Stream temperature criteria for Oregon's Lahontan cutthroat trout *Oncorhynchus clarki henshawi*

Final Report

Jason Dunham

Department of Biology and

Biological Resources Research Center

University of Nevada

Reno, NV 89557

Submitted to:

Bruce Hammon

Senior Aquatic Biologist

Oregon Department of Environmental Quality

Eastern Region

1 SW Nye, Suite B

Pendleton, OR 97801

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Summary

This document reviews available information on Lahontan cutthroat trout that is relevant to establishing stream temperature criteria for this subspecies in the state of Oregon. Provided are: 1) summaries of relevant details of the natural history of Lahontan cutthroat trout; 2) a review of existing water temperature criteria that may apply to Lahontan cutthroat trout in the context of the Endangered Species Act and Clean Water Act; 3) a review what is known about the thermal biology of Lahontan cutthroat trout; 4) an analysis of existing thermal regimes to recommend revised criteria; 5) recommendations for temperature criteria; and 6) an outline of important issues and uncertainties to be considered in future revision of temperature criteria.

Scope and Purpose of This Document

This document reviews available information on Lahontan cutthroat trout that is relevant to establishing stream temperature criteria for this subspecies in the state of Oregon. Until about 1997, there were very few data to quantitatively describe the thermal biology of Lahontan cutthroat trout. A large amount of research in progress since then has been dedicated to this purpose, however, and results of this work will contribute to improved temperature criteria. Accordingly, much of the information currently available on the thermal biology of Lahontan cutthroat trout is unpublished, or in the process of being collected or analyzed. Completion of this research will have implications for temperature criteria in the future.

Conclusions and recommendations from this report may be considered interim guidelines to be applied until significant new information is received to motivate revision of temperature criteria.

Here, I begin with a summary of relevant details of the natural history of Lahontan cutthroat trout to provide an ecological and evolutionary context for understanding the thermal biology of this subspecies. Next, I briefly review of existing water temperature criteria that may apply to Lahontan cutthroat trout in the context of the Endangered Species Act (ESA) and Clean Water Act (CWA). I then move on to review what is known about the thermal biology of Lahontan cutthroat trout, and outline important issues and uncertainties. I conclude with recommendations to revise existing water temperature criteria in light of this information and provide a brief discussion of uncertainties and issues for future revision of temperature criteria.

Natural history of Lahontan cutthroat trout in Oregon: ecological and evolutionary context

Lahontan cutthroat trout is a threatened subspecies of cutthroat trout endemic to the Great Basin of southeast Oregon, northern Nevada, and northeastern California (Coffin and Cowan 1995). In the state of Oregon, the natural range for Lahontan cutthroat trout includes the Coyote Lake or Willow/Whitehorse basin, including Willow and Whitehorse Creeks; and the northwest Lahontan basin, which is drained by the upper Quinn River basin, including McDermitt and Sage Creeks (see Hanson et al. 1993; Coffin and Cowan 1995; Jones et al. 1998).

Cutthroat trout colonized the Lahontan basin by at least 30,000 years ago (Trotter 1987), and perhaps as early as the Pliocene (Taylor and Smith 1981). Through this long history in the basin, cutthroat trout had access to a variety of stream and lacustrine habitats. The high stand of Lake Lahontan occurred about 14,000 years ago, when the lake itself covered approximately 22,100 km^2 in a drainage basin of about 117,000 km^2 (LaRivers 1962, Thompson et al. 1986). Following its high stand, Lake Lahontan rapidly desiccated to contemporary levels by about 8,000 years ago, isolating cutthroat trout populations in the eastern (Quinn and Humboldt River) basins from those in the western (Truckee, Carson and Walker River) Lahontan basins.

The Coyote Lake basin in southeast Oregon is an isolated endorheic basin with no direct connection to the Lahontan basin to the south. Little is known of the history of colonization by cutthroat trout in the Coyote Lake basin, but Behnke (1992) believed the most plausible explanation was a headwater stream transfer of cutthroat trout from the neighboring Quinn River basin. Recent genetic analysis using mitochondrial restriction site markers indicated Lahontan cutthroat trout in the Coyote Lake basin and Quinn River basin are genetically distinctive (R. Williams et al. 1998). Lahontan cutthroat trout in the Coyote Lake basin also are ecologically distinctive, since they are the only fish species in the basin (Jones et al. 1998).

