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Influence of Maximum Water Temperature on Occurrence of Lahontan Cutthroat Trout within Streams

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Abstract.—We measured water temperature at 87 sites in six streams in two different years (1998 and 1999) to test for association with the occurrence of Lahontan cutthroat trout *Oncorhynchus clarki henshawi*. Because laboratory studies suggest that Lahontan cutthroat trout begin to show signs of acute stress at warm (>22°C) temperatures, we focused on the maximum daily temperature. The maximum daily temperature associated with the occurrence of Lahontan cutthroat trout ranged from 18.9°C to 28.5°C. Occurrence was more likely at colder (<26°C) sites. In two streams, the maximum daily temperature associated with the occurrence of these trout was relatively cool (≤20°C). In these streams, the response to temperature may have been modified by extreme declines in streamflow in late summer. The air temperatures measured during the study were not consistently related to maximum water temperatures, but air temperature is useful for predicting the distribution of Lahontan cutthroat trout at larger scales (e.g., the geographic pattern of fish distribution among streams as distinct from occurrence within streams). The results of this work suggest a link between the thermal tolerance of individuals in the laboratory and the occurrence of fish within streams and a provide a mechanism for the observed geographic patterns in the distribution of local populations of Lahontan cutthroat trout.

Temperature plays a key role in determining the distribution of many aquatic organisms (Magnuson et al. 1979). Temperature has been a particular focus for salmonid fishes due to their requirement for relatively cold water (Elliott 1981). Past research has linked salmonid distributions to several indicators of temperature, including elevation gradients associated with climate (Fausch et al. 1994; Flebbe 1994), modeled air temperature (Keleher and Rahel 1996; Rieman et al. 1997), measured (Nakano et al. 1996) and modeled (Meisner 1990) groundwater temperature, and measured stream temperature (Torgerson et al. 1999). While the latter most directly affects fish, detailed information on stream temperatures is often limited or expensive to obtain, so alternative indicators (e.g., air temperature) can be useful (e.g., Stoneman and Jones 1996). The utility of a particular indicator may depend on the scale of inference. For example, the distribution of fish within a local area may be related to small gradients in stream temperature (e.g., Ebersole et al. 2001), but regional distributions may be indicated by broad-scale climatic gradients (e.g., Fausch et al. 1994; Rieman et al. 1997; Dunham et al. 1999).

In this study, we focused on patterns of occurrence of Lahontan cutthroat trout *Oncorhynchus clarki henshawi* within streams and the possible influence of temperature on those patterns. This subspecies of cutthroat trout is distributed within the Great Basin desert along the southern margin of the species' range (Behnke 1992). The climates of this region are believed to be only marginally suitable for salmonids in general because of their relatively warm temperatures, and populations may occur only at higher elevations (Keleher and Rahel 1996; Dunham et al. 1999). Previous laboratory work on thermal tolerance suggests that the occurrence of Lahontan cutthroat trout is related to temperature because fish can show signs of stress (e.g., decreased growth and appetite and increased mortality) when the maximum water temperature exceeds 22°C, even for short (<1 d) periods of time (Vigg and Koch 1980; Dickerson and Vinyard 1999; Meeuwig 2000). The distribution of Lahontan cutthroat trout in streams across the eastern Lahontan basin can be predicted

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by large-scale elevation and climatic (summer air temperature) gradients (Dunham et al. 1999), but there is no direct evidence to link fish occurrence in the field to air or stream temperature gradients at a local scale (e.g., within streams).

To better understand thermal habitat relationships on a local scale, we studied the occurrence of Lahontan cutthroat trout at sites within streams in relation to stream temperature. Patterns of thermal habitat use in the field were compared with the results of laboratory studies of the responses of Lahontan cutthroat trout to temperature (Vigg and Koch 1980; Dickerson and Vinyard 1999; Meeuwig 2000). We also examined the correlation between air and water temperatures at this scale. Our results allowed us to assess the utility of stream temperature as an indicator of the distribution of Lahontan cutthroat trout within streams. Finally, we contrasted our results with previous work on Lahontan cutthroat trout distributions at larger spatial scales (e.g., Dunham et al. 1999) to better understand scale-dependent relationships with different indicators of temperature.

