can survive short-term (1 h) exposure to water temperatures of up to 26°C and weekly exposure to constant temperatures of up to 24°C. Patterns of growth and survival suggested an upper chronic exposure limit of 24–25°C, which is not substantially different from information available on closely related salmonids (Dickerson and Vinyard 1999). Our field observations (e.g., Figure 2) also strongly suggest the distribution of Lahontan cutthroat trout in streams is restricted by unsuitably warm summer water temperatures. Finally, we believe temperature deserves further consideration as an important limiting factor because it has a clear mechanistic (physiological) basis relating it to fitness

and habitat quality for salmonids (e.g., Van Winkle et al. 1997).

Another obvious factor potentially affecting the distribution of Lahontan cutthroat trout in streams is occurrence of nonnative trout. Nonnative trout are widespread throughout the range of Lahontan cutthroat trout (Coffin and Cowan 1995). Previous work on geographic variation in salmonid distributions in the region (Keleher and Rahel 1996) considered a coldwater guild consisting of rainbow trout *Oncorhynchus mykiss*, brown trout *Salmo trutta*, brook trout, and cutthroat trout (various subspecies) without considering potential interactions within this guild. Similarly, previous work on Lahontan cutthroat trout and brook trout in streams (Nelson et al. 1992) did not quantitatively analyze potential interactions between these two species.

In this study, we analyzed downstream distribution limits of Lahontan cutthroat trout in relation to geographic variability and local factors, including occurrence of nonnative salmonids and downstream barriers (e.g., water diversions or natural dewatering). Geographic variability of Lahontan cutthroat trout distributions also was related to thermal distribution limits for trout proposed by Keleher and Rahel (1996) for the region based on air temperature. Classification of geologic or geomorphic landscape characteristics (Nelson et al. 1992) within the vast study area (Figure 1) was beyond the scope of this work. As mentioned above, however, it is likely these landscape characteristics and thermal gradients covary with elevation. We did not therefore attempt to distinguish these “alternatives” in this work. Rather, we were interested in the evidence to support the hypothesis that temperature and nonnative salmonids are important factors limiting the distribution of Lahontan cutthroat trout in streams.

We also considered upstream distribution limits of Lahontan cutthroat trout and evidence for geographic variability. Geographic variation in climate (e.g., Mitchell 1976; Keleher and Rahel 1996) may affect upstream distributions, which may be limited by freezing temperatures in winter (e.g., Cunjak 1996) or by reduced growth and survival associated with colder temperatures and shorter growing seasons at higher latitudes and elevations (Scarnecchia and Bergerson 1987; Shuter and Post 1990; but see Conover 1990). Effects of local factors, including dispersal barriers, channel geometry, and stream gradient were analyzed as well. Dispersal barriers in the form of high stream gradients, steep cascades, or waterfalls

(Kruse et al. 1997) may restrict the upstream distribution of cutthroat trout. Stream size may affect trout distributions if fish prefer larger or more complex stream habitats (Kruse et al. 1997; Dunham and Rieman 1999). Stream size also may be related to water temperature (Stefan and Preud'homme 1993).

Methods

Study Area and Organisms

The Lahontan cutthroat trout is endemic to the Lahontan basin of northeastern California, southeastern Oregon, and northern Nevada (Figure 1), and it did not co-occur with other trout species until translocations of nonnative salmonids began in the late 19th century (Miller and Alcorn 1943; LaRivers 1962). In the last 150 years, Lahontan cutthroat trout has been virtually eliminated from its historical distribution within the western Lahontan Basin, which includes the Truckee, Carson, and Walker River basins and their lakes (Coffin and Cowan 1995).

Our study focused on stream habitats in the eastern Lahontan basin, including the Quinn and Humboldt River basins of Nevada and the Coyote Lake basin of Oregon (Figure 1). Here, Lahontan cutthroat trout populations persist as isolated enclaves in low-order stream habitats, with the exception of a few basins where favorable conditions in larger downstream habitats may provide demographic connectivity among tributary populations (Coffin and Cowan 1995; Dunham 1996; Dunham et al. 1997).

Descriptions of stream habitats in the eastern Lahontan basin can be found in Nelson et al. (1987), Platts and Nelson (1989), Nelson et al. (1992), Dunham (1996), and Jones et al. (1998). Generally, stream habitats are highly variable in space and time. Within years, however, seasonal fluctuations in stream discharge are fairly predictable. With the exception of episodic flooding from summer thunderstorms, peak discharges generally coincide with spring snowmelt and runoff in March–June. Among years, periodic droughts and cooler, wetter periods bring dramatic changes in the frequency and magnitude of stream discharges, water temperature, and physical characteristics of stream channels.

Spatial variation in habitat conditions is also very pronounced. Higher-elevation streams are cooler in the summer (<20°C) and often have abundant riparian vegetation, pool-forming rocks, and (sometimes) large wood in the channel. Low-

er-elevation streams typically flow through permeable alluvial deposits (Nelson et al. 1992) with degraded (downcut) channels and higher maximum summer water temperatures (>20°C). Stream flows in many lower-elevation streams may become intermittent during summer droughts (Dunham 1996). In winter, colder water temperatures and anchor ice formation might cause high fish mortality in some years.

Stream habitats in the Lahontan basin support a variety of native and nonnative fishes (LaRivers 1962). Nonnative fishes encountered in this study included rainbow trout, brown trout, and brook trout. Brook trout were by far the most common nonnative salmonid present. Brook trout were upstream of other sympatric salmonids except for Lahontan cutthroat trout. Native nonsalmonid fishes most frequently encountered were Paiute sculpin *Cottus beldingi*, speckled dace *Rhinichthys osculus*, mountain sucker *Catostomus platyrhynchus*, Tahoe sucker *C. tahoensis*, and Lahontan reddsider *Richardsonius egregius*.

The primary land use in the eastern Lahontan basin is livestock grazing (Coffin and Cowan 1995) with localized mining and irrigated agriculture. Recreational fishing for Lahontan cutthroat trout is allowed in Nevada, but is not considered intensive enough to have significant effects on Lahontan cutthroat trout populations (Coffin and Cowan 1995). We rarely observed anglers on streams in five summers of field work conducted prior to and during this study.

Sampling of Distribution Limits

Sampling of Lahontan cutthroat trout distributions was conducted from 18 July to 24 September 1997 during summer base flows. We assumed annual air and water temperatures were at a maximum sometime during this time period. Sampling began in the southern portion of the eastern Lahontan basin and proceeded northward, though time of sampling and distance north were not strongly correlated ($r = 0.42$; $P = 0.03$). We started sampling in the south because streams there approached summer base flows earlier in the summer of 1977. We expected Lahontan cutthroat trout to be well distributed throughout suitable stream habitats in 1997 because the region had experienced three relatively wet and cool years since a drought in 1994, and density of fish in many streams in the area has generally increased since 1993 (Dunham 1996; J.B.D unpublished data). No attempt was made to collect a random sample of occupied habitats, but samples were interspersed

throughout the geographic range of Lahontan cutthroat trout in the eastern Lahontan basin (Figure 1). A relatively large number of streams was sampled, however (Figure 1), and we believe our sampling was representative of the range of the subspecies in the eastern Lahontan basin.