It is evident that populations of Lahontan cutthroat trout have experienced dramatic changes in climatic and hydrologic conditions over time. Spatial variability in these conditions is also evident. Before population declines dramatically reduced the range of Lahontan cutthroat trout, it was found in a remarkable diversity of habitats and thermal environments, including small desert streams (e.g. Willow and Whitehorse Creeks), larger rivers draining the eastern Sierra-Nevada range (e.g. the Walker, Carson, and Truckee Rivers), high-elevation oligotrophic lakes (e.g. Lake Tahoe and Independence Lake), and lower-elevation eutrophic lakes (e.g. Pyramid and Walker Lakes). Therefore, it seems reasonable to assume different populations have experienced a variety of different selective pressures. This diverse ecological context may have provided a selective arena favoring local adaptation of some populations (e.g. Hendry et al. 1998).

In Oregon, it seems likely in recent history that all populations of Lahontan cutthroat trout were restricted to living in stream habitats, though fish may have inhabited Coyote Lake in pluvial times (Behnke 1992). In these stream habitats, the opportunity for expression of different migratory life histories was available. Cutthroat trout in streams may adopt a "resident" life history, defined here as fish that spend their entire lives within a restricted zone of a stream very near, or entirely within spawning and rearing areas. Alternatively, some individuals may adopt a "fluvial" life history, where adults make extensive annual or seasonal migrations to feed in downstream habitats, returning to natal streams to reproduce (e.g. Northcote 1997).

It is believed that many Lahontan cutthroat trout populations historically interacted as metapopulations (Coffin and Cowan 1995). The term "metapopulation" refers to a collection of discrete local breeding populations. In the case of Lahontan cutthroat trout, metapopulation dynamics may result when local breeding populations in tributary streams are interconnected by larger downstream habitats. Interaction among tributary populations may have occurred through "straying" or dispersal of resident and/or fluvial fish (see Rieman and Dunham 1999). This was more likely historically, as fragmentation of habitats in the past 150 years has isolated local populations in many tributary habitats (Dunham et al. 1999). Loss of connectivity among local populations has been linked to increased risk of local extinction (Dunham et al. 1997).

In Oregon, it is unclear whether or not Lahontan cutthroat trout populations in Willow and Whitehorse Creeks functioned as a metapopulation, but metapopulation dynamics were much more likely historically in the Quinn River basin, including McDermitt Creek. Today, the potential for metapopulations in this basin is compromised by nonnative salmonids and widespread habitat degradation (Coffin and Cowan 1995).

Human impacts on aquatic habitats are evident everywhere in the Lahontan basin. Changes in aquatic habitats related to human developments over the past 200 years were reviewed by Minshall et al. (1989). They point out that while very little information is available on historic habitat condition, a variety of lines of evidence strongly demonstrate that contemporary and historical land uses have dramatically degraded aquatic habitats in the region.

Degradation and loss of habitat are risk factors identified by U.S. Fish and Wildlife Service (USFWS), which estimates that Lahontan cutthroat trout inhabit only about 15% of historically occupied habitat in the eastern Lahontan basin (Coffin and Cowan 1995). Lahontan cutthroat trout initially were listed as endangered by USFWS in 1970, and subsequently reclassified as threatened in 1975 to facilitate management and allow regulated angling (Coffin and Cowan 1995).

It was not until the early 1990s that basin-wide habitat restoration efforts to benefit Lahontan cutthroat trout were initiated on the ground. Two positive examples of restoration efforts include Willow and Whitehorse Creeks in southeast Oregon (Dufferena 1996), and Marys River in northeast Nevada (Gutzwiller et al. 1998).

As will become evident from this review, a critical part of habitat recovery will involve restoration of an appropriate thermal regime for Lahontan cutthroat trout. Attainment of this objective must be determined through effectiveness monitoring of restoration efforts (Coffin and Cowan 1995; Kershner 1998) and therefore requires a suite of quantitative and measurable temperature criteria (sensu J. Williams et al. 1998).

Review of Existing Water Quality Criteria for Lahontan Cutthroat Trout

Currently, three suites of temperature criteria have been proposed that may apply to Lahontan cutthroat trout in the state of Oregon. The first is listed in the USFWS recovery plan (Coffin and Cowan 1995). The states of Oregon and Nevada also have established stream temperature criteria for CWA compliance. I consider the state of Nevada's temperature criteria because many streams with occupied or potentially occupied habitat in the state of Oregon flow south into Nevada.