Methods

Study system.—The Lahontan cutthroat trout is endemic to the Lahontan basin of northeastern California, southeastern Oregon, and northern Nevada. The Lahontan basin is part of the Great Basin desert, which is characterized by hot summers, cool winters, and the majority of precipitation falling as snow at higher elevations in the winter (Peterson 1994). The topography in this region is characterized as ''basin and range,'' with north−south trending mountain ranges and intervening alluvial valleys (Morris and Stubben 1994). Under current conditions, streams draining these mountain ranges often lose surface flow in the summer as they flow onto alluvial valley floors. The stream habitats occupied by Lahontan cutthroat trout are typically small, with summer low-flow wetted widths of less than 6 m (Jones et al. 1998; Dunham et al. 2002a).

Study streams were dispersed throughout the eastern half of the Lahontan basin, including the Coyote Lake, Quinn River, and Humboldt River basins (Figure 1). The broad geographic distribution of the study streams was chosen to capture a wide range of conditions. In selecting streams for this work, however, we avoided those with known movement barriers or populations of nonnative trout that could confound the influences of temperature (Dunham et al. 1999, 2002a). Three streams with populations of Lahontan cutthroat trout (Frazer, Threemile, and Willow creeks) were studied in both 1998 and 1999. In addition, Edwards Creek was studied in 1998 and Carville and Dixie creeks in 1999. The populations in one stream (Edwards Creek) were derived from transplants of Lahontan cutthroat trout (Nielsen and Sage 2002). Edwards Creek lies just outside of the Lahontan basin (Figure 1).

Sampling water and air temperatures.—We used a standardized protocol to sample temperatures with digital temperature data loggers (Chandler et al., in press). The model of data logger that we used (Hobo Temp; Onset Computer Corporation, Pocasset, Massachusetts) measures temperature to within 0.7°C and records temperatures within a range of 0–43°C. To correct for instrument bias, we calibrated the temperature loggers before or after sampling (or both) following the manufacturer's specifications.

We attempted to characterize the temperatures of streams as opposed to those of the groundwater or localized thermal refugia (Ebersole et al. 2001). The water temperature at each site was measured with a handheld thermometer to check for localized heterogeneity. Data loggers were placed within the well-mixed portion of the main flow (thalweg) of the active stream channel and out of contact with direct solar radiation. This allowed us to measure the stream temperatures that should more generally be of importance to the distribution of fishes. Our definition of ''stream'' temperature is not the same as the temperature at the surface of the water, which is often measured by remote sensing methods (see Torgerson et al. 1999).

Air temperature data loggers were suspended from streamside trees or shrubs and out of contact with direct solar radiation. In 1998, air temperature loggers were placed at every water temperature sampling location. In 1999, a single air temperature logger was placed at the midpoint (up- and downstream direction) of sampling within each stream. Data loggers were programmed to record the temperature every 30 min.

Data loggers were placed in a longitudinal (up- and downstream) array of sites within streams to bracket the known or suspected downstream distribution limits of Lahontan cutthroat trout. This focused sampling at or near the areas where thermal regimes were expected to exceed the tolerance of this subspecies. Within each stream, we sampled 7–10 sites, depending on access, time, and physical constraints (e.g., lack of surface flow). Sites were generally 600 m apart, but spacing varied due to the loss or failure of data loggers.