Additional data on downstream distribution limits of Lahontan cutthroat trout were obtained from stream survey reports on file at the Nevada Division of Wildlife and the Oregon Department of Fish and Wildlife. These data were from various years and served as a baseline for evaluating results of surveys conducted in 1997. We also used data on upstream distribution limits for three streams surveyed by the Nevada Division of Wildlife in 1997 (J. Elliott, Nevada Division of Wildlife, personal communication). Some populations sampled originated from translocations either within or from outside the Lahontan basin. Translocated populations occurred in 8 of 44 streams sampled for lower distribution limits and 5 of 45 streams sampled for upstream distribution limits. Translocated populations were carefully scrutinized for their potential influence on the outcome of statistical analyses of the data.

Field sampling of Lahontan cutthroat trout distributions involved locating fish by electrofishing, and then proceeding in an upstream or downstream direction until no fish were encountered for 300 m. Sampling generally proceeded in an upstream direction to maximize the probability of detecting fish. Electrofishing small streams in this manner is an highly efficient method of fish capture. In other work on Lahontan cutthroat trout, capture probabilities from three-pass removal electrofishing (estimated by the program CAPTURE; White et al. 1982) averaged 0.78 ± 0.14 across 138 sites sampled in 1993–1995 (J.B.D, unpublished data). In the final 300 m of sampling, at least 15 relatively high-quality pool habitats were fished. High-quality pool habitats were defined as those with exceptional cover (e.g., boulders, large wood, undercut banks), deep water, or both.

Initially, distribution limits were determined separately for small (≤ 100 mm standard length) and large (> 100 mm) fish. Length-frequency distributions for Lahontan cutthroat trout from low- and high-elevation habitats (Dunham 1996) and age-length relationships from otoliths (J.B.D, unpublished data) indicate fish shorter than 100 mm may be reasonably classified as juveniles in their first to second year of life (age 0–1 year). This stratification was employed to distinguish the distribution of spawning and early rearing habitat

from that used exclusively by larger subadult and adult fish. In all cases, however, the distributions of these two size-classes overlapped almost completely, so stratification was unnecessary.

Wetted widths and depths of streams at upstream distribution limits were sampled over a 100-m reach by means of 10 transects oriented perpendicular to the wetted stream channel and spaced 10 m apart, following recommendations of Myers (1995). Average depth at each transect was calculated from depth measurements taken at 25, 50, and 75% of the channel width beginning from one bank (depth = 0) (Overton et al. 1997). In a few cases, we encountered lack of surface flow or hazardous sampling conditions and fewer than 10 transects (5–9) were sampled. Maximum depths of all pools, defined according to Hawkins et al. (1993), also were recorded in the 100-m reach. Stream gradient was estimated directly from 1:24,000 scale topographical maps.

Potential natural and human-caused barriers were noted at distribution limits. Natural physical dispersal barriers consisted of high-gradient cascades, waterfalls, and lack of surface flows. Human-caused dispersal barriers included downstream water diversions, and high (> 1.5 m: Kruse et al. 1997) vertical headcuts. Presence of non-native salmonids was also documented in each stream. Elevations of upstream and downstream distribution limits were estimated with 1:24,000 scale topographical maps.

Analysis of Factors Affecting Distribution Limits

Downstream distribution limits.—We initially used ordinary least-squares (OLS) regression to develop a predictive model of the elevation of downstream distribution limits of Lahontan cutthroat trout. We considered three predictors: latitude, longitude, and occurrence of nonnative brook trout. Latitude and longitude were estimated by universal transverse Mercator (UTM) map projections as northings and eastings, respectively, measured in meters.

Best-subsets regression was used to select variables to be used in regressions. We used a variety of model selection criteria, including summed PRESS residuals, mean square error, Mallows' C_p , Akaike's information criterion, and coefficient of determination for selection of alternative regression models (Freund and Littell 1991). Although these diagnostics measure somewhat different dimensions of the data (see Freund and Littell 1991), they generally agree in practice. Variables screened for regressions included linear and qua-

dratic latitude and longitude effects and interaction terms.

Initially, we used data collected during our surveys in 1997 for regression analyses. Other data made available through consultation with state agency biologists were added in subsequent analyses. We initially restricted the analysis to data collected in our own surveys because many agency surveys were conducted in different years, potentially adding unexplained temporal as well as spatial variability; agency surveys used different survey protocols; and agency survey data were clustered geographically and produced a heteroscedastic distribution of errors.

Distributions of residuals were analyzed to ensure OLS model assumptions of normality and homogeneity of variances were satisfied. Tests for normality used studentized residuals and the W statistic, following the method of Shapiro and Wilk (1965), as implemented by the SAS UNIVARIATE procedure (Cody and Smith 1991). Homogeneity of variances was assessed by correlation of absolute values of studentized residuals with predicted values of the response variable.

When variances were not homogeneous, we compared results of OLS regressions to those generated by percentile regression based on median, rather than mean, values of the response (Terrell et al. 1996). Because median values are less affected by outliers and heteroscedastic errors, percentile regression may provide more robust estimates of parameters. We refer to this method as LAD regression, which uses least absolute deviations, rather than the squared deviations used for OLS regression (see Terrell et al. 1996). Confidence intervals for percentile regression estimates were generated by bootstrapping (StataCorp 1997).

The influence of individual observations on regression models was estimated by DFFITS (Myers 1990; Freund and Littell 1991). This diagnostic estimates the number of standard errors the fitted value changes if the i th observation is removed (Myers 1990; Freund and Littell 1991). We used a cutoff value of $DFFITS = 2(m/n)^{0.5}$, recommended by Belsley et al. (1980), where m is the number of parameters (intercept and slopes) and n is the number of observations, to judge whether or not observations qualified as influential. Particular attention was paid to streams with downstream diversions or dewatering, because downstream distributions may be truncated in such cases, possibly biasing the regression model.

Because the regression models were intended to

be used for predictive purposes, we wished to have a measure of how well our models predicted new observations. Typically model "validation" has involved reserving a subset of observations to be predicted by the original model constructed without these observations. In view of the limited number of data points in our samples, we opted for an alternative that more efficiently utilizes available information. To evaluate the predictive performance of regressions, we used prediction sum of squares (PRESS) residuals (Myers 1990). The PRESS residuals were estimated by withholding a single observation (y_i) and estimating a "residual" by subtracting the observed value from that predicted by a regression model constructed with the remaining ($n - 1$) observations. This avoids using the observation y_i to simultaneously create and evaluate the predictive performance of the regression model.

Upstream distribution limits.—The elevation of upstream distribution limits was analyzed as above with OLS regression. Regional variability in upstream distribution limits was modeled as a function of latitude and longitude based on UTM coordinates. Local factors, including stream gradient, stream width, average depth, and maximum pool depth, were included in the analysis. Analysis of covariance (ANCOVA) was initially used to test for the effects of presumptive dispersal barriers on upstream distribution limits. Screening for influential data points was conducted as above with the OLS regression model developed from the full data set. In screening for influential data points, we made special note of streams with potential barriers to upstream dispersal. Dispersal barriers might exclude fish from suitable upstream habitats and distort relationships between upstream distribution limits and other variables.