To begin with, a definition of the various temperature metrics referred to throughout this analysis is provided (Table 1).

Table 1. Definition of temperature metrics used in this review.

Metric	Abbreviation	Definition
Average daily temperature	None	Arithmetic average of temperature measurements within a day
Maximum average daily temperature	MDAT	Maximum of average daily temperature within a year
Maximum daily temperature	None	Maximum temperature within a day
Maximum daily maximum temperature	MDMT	Maximum of maximum daily temperature within a year
Average weekly average temperature	AWAT	Arithmetic average of average daily temperatures over any seven-day period
Maximum weekly average temperature	MWAT	Maximum value of AWAT within a year
Average weekly maximum temperature	AWMT	Arithmetic average of maximum daily temperatures over any seven-day period
Maximum weekly maximum temperature	MWMT	Maximum value of AWMT within a year

USFWS Temperature Criteria

Criteria proposed by USFWS (Coffin and Cowan 1995) were based on a literature review to parameterize habitat suitability models for cutthroat trout developed by Hickman and Raleigh (1982). For streams (fluvial habitats), Coffin and Cowan (1995, pg. 39) reported the following optimal thermal conditions:

"Optimal fluvial cutthroat trout habitat is characterized by: 1) Clear, cold water with an average maximum summer temperature of <22° C (72° F), and a relatively stable summer temperature regime averaging about 13° C (55° F) ± 4° C (7° F)."

For lakes (lacustrine habitats), Coffin and Cowan (1995, pg. 39) reported:

"Optimal lacustrine cutthroat habitat is characterized by: 1) Clear, cool/cold water with and average summer mid-epilimnion temperature of <22° C (72° F)."

Here, I focus on the USFWS stream temperature criteria. Temperature criteria proposed by Coffin and Cowan (1995) were motivated by listing of Lahontan cutthroat trout as a threatened species under the ESA. Temperature also is a key element of state water quality criteria, as directed by the CWA, Section 303. Temperature criteria adopted by the states of Oregon and Nevada are reviewed below.

State of Oregon Temperature Criteria

The state of Oregon Department of Environmental Quality (ORDEQ) has established water quality criteria for streams containing cold-water aquatic species:

"...the new criterion sets the temperature at 64 degrees [Fahrenheit] statewide unless there is cold-water fish spawning or bull trout habitat. These special habitat areas have criteria of 55 degrees and 50 degrees respectively."

(ORDEQ 1998). The criterion of 64° F (17.8° C) applies to Lahontan cutthroat trout as defined by the "Total Maximum Daily Load" or TMDL, which is defined as follows:

"Determining whether the stream temperature is above or below the temperature criterion is based on the average of the maximum daily water temperatures for the stream's warmest, consecutive 7-day period during the year. A one time measurement above the criterion will NOT be considered a violation of the criterion."

(ORDEQ 1998). To summarize, according to ORDEQ criteria, water temperatures in streams must not exceed an average maximum daily water temperature of 17.8° C for the warmest 7-day period of the year (hereafter, average maximum daily water temperature during the *warmest week of the year* is referred to as "MWMT"), unless cold-water fish spawning may potentially occur. In the latter case, MWMT cannot exceed 55° F (12.8° C).

State of Nevada Temperature Criteria

Water body classifications

Water temperature criteria for the state of Nevada are designated using a water body classification system listed in the State of Nevada Administrative Codes. Class "A" waters are defined to include:

"…waters or portions of waters located in areas of little human habitation, no industrial development or intensive agriculture and where the watershed is relatively undisturbed by man's activity."

Class "B" waters are defined to include:

"…waters or portions of waters which are located in areas of light or moderate human habitation, little industrial development, light-to-moderate agricultural development and where the watershed is only moderately influenced by man's activity."

Class "C" waters are defined to include:

"… waters or portions of waters which are located in areas of moderate-to-urban human habitation, where industrial development is present in moderate amounts, agricultural practices are intensive and where the watershed is considerably altered by man's activity."

Class "D" waters are defined to include:

"…waters or portions of waters located in areas of urban development, highly industrialized or intensively used for agriculture or a combination of all the above and where effluent sources include a multiplicity of waste discharges from the highly altered watershed."