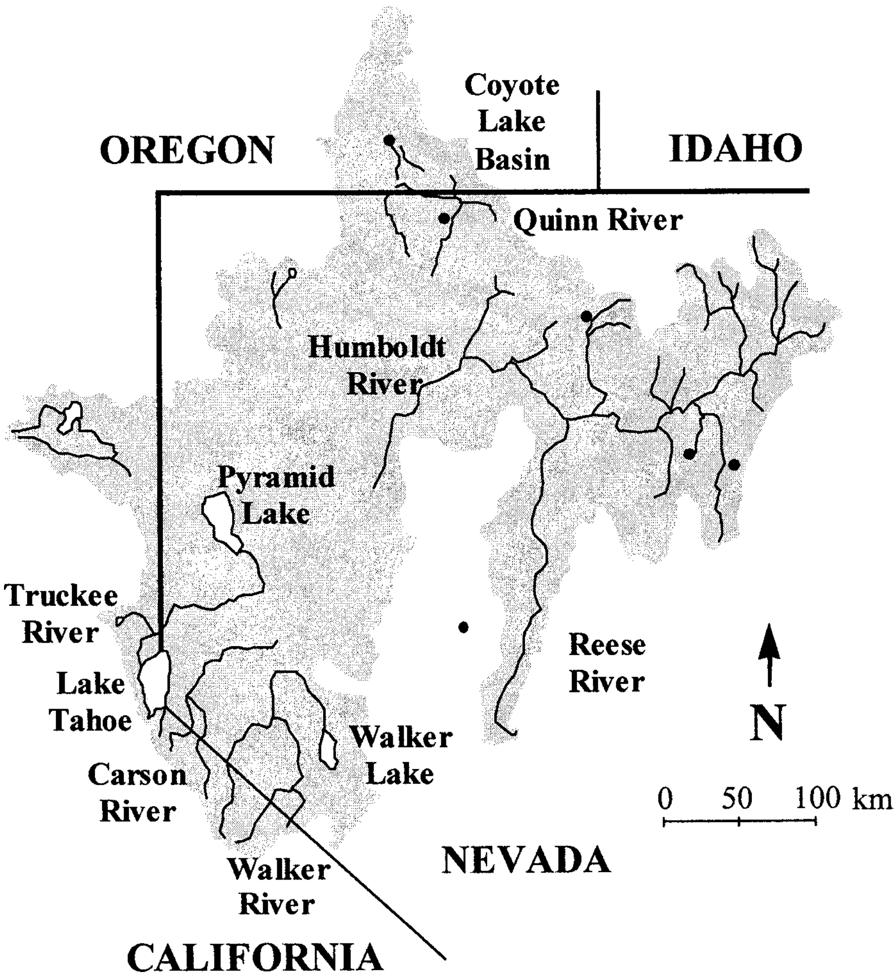

FIGURE 1.—Map of study stream locations in the Lahontan basin system (gray shading). Dots denote the study streams; their names, from north to south, are as follows: Willow Creek, Threemile Creek, Frazer Creek, Dixie Creek, Carville Creek, and Edwards Creek.

Water temperatures were sampled from 15 July to 15 September in 1998 and from 1 July to 15 September in 1999. We assumed that the maximum water temperatures occurred within this temporal window. (Prior to the study, we examined long-term climate records from monitoring stations throughout the region to confirm that maximum air temperatures were likely to be observed at this time of year.) Long-term water temperature data are not widely available, but we assumed that the coincidence of high levels of solar radiation and long photoperiods, coupled with declining streamflows in the latter part of the summer, would lead to maximum water temperatures during this time period.

Fish sampling.—Fish sampling followed procedures established by Dunham et al. (1999). We used backpack electrofishers to survey for the occurrence of Lahontan cutthroat trout within 150 m up- and downstream of each temperature sampling site. If fish were found within this 300-m reach, the cutthroat trout were scored as ‘‘present.’’ In 1998, fish occurrence was determined once during the summer season (15 July−15 September). In 1999, streams were sampled several (≥3) times during the summer to confirm that fish distributions were consistent (i.e., that fish presence or absence remained the same within 150 m of the sites sampled for temperature) over the summer season. Previous work on redband trout *O. mykiss* and Bonneville cutthroat trout *O. c. utah* in adjacent areas with similar conditions also found that downstream fish distributions in streams were constant over the summer season (Zoellick 1999; Schrank et al. 2003).

Data screening and analysis.—Water temperature data were screened visually for unusual "spikes," that is, large fluctuations associated with instrument malfunction or stream desiccation (Chandler et al., in press). We used the maximum daily water temperature (i.e., the warmest single observation recorded during the summer) to relate to the occurrence of Lahontan cutthroat trout. This measure of temperature provided an indication of acute temperature exposure, which has been shown to have important influences on the behavior of Lahontan cutthroat trout in the laboratory (Meeuwig 2000).