Because maximum elevations of mountain ranges in our study area follow geographic clines (Grayson 1993), we also tested for geographic variation in the maximum elevation of catchment basins for streams in this study. In other words, it may not be physically possible for Lahontan cutthroat trout to occupy higher elevation habitats in the northern portion of their range because such habitats do not exist. This possibility was considered by analysis of correlations between maximum basin elevation and variables explaining upstream distribution limits of Lahontan cutthroat trout (UTM eastings, northings, and stream gradient).

Correspondence of downstream distribution limits to thermal gradients.—Because data on stream temperatures were unavailable, we used mean July

TABLE 1.—Regression models of downstream distribution limits (elevation, in meters) of Lahontan cutthroat trout. Abbreviations: UNR = University of Nevada–Reno; agency = Nevada Division of Wildlife and Oregon Department of Fish and Wildlife; OLS = ordinary least squares; LAD = least absolute deviation; UTMN and UTME = universal transverse mercator northing and easting, respectively.

| Parameter or variable | df | Parameter estimate | <i>t</i> | <i>P</i> | 95% confidence limit | |
|--|----|--------------------|----------|----------|------------------------|----------|
| | | | | | Lower | Upper |
| UNR data, OLS regression | | | | | | |
| Constant | 1 | 6716.13 | 7.33 | 0.0001 | 4773.45 | 8658.81 |
| UTMN | 1 | -0.0011 | -5.57 | 0.001 | -0.0016 | -0.00071 |
| UTME | 1 | 0.00067 | 2.11 | 0.051 | -4.00·10 ⁻⁶ | 0.0013 |
| UNR + agency data, OLS regression | | | | | | |
| Constant | 1 | 7579.17 | 8.46 | 0.0001 | 5740.97 | 9417.38 |
| UTMN | 1 | -0.0014 | -7.11 | 0.0001 | -0.0018 | -0.00098 |
| UTME | 1 | 0.00097 | 3.62 | 0.001 | 0.00042 | 0.0015 |
| UNR + agency data, LAD regression | | | | | | |
| Constant | 1 | 6675.60 | 8.31 | 0.0001 | 5026.49 | 8324.70 |
| UTMN | 1 | -0.0011 | -6.49 | 0.0001 | -0.0015 | -0.00077 |
| UTME | 1 | 0.00059 | 2.40 | 0.024 | 0.000086 | 0.0011 |

air temperature as a surrogate measure, after Keleher and Rahel (1996) and Rahel et al. (1996). We compared our observed downstream distribution limits of Lahontan cutthroat trout to predictions corresponding to the Keleher and Rahel (1996) temperature model:

$$\text{JulyC} = -11.468 + 2.812(\text{latitude}) - 0.007(\text{elevation}) - 0.043(\text{latitude})^2.$$

This model was developed from an extensive air temperature database (615 stations) that included stations from Nevada, Idaho, Montana, Wyoming, Utah, Colorado, Arizona, and New Mexico. This equation was rearranged to predict elevation (meters) from mean July air temperature (JulyC, °C) and latitude (decimal degrees). Latitudes corresponded to coordinates from our observed downstream distribution limits, and predicted elevations of downstream distribution limits were generated with nine temperature models corresponding to mean July air temperatures of 16–24°C. The sum of squared deviations between predicted and observed elevations corresponding to each model was calculated to assess fit (Hilborn and Mangel 1997). The temperature model with the smallest sum of squared deviations was selected as that most closely approximating the air temperature corresponding to the downstream distribution limit of Lahontan cutthroat trout.

Results

Downstream Distribution Limits

Regression models of downstream distribution limits for streams with and without brook trout

were analyzed separately because Levene's test on absolute residuals from ANCOVA (Kuehl 1994) indicated that the variability of limits was strongly affected by the presence of brook trout, even when an outlier data point from a stream with a translocated population of Lahontan cutthroat trout was omitted from the data set ($F = 5.72$; $P = 0.02$; $df = 43$). This effect (unequal variances) violated standard analysis-of-variance (ANOVA) and regression assumptions (Kuehl 1994), thus invalidating parametric hypothesis tests on all streams combined.

Streams with Lahontan cutthroat trout only.—We recorded the elevations of downstream distribution limits of Lahontan cutthroat trout in 19 streams without brook trout across northern Nevada in 1997 (Figure 1). Data for an additional 11 streams were available from information on file with the Nevada Division of Wildlife and the Oregon Department of Fish and Wildlife.

Variable screening selected a two-variable model with linear latitude and longitude effects (Table 1). Initially, the regression analysis was restricted to the 19 streams we surveyed in 1997. Overall, the OLS regression model explained over 67% of the variability in downstream distribution limits of Lahontan cutthroat trout. A regression of absolute values of studentized residuals in relation to predicted distribution limits from the model showed no relationship ($F = 0.98$; $P = 0.34$; $df = 18$), indicating homogeneity of variances. Tests for normality of studentized residuals indicated model errors were normally distributed ($W = 0.92$; $P = 0.09$). The model predicted observations well;

PRESS residuals averaged 1.20 ± 114.55 m of elevation.

Next, we extended the regression analysis to include all 30 streams for which data were available. The OLS model explained over 71% of the variability in downstream distribution limits. A regression of absolute values of studentized residuals in relation to predicted distribution limits from the model indicated heterogeneity of variances ($F = 9.06$; $P = 0.001$; $df = 29$). This heterogeneity likely arose because agency surveys of distribution limits were concentrated in the northern and eastern portions of the range of Lahontan cutthroat trout (Figures 1, 3). Model errors were normally distributed ($W = 0.97$; $P = 0.67$). Inspection of influence diagnostics indicated that two streams in the Coyote Lake basin, the northern-most streams in our sample (Figure 1), qualified as influential outliers ($DFITs < -0.63$ or > 0.63) with $DFITs$ values of -0.73 and -0.95 .

The presence of influential outliers and heterogeneous variances in the OLS model prompted us to conduct LAD regression with the full data set. Results of this analysis corroborated those obtained by OLS regressions (Table 1). As might be expected, there was some variability in the precision (width of confidence intervals) for parameter estimates among the three regression models (Table 1). In particular, the weaker effect of longitude ranged from marginally nonsignificant ($P = 0.051$) in the original analysis of 19 streams to highly significant ($P = 0.001$) in the OLS model of all 30 streams.

Streams with both Lahontan cutthroat trout and brook trout.—Distribution limits for Lahontan cutthroat trout in streams with brook trout were highly variable (Figure 3) and not significantly related to latitude or longitude ($F = 2.10$; $P = 0.17$; $df = 13$). A decreasing trend in the elevation of lower distribution limits with latitude, similar to that of streams without brook trout, was evident, however (Figure 3). The statistical significance of this trend was not changed by removal of an outlier data point from a stream with a translocated population of Lahontan cutthroat trout. On average, downstream distribution limits for Lahontan cutthroat trout were 226.79 m higher in streams with brook trout than in streams without brook trout. This difference was highly significant (Wilcoxon rank-sum test: $P < 0.0001$; see also Figure 3).