Temperature criteria

There are no temperature criteria listed for Class D waters, and no mention is made of cool-water aquatic life, such as trout. For Class C waters with trout, temperature criteria are as follows:

"Must not exceed 20° C for waters with trout or 34° C for waters without trout. Allowable temperature increase above normal receiving water temperature: 3° C."

For Class B waters, temperature criteria are as follows:

"Must not exceed 20° C for trout waters or 24° C for nontrout waters. Allowable temperature increase above natural receiving water temperatures: None."

For Class A waters, temperature criteria are as follows:

"Must not exceed 20° C. Allowable temperature increase above natural receiving water temperature: None."

The Nevada Administrative Code makes no distinction between nontrout waters, and waters known to support trout historically. In the case of Lahontan cutthroat trout, many presently unoccupied ("nontrout") waters were occupied in the mid 19th to early 20th century. In fact, local extinctions of Lahontan cutthroat trout appear to be a continuing phenomenon (Dunham et al. 1997).

Historically occupied habitat in the eastern Lahontan basin included streams in the Humboldt and Quinn River subbasins downstream to about 1500 m in elevation (Snyder 1917, Dunham et al. 1997). Coffin (1981) estimated that "…of the estimated 2,469.84 miles of stream within the Humboldt River indicates that the Lahontan/Humboldt cutthroat trout may have existed in as much as 2,210.0 miles or 90 percent of the basin."

The temperature threshold of 20° C is not specified to be a daily or weekly average, and is assumed to be a point temperature value not to be exceeded in water bodies supporting trout, except in the case of Class C streams, where there is an allowable increase of 3° C above normal. "Normal" is assumed to be the long-term average temperature of a water body (must be <20° C for trout-bearing waters) at a specific point in time.

When temperatures exceed normal by 0-10% (a percentage of total observations available from past temperature measurements), thermal requirements for beneficial use (e.g. sustain trout life) are considered to be satisfied. When temperatures exceed normal by 10-25%, beneficial use is only partially met, while "exceedance" of greater than 25% is considered to not satisfy beneficial use criteria (G. Gentry, Nevada Division of Environmental Protection, personal communication).

Comparison of temperature criteria

In conclusion, it appears the state of Oregon's temperature criterion is the most "conservative," in the sense that it requires coldest maximum water temperatures (MWMT = 17.8° C). While somewhat unclear, the state of Nevada's temperature criteria appear to lie between Oregon's criteria, and that proposed by USFWS (average maximum summer temperature < 22° C). The USFWS criteria specify a maximum temperature, an average temperature, and a measure of variability, assumed to be the daily range herein.

Temperature criteria for the state of Nevada and USFWS are not clear as to how they should be measured or estimated, while Oregon's temperature criteria are specifically defined, in terms of time frame and mathematical estimation. Oregon's temperature criteria are specific to potentially different thermal requirements for spawning and non-reproductive stages of the salmonid life cycle, but uniform criteria apply statewide for most water bodies and salmonid species, except bull trout (*Salvelinus confluentus*). Nevada's temperature criteria are specific to waters with different use classifications (e.g. Class A-D waters), but requirements for species and/or life history stages are not specified.

Thermal biology of Lahontan cutthroat trout: review of published literature and available unpublished data

Temperature is one of the most important factors affecting the quantity and quality of aquatic habitats in deserts of western North America. Many factors operate to determine stream temperature regimes (Beschta et al. 1987; Sullivan et al. 1990). Solar radiation, air temperature, vegetation cover, groundwater, stream discharge, stream channel shape and orientation, and local and regional climatic gradients are among the host of potentially important factors that interact to determine the thermal regime of a stream. Stream temperature can be dramatically affected by land use (Beschta et al. 1987; Platts 1991; Sullivan et al. 1990) and is therefore a potential indicator of overall water quality and habitat condition.

In desert regions, streams that are cooler in summer are more likely to have perennial flow, good vegetation cover and forage, and more productive fish and wildlife populations. However, summer stream temperatures in Nevada and elsewhere in the Great Basin region have likely increased over the past 150 years (Minshall et al. 1989; Platts and Nelson 1989; Platts 1991), and may possibly continue increase in the future in response to regional increases in air temperatures attributed to global warming (Keleher and Rahel 1996). It is generally believed that increases in summer stream temperatures in the region are associated with climatic variability and past and continuing impacts of various land uses and changes in riparian landscapes (Platts and Nelson 1989; Platts 1991).