Parametric methodswere found to be inappropriate for analyzing the associations between fish occurrence and temperature, so we opted for a nonparametric Kruskal–Wallis analysis of variance (ANOVA) to test for differences in temperatures between sites with and without Lahontan cutthroat trout sampled in both years. The results of this overall test were complemented by direct interpretation of the data for each stream and year.

For data on water and air temperatures collected at paired sites in 1998, we used Spearman rank correlation to relate maximum daily temperatures in each medium. Our objective was to test the correspondence between the maximum air and water temperatures observed over the entire summer, not to relate those temperatures on a daily basis. Air temperatures were not modeled directly in relation to the occurrence of Lahontan cutthroat trout because the correlations between air and water temperatures were not consistent (see below).

Results

The mean dates for maximum daily water temperature in streams were 5 August and 29 July in 1998 and 1999, respectively. Because we did not begin monitoring temperatures until 15 July in 1998, there is some possibility that the maximum temperature occurred prior to that date. In 1998, the earliest date for which the maximum daily temperature was observed in a stream was 18 July, only 3 d after sampling was initiated. In 1999, water temperature monitoring was initiated by 1 July. Maximum water temperatures were generally observed after 15 July, but there were exceptions in some streams. In Frazer Creek, the maximum water temperature at sites occupied by Lahontan cutthroat trout occurred on 12 July and after 15 July 1999. Maximum water temperatures in unoccupied sites were also observed on 12 July in Frazer Creek in 1999. The correlation between maximum water and air temperatures measured at paired sites in four streams (Edwards, Frazer, Threemile, and Willow creeks) in 1998 was highly variable (Figure 2). Spearman rank correlations ranged between 0.17 and 0.88 (mean = 0.48). Only one of these correlations (r_s = 0.88) was statistically significant (P = 0.002), but the overall correlation between air and water temperatures was moderate and statistically significant (r_s = 0.63, $P < 0.001$, n = 33).

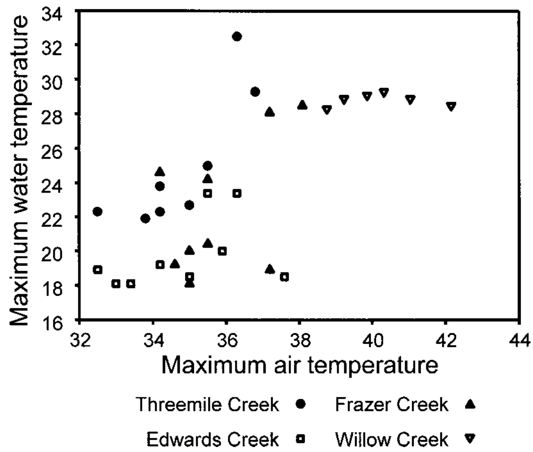

FIGURE 2.—Relationships between the maximum water and air temperatures (°C) recorded at paired sites in four streams in 1998.

In four streams (Carville, Edwards, Frazer, and Threemile creeks), streamflows declined dramatically during the summer season, particularly in downstream sites where the warmest temperatures were also observed (Figure 3). The flows at downstream sites in these streams occasionally became intermittent. The flows in Dixie and Willow creeks also declined during the summer, but not nearly to the extent observed in other streams. In Edwards Creek, a large influx of groundwater caused a large (>4°C) drop in temperature at the third-most downstream site (Figure 3). In general, however, stream temperatures increased from up- to downstream, with particularly rapid increases between sites in streams with the greatest loss of streamflow (Figure 3).