Upstream Distribution Limits

Elevations of upstream distribution limits varied significantly as functions of latitude, longitude,

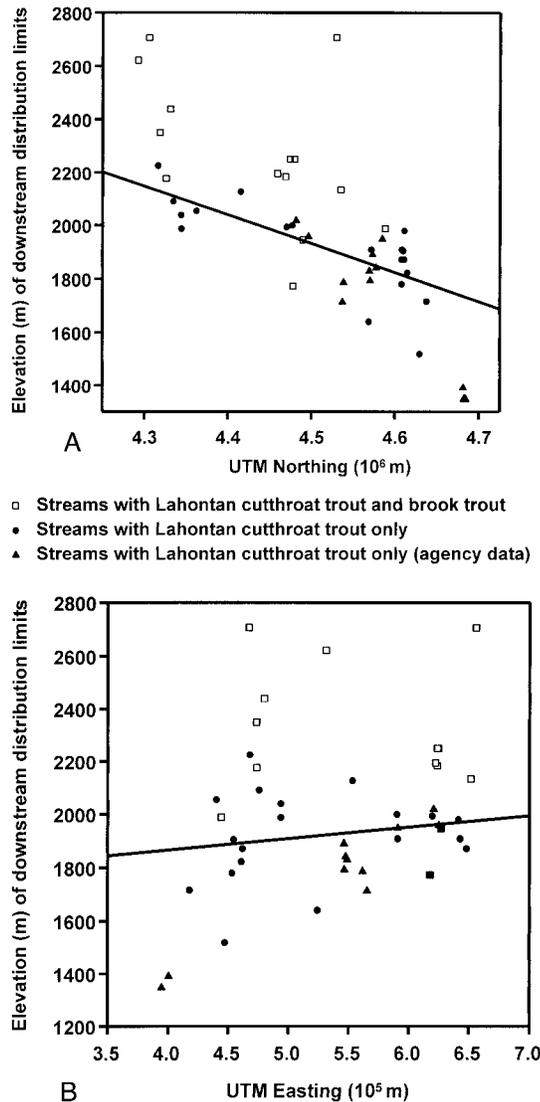


FIGURE 3.—Scatter plots showing elevations of downstream distribution limits of Lahontan cutthroat trout in streams of the eastern Lahontan basin (Figure 1) in relation to (upper panel) latitude (UTM northings) and (lower panel) longitude (UTM eastings). Univariate regression lines are fitted to streams with only Lahontan cutthroat trout surveyed in 1997 (solid circles). Lines are fitted for visual reference only (see Table 1 for multiple regression results).

and gradient, but ANCOVA indicated barrier effects were not significant ($P = 0.13$). Upstream distribution limits varied most strongly as an inverse function of latitude ($P = 0.0001$) and gradient ($P = 0.002$) and less so as a positive function of longitude ($P = 0.01$). Upstream distribution

limits were not related to stream size as measured by wetted stream width, maximum pool depth, or average depth. The model with latitude, gradient, and longitude explained 61% of the variation in the elevation of upstream distribution limits. Values of studentized residuals and DFFITS did not suggest major problems with outliers or highly influential data points. Only three data points qualified as influential outliers (DFFITS < -0.61 or > 0.61): two (DFFITS = -1.00 and 0.65) from streams with a dispersal barrier (subsurface flow and waterfall, respectively) and one (DFFITS = -0.64) from a stream with no identifiable barriers. Regressions of absolute residuals indicated no problems with heteroscedastic errors ($F = 0.89$; $P = 0.45$; $df = 42$). The Shapiro–Wilk test indicated errors were not normally distributed ($W = 0.93$; $P = 0.01$), however. Log transformation of the data failed to remedy nonnormality, but ANOVA is robust to departures from this assumption (Underwood 1997), so we did not attempt further analyses. Pearson correlation analysis revealed significant associations of maximum basin elevation with upper distribution limit of cutthroat trout ($r_s = 0.85$; $P = 0.0001$), latitude ($r_s = -0.70$; $P = 0.0001$), and gradient $r_s = 0.36$; $P = 0.02$), but not with longitude ($r_s = -0.003$; $P = 0.98$).

Correspondence of Downstream Distribution Limits to Thermal Gradients

We tested the fit of nine air temperature models to observed downstream distribution limits of Lahontan cutthroat trout. Each temperature model estimated the elevation corresponding to mean July air temperatures ranging from 16 to 24°C. Of the nine models, the data were best explained by the model corresponding to a mean July air temperature of 18°C (Figure 4). The sum of squared deviations from model predictions of our latitude–longitude model (UNR–OLS; Table 1) was 174,610 m², where the sum of squared deviations from the 18°C temperature model was 254,173 m². Squared deviations for the two next best models (19 and 17°C) were considerably larger: 460,814 m² and 823,043 m², respectively (Figure 4). Predicted elevations of downstream distribution limits from climate models paralleled those predicted by our geographic model (Figure 4).

Discussion

We found major geographic gradients in the distribution of stream-living Lahontan cutthroat trout except for populations co-occurring with nonnative brook trout. In the latter case, a geographic

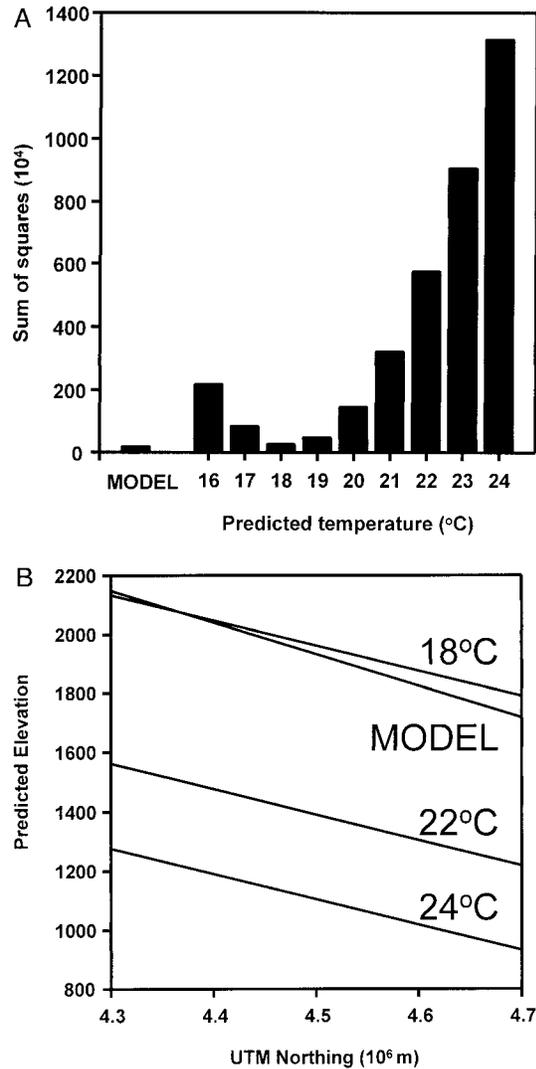


FIGURE 4.—(Upper panel) Deviations between model predictions of elevation (m) corresponding to nine mean July air temperatures (Keleher and Rahel 1996) and observed elevations of downstream distributions of Lahontan cutthroat trout surveyed in 1997. The bar corresponding to “MODEL” refers to the sum of squared deviations for the best-fitting latitude–longitude regression model of downstream distribution limits (UNR–OLS; Table 1). (Lower panel) Plots of predicted downstream elevations from three temperature models (18, 22, and 24°C) and MODEL in relation to latitude.