The critical importance of temperature to the health of Lahontan cutthroat trout populations was not fully appreciated until recently. In earlier reviews, persistence of Lahontan cutthroat trout in desert climates often was tied to adaptation for increased thermal tolerance. For example, Trotter (1987) speculated that stream-living Lahontan cutthroat trout were less likely to be displaced by nonnative salmonids (e.g. brook trout, *Salvelinus fontinalis*; brown trout, *Salmo trutta*; rainbow trout, *Oncorhynchus mykiss*) in habitats where temperatures exceed the tolerance level for most salmonids. Behnke (1992) believed it was likely that Lahontan cutthroat trout in the Coyote Lake sub-basin have "evolved physiological adaptations to exist at extreme temperatures." In a study of Lahontan cutthroat trout in the North Fork Humboldt River sub-basin of northeast Nevada, Nelson et al. (1992) stated that "neither temperature nor dissolved oxygen currently limit cutthroat trout distributions."

Unfortunately, these impressions of Lahontan cutthroat trout and thermal tolerance were based on limited and correlative evidence. Point observations of fish occurrence at "extreme" temperatures were sometimes extrapolated to inferences about local adaptation for increased thermal tolerance or preference. Indeed, it is tempting for biologists who personally experience the dramatic diurnal temperature changes in the Great Basin to internalize the feeling of "extreme" tolerance on behalf of other organisms. This is not to imply that stream habitats in the Great Basin are not stressful environments, however.

Laboratory experiments on thermal response of Lahontan cutthroat trout

Vigg and Koch (1980). Experimental assessments of thermal tolerance of Lahontan cutthroat began with the work of Vigg and Koch (1980). Vigg and Koch sought to determine the upper lethal temperature tolerance of Lahontan cutthroat trout from two sources: Summit Lake and Pyramid Lake (Marble Bluff) Hatchery Stock. Experiments were conducted in a controlled laboratory environment. Survival of cutthroat trout from these two sources was measured as temperatures were gradually raised (about 1° C per day) from an acclimation temperature of 16° C, and then held for 96 hours at each of the following temperatures (in sequence): 20, 21, 22, and 23° C. Three different water sources, varying in alkalinity and pH were tested as well. Water sources included Pyramid Lake (highest alkalinity and pH), Dunn Hatchery well water (intermediate alkalinity and pH), and Truckee River water (lowest alkalinity and pH).

Results of these experiments yielded the following results:

1) Thermal tolerance was reduced in alkaline water of higher pH.

2) Differences in thermal tolerance were statistically significant between strains in Truckee River and Pyramid Lake water treatments, but not Dunn Hatchery well water.

3) In all cases, Summit Lake fish exhibited higher thermal tolerance, both in terms of average lethal temperature, and average survival time.

4) Increased mortality under higher pH conditions may have been due to increased toxicity of ammonia (conversion from less toxic ionized form [NH_3-N] to the toxic un-ionized form [NH_3]).

5) Levels of un-ionized ammonia may have approached or exceeded lethal levels in Dunn Hatchery well and Pyramid Lake water, but not in Truckee River water.

These results clearly point to the importance of interacting factors in determination of thermal tolerance. In particular, the potential effects of sublethal or lethal levels of ammonia were believed to have modified survival of Lahontan cutthroat trout exposed to thermal stress (see also Reid et al. 1998). Under the most optimal conditions (Truckee River water) in this study, an upper lethal temperature of 22.3 to 22.6° C was observed. Statistically significant differences in lethal temperatures were observed between strains, but the average difference was small (0.3° C), and probably not detectable under most field conditions.

Behnke (1992) questioned the validity of this work, claiming that fish were held without food during the experiments. This is not correct because Vigg and Koch (1980) fed fish daily until they stopped feeding and examined feeding inhibition as a stress symptom during the experiments. Furthermore, results of subsequent experiments (Dickerson and Vinyard 1999) have confirmed Vigg and Koch's results.

Dickerson, Vinyard, and Weber (1999 and unpublished data). Dickerson and Vinyard (1999) performed experiments to assess thermal tolerance of Lahontan cutthroat trout under exposure to chronic and fluctuating temperatures in controlled laboratory conditions. Their experiments utilized hatchery-reared, Pyramid Lake strain Lahontan cutthroat trout. This strain is derived from a mixture of fish originating from sources in the western Lahontan basin and Summit Lake (Coffin and Cowan 1995), and may be genetically different from the original population of Lahontan cutthroat trout in Pyramid Lake and the eastern Lahontan basin, including populations in Oregon (Dunham et al. 1998, R. Williams et al. 1998).