Maximum temperatures were significantly different at sites with and without Lahontan cutthroat trout (Kruskal–Wallis test; χ^2 = 15.8, df = 1, $P <$ 0.0001). Lahontan cutthroat trout occurred most often at cooler sites (<26°C, Figure 3) but also occurred at sites with maximum daily temperatures

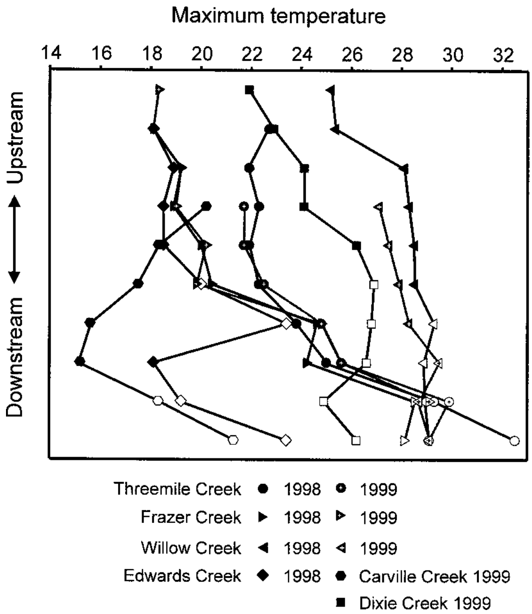

FIGURE 3.—Maximum water temperatures recorded at sites with Lahontan cutthroat trout present (solid symbols) or absent (open symbols) in five streams sampled in 1998 and 1999. Symbols are connected by lines to facilitate tracking of temperatures along the up- and downstream gradient sampled in each stream. Lighter lines connect symbols for streams sampled in 1999 that were also sampled in 1998.

up to 28.5°C and were found to be absent from sites with summer maximum temperatures as low as 18.9°C (Figure 3). The occurrence of cutthroat trout at the site with the highest temperature (28.5°C) was confirmed on the day that temperature was observed (A. Talabere, Oregon Department of Fish and Wildlife, personal communication). The thermal profiles of the streams sampled in both 1998 and 1999 were similar (Figure 3), as were the maximum temperatures associated with the occurrence of Lahontan cutthroat trout. For streams sampled in 1998 and 1999, the difference in maximum daily temperature associated with the occurrence of cutthroat trout ranged from 0.2°C to 0.6°C.

Discussion

Based on the responses of cutthroat trout to temperature in the laboratory, we expected the occurrence of fish within streams to be constrained by stream temperature. Within most of the streams that we studied, Lahontan cutthroat trout occurred at sites with temperatures observed to cause sublethal stress (>22°C; Vigg and Koch 1980; Dickerson and Vinyard 1999; Meeuwig 2000) or mortality (>24°C; Dickerson and Vinyard 1999) in the laboratory under relatively optimal conditions (e.g., unlimited food, dissolved oxygen saturation, low ammonia levels; Poole et al. 2001). The warmest temperatures associated with the occurrence of cutthroat trout were in observed in Willow Creek (Figure 3), but these temperatures did not exceed 28°C for more than two consecutive hours (our unpublished data). In laboratory tests, about 20% of Lahontan cutthroat trout survived up to 24 h of exposure to a constant temperature of 28°C and showed no mortality over a week of exposure to a variable thermal regime with temperatures exceeding 26°C for only 1 h within a day (Dickerson and Vinyard 1999). With such short exposures to very warm (>28°C) temperatures, it is possible that fish could survive, albeit with lower probability than at cooler temperatures.

The absence of Lahontan cutthroat trout from sites with warmer temperatures could be due to emigration to cooler sites or to mortality resulting directly or indirectly from temperature. We did not collect information to explore these mechanisms, but observations at sites where the maximum temperature exceeded 28°C in Willow Creek indicate that abundance was reduced substantially as the stream warmed over the summer (Talabere, personal communication). Schrank et al. (2003) examined the abundance, movements, and mortality of Bonneville cutthroat trout in an enclosed section of stream and found no responses, in spite of water temperatures near the lethal maximum of 27°C (Johnstone and Rahel 2003) on three separate days. The survival of Lahontan cutthroat trout is also severely reduced at such temperatures (Dickerson and Vinyard 1999), but more detailed study of individual and population responses of Lahontan cutthroat trout to differing thermal conditions in the field is needed to better understand how the patterns of occurrence are generated.