gradient was not evident, and the distribution of Lahontan cutthroat trout was significantly reduced when brook trout were present. Geographic gradients in downstream distribution limits of Lahontan cutthroat trout were concordant with regional thermal gradients (Figure 4), but distribu-

tion patterns differed substantially from those predicted by recent climate models for salmonids in the Rocky Mountain region (Figure 4). Below, we discuss each of these results in more detail, with an emphasis on downstream distribution limits.

Downstream Distribution Limits

Changes in downstream distribution limits may have especially important implications for the productivity and viability of trout populations. In the Basin and Range physiographic province (Grayson 1993), which includes all of the eastern Lahontan basin, streams drain north–south trending mountain ranges, flowing into alluvial valleys with gentle slopes. As a result, the vertical profile of streams is generally *j*-shaped with higher-gradient headwater reaches and lower-gradient reaches downstream. Accordingly, an increase in the elevation of downstream distribution limits will result in a much greater loss of linear stream habitat than a comparable lowering of upstream distribution limits. Loss of downstream habitats also increases the isolation of fish populations in headwater habitats, which may reduce the probability of population rescue or recolonization and thus the probability of habitat occupancy (Rieman and McIntyre 1993; Dunham et al. 1997; Dunham and Rieman 1999).

Streams with Lahontan cutthroat trout only.—In the absence of other salmonids, variability in the downstream distribution limits of stream-living Lahontan cutthroat trout populations was best explained by a model with linear latitude and longitude effects. Our model predictions were robust to the addition of distribution data collected in different streams and years (Table 1), suggesting distribution limits may be relatively constant, at least across the 20-year period over which distribution data were collected (1977–1997). Some fluctuation in distribution limits may be expected, however, because about 30% of the total variation is not explained by our model. A recent long-term study of brook and rainbow trout over a similar time period in eastern Tennessee streams similarly showed no net change in distribution limits (Strange and Habera 1998). Future annual and seasonal monitoring of distribution limits will be needed to validate predictions of the geographic model proposed here, however.

Geographic variability in downstream distribution limits of Lahontan cutthroat trout closely paralleled regional thermal gradients. Previous work on climate variability in the region has shown July air temperatures to vary geographically, being

colder in the northern and warmer in the eastern Lahontan basin (Mitchell 1976). This qualitative pattern corresponds well with patterns in the downstream distribution limit we observed for Lahontan cutthroat trout. The form of the regional model of mean July air temperatures developed by Keleher and Rahel (1996) differs somewhat from our models in that temperatures were predicted by the Keleher–Rahel model with quadratic as well as linear latitude effects but not with longitude effects. In our regression analysis of distribution limits, we screened a quadratic model of the form used by Keleher and Rahel to predict regional air temperatures, but model selection criteria favored a linear latitude–longitude model.

We expected the downstream distribution limit of Lahontan cutthroat trout to correspond with geographically defined thermal limits as modeled by Keleher and Rahel (1996) and Rahel et al. (1996). Their studies used trout distribution data from Wyoming Game and Fish Department surveys to establish a thermal limit corresponding to mean July air temperatures of 22–24°C. Our analysis of correspondence between distribution limits predicted by the regional Keleher–Rahel air temperature model and those observed for Lahontan cutthroat trout revealed, however, that downstream distribution limits corresponded most closely with a model based on a mean July air temperature of 18°C, about 4–6°C cooler than generally expected for salmonids in the Rocky Mountain region.

Why do downstream distribution limits of Lahontan cutthroat trout correspond with such cooler air temperatures? One possibility is that Lahontan cutthroat trout are unusually intolerant of warm temperatures, but this is not supported by laboratory research (Dickerson and Vinyard 1999). A second possibility is that relationships between mean July air temperature, elevation, and latitude may be unique in Nevada, and regional air temperature models developed by Keleher and Rahel (1996) may not apply. This seems unlikely as well, because Keleher and Rahel (1996) modeled an extensive 30-year (1951–1980) database of air temperatures from 615 meteorological stations throughout the Rocky Mountain region, including Nevada. A more formal analysis of geographic patterns in air temperatures may be needed, however, to explore this alternative in more detail.

A third and related possibility is that air temperature–water temperature relationships in the study area differ fundamentally from those in other parts of the region. Daily thermal maxima in the eastern Lahontan basin may exceed short-term

preference or tolerance limits for Lahontan cutthroat trout while mean temperatures remain within a suitable range. If such is the case, mean temperature may be less meaningful in terms of describing suitable thermal habitat. Variability or time of exposure to critical temperatures may be more important.

Another regional difference could be that many stream habitats in Nevada are relatively small. Accordingly, small-scale climate influences may be critical. On a local scale, air temperature–water temperature relationships can be profoundly influenced by topographic shading and by natural and human-caused variability in stream channel morphology or riparian vegetation (e.g., Beschta et al. 1987; Platts and Nelson 1989; Armour et al. 1991; Li et al. 1994). Channel and riparian alterations by activities associated with livestock grazing and agricultural development are particularly evident in the Great Basin, including the eastern Lahontan basin (Platts and Nelson 1989; Platts 1991; Nelson et al. 1992; Coffin and Cowan 1995; Myers and Swanson 1995; Gutzwiller et al. 1997; Jones et al. 1998). It generally is believed such changes have elevated summer water temperatures in streams throughout the western United States, and increased temperature has been identified as one of the primary sources of water quality impairment affecting native salmonids in the Rocky Mountain region (see papers in Gresswell 1988; Young 1995; Duff 1996) and elsewhere (e.g., Meisner 1990a, 1990b; Regier and Meisner 1990; Flebbe 1994; Eaton et al. 1995; Nakano et al. 1996).

In the preceding discussion, we have emphasized the potential influence of thermal gradients. Geographic gradients in geologic and geomorphic features of stream catchments could alternatively explain variability in downstream distribution limits observed for Lahontan cutthroat trout in this study (Nelson et al. 1992). It seems more likely, however, that thermal, geologic, and geomorphic conditions covary in the Lahontan basin and may be interrelated. As streams flow from their headwaters high on mountain slopes through different geologic and geomorphic gradients (Nelson et al. 1992), they also become warmer as stream temperatures track corresponding increases in air temperature at lower elevations (Rahel et al. 1996). Geologic and geomorphic effects on surface and groundwater discharge also may be important (Baxter et al. 1999, this issue). Further study of relationships among these factors is needed to more clearly resolve their direct and indirect re-

lationships to downstream distribution limits of Lahontan cutthroat trout.