Fish in experimental tanks were acclimated to 13^{o} C, and temperatures were increased at a rate of 4^{o} C per day until experimental temperatures were attained. Experimental temperatures included 13 (control), 20, 22, 24, 26, and 28^{o} C treatments. Fish were exposed to these constant temperatures for one week. Water quality was carefully monitored and controlled, and ammonia levels were virtually undetectable (B. R. Dickerson, personal communication). Fish were fed a daily ration of 4% of body weight twice per day. Both survival and growth were monitored.

Survival varied dramatically among temperature treatments. Survival was virtually 100% for temperatures less than or equal to 24^{o} C, but declined to 35% at 26^{o} C. Mortality was 100% within 48 hours for fish held at a constant temperature of 28^{o} C. Growth in 13, 20, and 22^{o} C treatments was not different, but a significant reduction in growth occurred at 24^{o} C.

In a second series of experiments, groups of fish were exposed to one week of fluctuating temperatures mimicking diurnal fluctuations observed in the lower Truckee River (20-26^{o} C; mean = 23^{o} C), and to constant temperatures of 13, 20, and 23^{o} C. Two groups of these fish (20-26^{o} C fluctuation, and constant 20 and 23^{o} C) were exposed to a subsequent week of exposure to constant 24^{o} C temperatures.

Mortality did not occur during the initial seven-day exposure of fish to fluctuating temperatures, even though temperatures exceeded 26^{o} C for one hour during each day. Growth rates of fish exposed to fluctuating temperatures were lower than for groups of fish exposed to constant temperatures of 13 and 20^{o} C, but were similar to groups of fish held at a constant 23^{o} C (the mean temperature of the fluctuating cycle). During the second week of exposure to constant 24^{o} C temperatures, there was no mortality, and no difference in growth among the three groups examined (those previously exposed to 20-26^{o} C fluctuation, and constant 20 and 23^{o} C).

Work on heat shock proteins supports results of the research by Dickerson and Vinyard (1999). Heat shock proteins are major indicators of stress in vertebrates (reviewed by Sanders 1993). Heat shock proteins play a role in refolding denatured proteins when organisms are stressed by a number of factors, including temperature. Experimental data show that Lahontan cutthroat trout begin to synthesize detectable amounts of heat shock proteins immediately at 26^{o} C, within 24 hours of chronic exposure to temperatures of 24^{o} C, but not at 22^{o} C, even after 5 days of exposure (L. Weber, University of Nevada-Reno, personal communication).

Additional research is underway at the University of Nevada-Reno to further address the issue of fluctuating temperatures and the potential for differences in thermal responses among size classes of Lahontan cutthroat trout (M. Meeuwig, University of Nevada-Reno, personal communication). This research is part of a graduate master's thesis, and will be completed by 2000.

Results of these experiments may be summarized as follows:

1) The upper thermal limit for growth and long-term survival lies somewhere between 22 and 23^{o} C when fish are exposed to chronic temperatures.

2) Lahontan cutthroat trout can survive weekly exposure to daily temperature fluctuations of 6^o C (20-26^o C), including 1 hour exposures to temperatures of up to 26^o C, but growth is significantly compromised at these high and fluctuating temperatures.

3) One week of acclimation to warmer temperatures does not appear to elicit increased thermal tolerance.