Until better evidence is available, we concur with the cautionary statements by Poole et al. (2001) suggesting that field observations of fish under thermal conditions that exceed laboratory tolerances must be supplemented with additional information if one is to make inferences about the health of individuals or populations. It is possible that at some times and in some places Lahontan cutthroat trout will be found under potentially stressful thermal conditions, but our results suggest that such cases will be uncommon and that even there the duration and extent of thermal exposure will be limited.

A further caution in interpreting field observations is the potential influence of modifying factors that are not easily mimicked by laboratory studies (Poole et al. 2001).The potential influence of modifying factors was highlighted by the spatial variation in the response of Lahontan cutthroat trout distributions to temperature (Figure 2). In two streams, the maximum daily temperature associated with the occurrence of these trout was relatively cool (≤20°C). In both of these streams, the response of fish to temperature may have been modified by extreme declines in streamflow in late summer (J. Dunham and R.Schroeter, personal observations). Loss of flow is common in streams of the Great Basin desert as they flow from mountain slopes onto alluvial valleys. As flows decline, fish are often trapped in intermittent pools and may be vulnerable to other stressors (e.g., predators and changes in water quality) that could individually or jointly modify their response to temperature gradients (Poole et al. 2001). Similarly, Sloat (2001) found that in small streams in Montana westslope cutthroat trout *O. c. lewisi* occurred only in cool (maximum daily temperature, ≤16.5°C) sites, possibly reflecting local influences of dispersal barriers and nonnative trout rather than temperature. Our work on Lahontan cutthroat trout suggests that these influences can be locally important as well (Dunham et al. 1999, 2002a).

The utility of maximum air temperature for discriminating fish distributions in our study system was limited by inconsistent associations between maximum air and water temperatures at a local scale (Figure 2). Regional differences in the relationships between fish distribution and water and air temperature probably reflect the degree of correlation between the latter. In areas with strong air−water temperature correlations, either measure may prove useful for delineating suitable habitats (Stoneman and Jones 1996). The complexity of the relationships between air and water temperatures reflects a broad array of physical influences not considered in this study (Isaak and Hubert 2001; Poole and Berman 2001). In spite of the uncertain connection between air and water temperatures, air temperature has been shown to be useful for modeling salmonid distributions at larger spatial scales, where the variability in temperature should be larger and more informative. Examples include the distribution of Lahontan cutthroat trout among streams across the eastern Lahontan basin (Dunham et al. 1999), the distribution of bull trout *Salvelinus confluentus* in the interior Columbia River basin (Rieman et al. 1997), and the distribution of salmonids in general in the interior western United States (Keleher and Rahel 1996).

Conclusions and Management Implications

The importance of temperature to Lahontan cutthroat trout has been demonstrated at several spatial scales and levels of biological organization. Studies in the laboratory (Vigg and Koch 1980; Dickerson and Vinyard 1999; Meeuwig 2000) have examined the growth, survival, and behavior of individual fish exposed to different thermal regimes. In the field, fish distributions probably represent both individual and population-level responses to temperature. Within streams with perennial streamflow, summer maximum temperatures play a dominant role in determining fish occurrence. Among streams within the region, distribution limits are tied strongly to elevation and climatic (air temperature) gradients and thus to the amount of suitable habitat within a watershed (Dunham et al. 1999). Within the eastern Lahontan basin, watersheds with larger areas of potentially suitable habitat are more likely to support extant populations of Lahontan cutthroat trout (Dunham et al. 2002b).

Protection and restoration efforts to improve habitat for Lahontan cutthroat trout could benefit from a focus on temperature and streamflow as primary limiting factors. Monitoring of both streamflow (discharge) and temperature would provide useful indications of the effectiveness of management efforts. Future work to understand the nature, extent, and causes of seasonal drying in streams that offer current or potential habitat for Lahontan cutthroat trout would provide useful guidance for restoring perennial streamflows, where possible. Strategies to improve the suitability of thermal habitat could focus on changes in the availability of such habitat caused by contemporary human influences (e.g., the dewatering of stream channels and alteration of stream channel morphology and riparian vegetation; Poole and Berman 2001) in the context of natural influences and potential future scenarios, such as climate change, that may lead to increased fragmentation of suitable habitat (Keleher and Rahel 1996; Poff et al. 2002).

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