Finally, our analysis indicated water diversions did not significantly influence downstream distribution limits, suggesting they occurred near contemporary downstream distribution limits. In three southern streams with complete irrigation diversions, however, we observed Lahontan cutthroat trout using habitats at the point where water was shunted out of the channel, suggesting that diversions were truncating downstream distribution limits to some degree. Obviously, downstream dewatering and diversions can have important impacts on fish populations by isolating upstream populations and constraining colonization and occupancy of downstream habitats, should such habitats be seasonally important dispersal corridors or become suitable following habitat restoration, for example.

Influence of nonnative brook trout on downstream distribution limits.—We found elevations of downstream distribution limits of Lahontan cutthroat trout to be significantly higher when brook trout were present. Other nonnative salmonids (brown trout, rainbow trout) were present in a few streams with brook trout, but these species occurred primarily in the lowermost reaches of streams, below brook and cutthroat occurrences. In every case, brook trout occurred directly downstream of Lahontan cutthroat trout, which tended to be concentrated in upstream reaches. This is a typical pattern of segregation among brook trout and cutthroat trout (Griffith 1988; Fausch 1989; Bozek and Hubert 1992), but specific mechanisms producing this pattern are not clear (Fausch 1988, 1989). More recent experimental evidence suggests temperature may play a role in upstream–downstream segregation of brook trout and Lahontan cutthroat trout (DeStaso and Rahel 1994).

Downstream distribution limits of Lahontan cutthroat trout in streams with brook trout did not follow the geographic patterns we observed for distribution limits in streams without brook trout, further evidence that brook trout exerts a strong effect on Lahontan cutthroat trout populations. The variability of this effect is large, however; the distribution of Lahontan cutthroat trout in some streams seems scarcely affected, whereas in others the distribution is dramatically reduced relative to streams without brook trout (Figure 3).

The large variability in the effect of brook trout on Lahontan cutthroat trout distribution suggests the possibility for habitat-specific interactions (sensu DeStaso and Rahel 1994; Harvey and Nak-

amoto 1997; Schroeter 1998). It also may be the case that variability in the timing of invasion by brook trout or the presence of dispersal barriers plays a role in the contemporary downstream distribution of Lahontan cutthroat trout. Timing of invasion may be important in some cases, but stocking records for many streams indicate brook trout have coexisted with Lahontan cutthroat trout for several decades (P. Coffin, U.S. Fish and Wildlife Service, personal communication). Dispersal barriers to upstream migration of brook trout may be locally important, but we found obvious barriers in only 3 of 15 streams with both Lahontan cutthroat trout and brook trout.

Upstream Distribution Limits

Upstream distribution limits of Lahontan cutthroat trout followed a geographic pattern that could be related to climatic variability, but strong covariation between longitude and maximum elevations of catchment basins suggested upstream distributions of Lahontan cutthroat trout may simply be a function of the latter. Three measures of stream size (mean wetted width, average maximum pool depth, average depth) did not explain any extra variability in upstream distribution limits, but stream size has been positively related to occurrence of other salmonids, including bull trout *Salvelinus confluentus* (Rieman and McIntyre 199; Dunham and Rieman 1999) and Yellowstone cutthroat trout *Oncorhynchus clarki bouvieri* (Kruse et al. 1997).

Upstream dispersal barriers did not significantly affect upstream distribution limits of Lahontan cutthroat trout. Work on upstream distribution limits of Yellowstone cutthroat trout (Kruse et al. 1997) has similarly suggested that dispersal barriers may not substantially reduce the distribution of occupied habitat. Kruse et al. (1997) pointed out that although translocated trout populations may be able to survive above barriers, natural populations are generally absent from such habitats. We followed Kruse et al. (1997) and classified vertical geologic structures higher than 1.5 m to be dispersal barriers, but cutthroat trout are capable of surmounting much higher structures (Dunham 1996). The general absence of fish populations above barriers may likely be a product of high extinction and low recolonization or population rescue probabilities in such small and isolated habitats (see Rieman et al. 1993). This result implies translocations of cutthroat trout above barriers in headwater habitats may only be viewed as a short-term strategy for population recovery or restora-

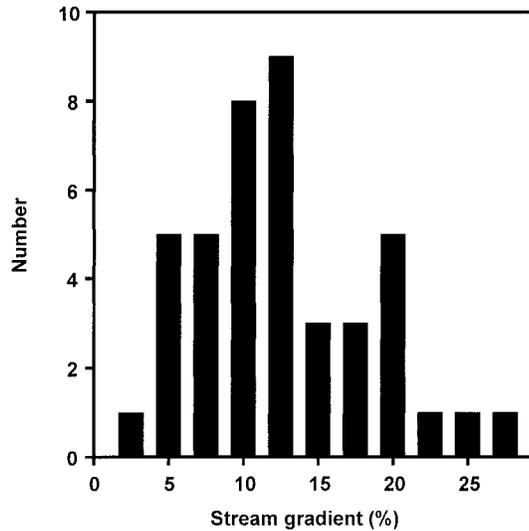


FIGURE 5.—Distribution of stream gradients observed at upstream distribution limits of Lahontan cutthroat trout.

tion, because such habitats are unlikely to support Lahontan cutthroat trout in the long term.

Stream gradient was positively correlated with upstream distribution limits, but also positively correlated with maximum basin elevation. The positive relationship between elevation of upstream distribution limits and stream gradient may therefore be an artifact of covariation between stream gradient and maximum basin elevation (as with longitude).

Stream gradients at upstream distribution limits generally were greater than those associated with upstream distribution limits of Yellowstone cutthroat trout (Kruse et al. 1997). Yellowstone cutthroat trout rarely occurred in stream habitats with gradients exceeding 10% (Kruse et al. 1997; see also Bozek and Hubert 1992). Stream gradients at upstream distribution limits in our study averaged 11.6%, ranging from 2.1 to 26.7% (Figure 5). Results of this study suggest upstream limits of Lahontan cutthroat trout may simply be constrained by the maximum elevation of stream basins and are little influenced by steep gradients.

Conclusions

Patterns of distribution limits observed for Lahontan cutthroat trout in this study suggest important local and geographic influences, particularly for downstream distribution limits. On a local scale, it is clear that Lahontan cutthroat trout occupy less potentially suitable habitat when brook

trout are present, but this effect is highly variable. The geographic model of downstream distribution limits for allopatric Lahontan cutthroat trout provided an important context for evaluating the effects of brook trout. On a geographic scale, we were able to accurately predict the downstream distribution limit of allopatric Lahontan cutthroat trout populations in streams using only latitude and longitude as predictors, but we were not able to unequivocally determine causes of this relationship. Correlative evidence suggests thermal gradients likely play a role in determining downstream distributions, but other factors such as geomorphology and geology may play a direct or indirect role as well. Large discrepancies between predictions of more generalized climate-based distribution models for trout (Keleher and Rahel 1996) and downstream distribution limits we observed for Lahontan cutthroat trout point to the need for a better understanding of causal mechanisms. Such will require more detailed experimental and observational field study. Upstream distribution limits varied as a function of latitude and stream gradient, but effects of these variables were likely confounded with topographical variability within the region. Local influences (stream gradient, size, and barriers) seemed to matter less in terms of upstream distribution limits, suggesting Lahontan cutthroat trout may be relatively opportunistic in regard to selection of summer habitats in headwater streams.

Acknowledgments

This research was supported in part by the U.S. Forest Service's Rocky Mountain (formerly Intermountain) Research Station (INT-96089-RJVA), and the U.S. Fish and Wildlife Service's Region 1 (DOI-FW-1960007). Additional support was provided by the Biological Resources Research Center, University of Nevada-Reno. We thank C. Carreno, G. Guscio, H. Miyagawa, M. Meeuwig, B. Prusha, and S. Williamson for long hours of field assistance, and the Nevada Division of Wildlife and the Oregon Department of Fish and Wildlife for sharing data on distribution limits. R. Bamford helped produce Figure 1. Work on Lahontan cutthroat trout was authorized by Region 1 of the U.S. Fish and Wildlife Service and the Nevada Division of Wildlife (permits S-9039, S-0153, S-12357, S-14065, and S-15425). Three anonymous reviewers and P. Connolly provided helpful comments on an earlier version of this manuscript.

References

- Armour, C. L., D. A. Duff, and W. Elmore. 1991. The effects of livestock grazing on riparian and stream ecosystems. *Fisheries* 16(1):7-11.
- Baxter, C. V., C. A. Frissell, and F. R. Hauer. 1999. Geomorphology, logging roads, and the distribution of bull trout spawning in a forested river basin: implications for management, and conservation. *Transactions of the American Fisheries Society* 128: 854-867.
- Belsley, D. A., E. Kuh, and R. E. Welsch. 1980. *Regression diagnostics*. Wiley, New York.
- Beschta, R. L., R. E. Bilby, G. W. Brown, L. B. Holtby, and T. D. Hofstra. 1987. Stream temperature and aquatic habitat: fisheries and forestry interactions. Pages 191-132 in E. O. Salo, and T. W. Cundy, editors. *Streamside management: forestry and fishery interactions*. University of Washington, Institute of Forest Resources, Contribution 57, Seattle.
- Bozek, M. A., and W. A. Hubert. 1992. Segregation of resident trout in streams as predicted by three habitat dimensions. *Canadian Journal of Zoology* 70: 886-890.
- Cody, R. P., and J. K. Smith. 1991. *Applied statistics and the SAS programming language*, 2nd edition. Elsevier, New York.
- Coffin, P. D., and W. F. Cowan. 1995. Lahontan cutthroat trout (*Oncorhynchus clarki henshawi*) recovery plan. U.S. Fish and Wildlife Service, Region 1, Portland, Oregon.
- Conover, D. O. 1990. The relation between capacity for growth and length of growing season: evidence for and implications of countergradient variation. *Transactions of the American Fisheries Society* 119: 416-430.
- Cunjak, R. A. 1996. Winter habitat of selected stream fishes and potential impacts from land-use activity. *Canadian Journal of Fisheries and Aquatic Sciences* 53(Supplement 1):267-282.
- DeStaso, J., III, and F. J. Rahel. 1994. Influence of water temperature on interactions between juvenile Colorado River cutthroat trout and brook trout in a laboratory stream. *Transactions of the American Fisheries Society* 123:289-297.
- Dickerson, B. R., and G. L. Vinyard. 1999. Effects of high chronic temperatures and diel temperature cycles on the survival and growth of Lahontan cutthroat trout. *Transactions of the American Fisheries Society* 128:516-521.
- Duff, D. A., editor. 1996. *Conservation assessment for inland cutthroat trout status and distribution*. USDA Forest Service, Intermountain Region, Ogden, Utah.
- Dunham, J. B. 1996. The population ecology of stream-living Lahontan cutthroat trout (*Oncorhynchus clarki henshawi*). Doctoral dissertation. University of Nevada, Reno.
- Dunham, J. B., and B. E. Rieman. 1999. Metapopulation structure of bull trout: influences of habitat size, isolation, and human disturbance. *Ecological Applications* 9:642-655.
- Dunham, J. B., G. L. Vinyard, and B. E. Rieman. 1997.

- Habitat fragmentation and extinction risk of Lahontan cutthroat trout (*Oncorhynchus clarki henshawi*). *North American Journal of Fisheries Management* 17:910–917.
- Eaton, J. G., and six coauthors. 1995. A field information-based system for estimating fish temperature tolerances. *Fisheries* 20(4):10–18.
- Fausch, K. D. 1988. Tests of competition between native and introduced salmonids in streams: what have we learned? *Canadian Journal Fisheries and Aquatic Sciences* 45:2238–2246.
- Fausch, K. D. 1989. Do gradient and temperature affect distribution of, and interactions between juvenile brook char and other salmonids in streams? *Physiology and Ecology Japan 1* (Special Volume):303–322.
- Flebbe, P. A. 1994. A regional view of the margin: salmonid abundance and distribution in the southern Appalachian mountains of North Carolina and Virginia. *Transactions of the American Fisheries Society* 123:657–667.
- Freund, R. J., and R. C. Littell. 1991. SAS system for regression. SAS Institute, Cary, North Carolina.
- Grayson, D. K. 1993. *The desert's past: a natural prehistory of the Great Basin*. Smithsonian Institution Press, Washington, D.C.
- Gresswell, R. E., editor. 1988. Status and management of cutthroat trout. American Fisheries Society, Symposium 4, Bethesda, Maryland.
- Griffith, J. S. 1988. Review of competition between cutthroat trout and other salmonids. Pages 134–140 in R. E. Gresswell, editor. Status and management of cutthroat trout. American Fisheries Society, Symposium 4, Bethesda, Maryland.
- Gutzwiller, L. A., R. M. McNatt, and R. D. Price. 1997. Watershed restoration and grazing practices in the Great Basin: Marys River of Nevada. Pages 360–380 in J. E. Williams, C. A. Wood, and M. P. Dombek, editors. *Watershed restoration: principles and practices*. American Fisheries Society, Bethesda, Maryland.
- Hall, J. D., P. A. Bisson, and R. E. Gresswell. 1997. Sea-run cutthroat trout: biology, management and future conservation. American Fisheries Society, Oregon Chapter, Corvallis.
- Harvey, B. C., and R. J. Nakamoto. 1997. Habitat-dependent interactions between two size-classes of juvenile steelhead in a small stream. *Canadian Journal of Fisheries and Aquatic Sciences* 54:27–31.
- Hawkins, C. P., and ten coauthors. 1993. A hierarchical approach to classifying stream habitat features. *Fisheries* 18(6):3–11.
- Hilborn, R., and M. Mangel. 1997. *The ecological detective: confronting models with data*. Monographs in Population Biology 28.
- Jones, K. K., J. M. Dambacher, B. G. Lovatt, A. G. Talabere, and W. Bowers. 1998. Status of Lahontan cutthroat trout in the Coyote Lake basin, southeast Oregon. *North American Journal of Fisheries Management* 18:308–317.
- Keleher, C. J., and F. J. Rahel. 1996. Thermal limits to salmonid distributions in the Rocky Mountain region and potential habitat loss due to global warming: a geographic information system (GIS) approach. *Transactions of the American Fisheries Society* 125:1–13.
- Kruse, C. G., W. A. Hubert, and F. J. Rahel. 1997. Geomorphic influences on the distribution of Yellowstone cutthroat trout in the Absaroka Mountains, Wyoming. *Transactions of the American Fisheries Society* 126:418–427.
- Kuehl, R. O. 1994. *Statistical principles of research design and analysis*. Duxbury Press, Belmont, California.
- La Rivers, I. 1962. *Fishes and fisheries of Nevada*. Nevada State Fish and Game Commission, Reno.
- Li, H. W., G. A. Lamberti, T. N. Pearsons, C. K. Tait, J. L. Li, and J. C. Buckhouse. 1994. Cumulative effects of riparian disturbances along high desert trout streams of the John Day basin, Oregon. *Transactions of the American Fisheries Society* 123:627–640.
- Meisner, J. D. 1990a. Potential loss of thermal habitat for brook trout, due to climatic warming, in two southern Ontario streams. *Transactions of the American Fisheries Society* 119:282–291.
- Meisner, J. D. 1990b. Effect of climate warming on the southern margins of the native range of brook trout, *Salvelinus fontinalis*. *Canadian Journal of Fisheries and Aquatic Sciences* 47:1065–1070.
- Miller, R. R., and J. R. Alcorn. 1943. The introduced fishes of Nevada, with a history of their introduction. *Transactions of the American Fisheries Society* 73:173–193.
- Mitchell, V. L. 1976. The regionalization of climate in the western United States. *Journal of Applied Meteorology* 15:920–927.
- Myers, R. H. 1990. *Classical and modern regression with applications*, 2nd edition. Duxbury Press, Belmont, California.
- Myers, T. J. 1995. *The stochastic structure of rangeland streams*. Doctoral dissertation. University of Nevada, Reno.
- Myers, T. J., and S. Swanson. 1995. Impact of deferred rotation grazing on stream characteristics in central Nevada: a case study. *North American Journal of Fisheries Management* 15:428–439.
- Nakano, S., F. Kitano, and K. Maekawa. 1996. Potential fragmentation and loss of thermal habitats for charrs in the Japanese archipelago due to climatic warming. *Freshwater Biology* 36:711–722.
- Nelson, R. L., W. S. Platts, and O. Casey. 1987. Evidence for variability in spawning behavior of interior cutthroat trout in response to environmental uncertainty. *Great Basin Naturalist* 47:480–487.
- Nelson, R. L., W. S. Platts, D. P. Larsen, and S. E. Jensen. 1992. Trout distribution and habitat in relation to geology and geomorphology in the North Fork Humboldt River drainage, northeastern Nevada. *Transactions of the American Fisheries Society* 121:405–426.
- Overton, K. O., S. P. Wollrab, B. C. Roberts, and M. A. Radko. 1997. R1/R4 (Northern/Intermountain Regions) fish and fish habitat standard inventory

- procedures handbook. U.S. Forest Service, General Technical Report INT-GTR-346.
- Platts, W. S. 1991. Livestock grazing. Pages 389–423 in W. R. Meehan, editor. Influences of forest and rangeland management on salmonid fishes and their habitats. American Fisheries Society, Special Publication 19, Bethesda, Maryland.
- Platts, W. S., and R. L. Nelson. 1989. Stream canopy and its relationship to salmonid biomass in the intermountain West. *North American Journal of Fisheries Management* 9:446–457.
- Rahel, F. J., C. J. Keleher, and J. L. Anderson. 1996. Potential habitat loss and population fragmentation for coldwater fish in the North Platte River drainage of the Rocky Mountains: response to climate warming. *Limnology and Oceanography* 41:1116–1123.
- Regier, H. A., and J. D. Meisner. 1990. Anticipated effects of global climate change on freshwater fishes and their habitat. *Fisheries* 15(6):10–15.
- Rieman, B. E., D. Lee, J. D. McIntyre, K. Overton, and R. Thrown. 1993. Consideration of extinction risks for salmonids. U.S. Forest Service Technical Bulletin 14.
- Rieman, B. E., and J. D. McIntyre. 1993. Demographic and habitat requirements for conservation of bull trout. U.S. Forest Service, General Technical Report INT-GTR-302.
- Rieman, B. E., and J. D. McIntyre. 1995. Occurrence of bull trout in naturally fragmented habitat patches of varied size. *Transactions of the American Fisheries Society* 124:285–296.
- Scarnecchia, D. L., and E. P. Bergerson. 1987. Trout production and standing crop in Colorado's small streams, as related to environmental features. *North American Journal of Fisheries Management* 7:315–330.
- Schroeter, R. E. 1998. Segregation of stream-dwelling Lahontan cutthroat trout and brook trout: patterns of occurrence and mechanisms for displacement. Master's thesis. University of Nevada, Reno.
- Shapiro, S. S., and M. B. Wilk. 1965. An analysis of variance test for normality (complete samples). *Biometrika* 52:591–611.
- Shuter, B. J., and J. R. Post. 1990. Climate change, population viability, and the zoogeography of temperate fishes. *Transactions of the American Fisheries Society* 119:314–336.
- StataCorp. 1997. Stata statistical software: release 5.0. StatCorp, College Station, Texas.
- Stefan, H. B., and E. B. Preud'homme. 1993. Stream temperature estimation from air temperature. *Water Resources Bulletin* 29:27–45.
- Strange, R. J., and J. W. Habera. 1998. No net loss of brook trout distribution in areas of sympatry with rainbow trout in Tennessee streams. *Transactions of the American Fisheries Society* 127:434–440.
- Terrell, J. W., B. S. Cade, J. Carpenter, and J. M. Thompson. 1996. Modeling stream fish habitat limitations from wedge-shaped patterns of variation in standing stock. *Transactions of the American Fisheries Society* 125:104–117.
- Underwood, A. J. 1997. *Experiments in ecology*. Cambridge University Press, New York.
- Van Winkle, W., K. A. Rose, B. J. Shuter, H. I. Jager, and B. D. Holcomb. 1997. Effects of climatic temperature change on growth, survival, and reproduction of rainbow trout: predictions from a simulation model. *Canadian Journal of Fisheries and Aquatic Sciences* 54:2526–2542.
- White, G. C., D. R. Anderson, K. P. Burnham, and D. L. Otis. 1982. Capture–recapture and removal methods for sampling closed populations. Los Alamos National Laboratory, LA-8787-NERP, Los Alamos, New Mexico.
- Young, M. K., editor. 1995. Conservation assessment for inland cutthroat trout. U.S. Forest Service General Technical Report RM-256.