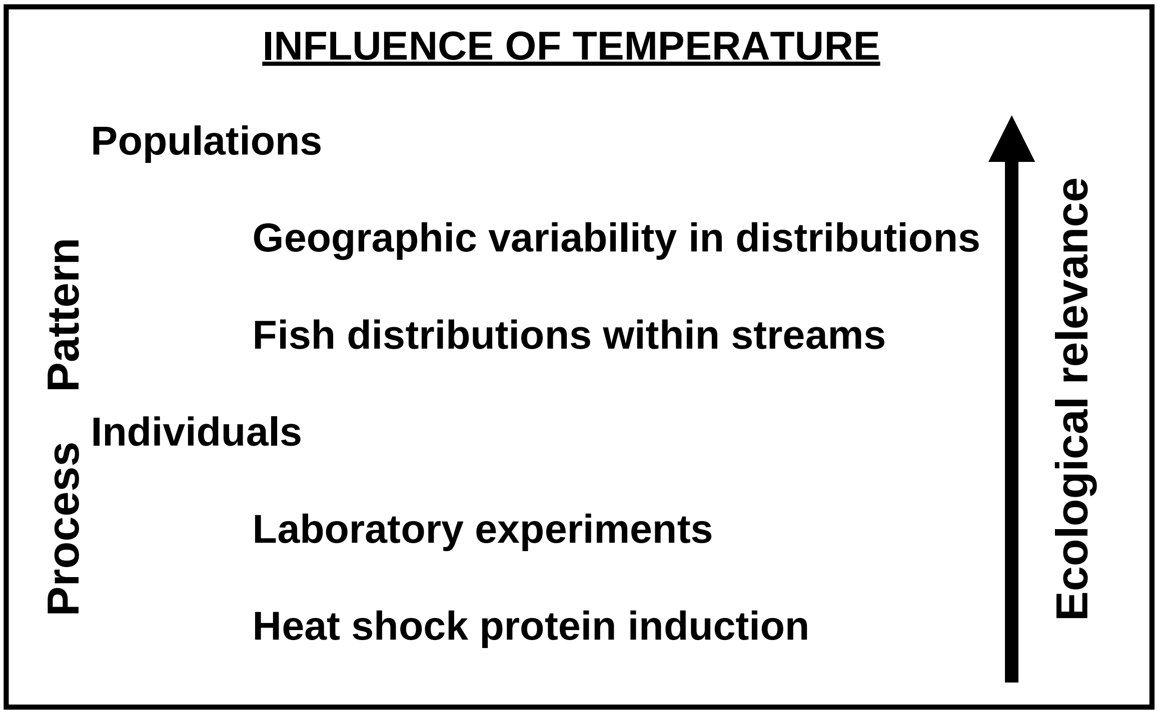
4) Results of these experiments apply only under relatively optimal conditions, e.g. high food availability, no other water quality problems, competitors, disease, etc.

5) Dramatic declines in growth that occur above the upper thermal limit of 22-23^o C correspond with a second indicator of stress, induction of heat shock proteins.

Evidence from the field: patterns of Lahontan cutthroat trout occurrence at broad scales and within streams

Laboratory experiments provide an important mechanistic basis for understanding the effects of temperature on Lahontan cutthroat trout. It is difficult, however, to extrapolate from results obtained under laboratory conditions to the field, where many uncontrolled factors interact simultaneously. Nonetheless, it is in the field where temperature plays a potentially important role to affect the productivity and viability of fish populations. Development of temperature criteria must therefore incorporate information from a combination of complementary approaches, including controlled laboratory experiments and correlative field studies. Figure 1 displays relationships between insights provided by these different approaches in regard to revealing patterns versus process, scale (e.g. individuals versus populations) and ecological relevance.

Figure 1.



In the following section, I briefly review published and preliminary results of research to relate distribution and occurrence of Lahontan cutthroat trout in the field to local and regional thermal variability.

Dunham et al. 1999. Dunham et al. (1999) surveyed the downstream distribution limits of Lahontan cutthroat trout in streams of the eastern Lahontan basin to develop a predictive geographic model of potentially suitable habitat. In streams without nonnative salmonids, latitude and longitude explained about 70% of the variation in elevation of the summertime downstream limit. Latitude was the strongest predictor, and as expected, Lahontan cutthroat trout occupied progressively lower elevation stream habitats at higher latitudes. This pattern closely tracked regional clines in mean July air temperature, but Lahontan cutthroat trout distribution limits most closely paralleled the 18^{o} C isocline, rather than 22-24^{o} C as proposed by Keleher and Rahel (1996).

Distribution limits in streams with both Lahontan cutthroat trout and nonnative trout (primarily brook trout, *Salvelinus fontinalis*) were highly variable and difficult to predict. Distribution limits did not vary geographically, but Lahontan cutthroat trout occurred significantly further upstream in habitats with nonnative trout. Distribution limits were not affected significantly by downstream water diversions, indicating that contemporary distributions of Lahontan cutthroat trout were at or upstream of diversions.

Dunham et al. (1999) hypothesized that distribution limits were determined in large part by unsuitably warm summer water temperatures in lower elevation stream habitats. As mentioned above, stream temperatures can be affected by a host of factors that may directly or indirectly influence habitat quality. Temperature may therefore be a good indicator of the collective influence of these factors on Lahontan cutthroat trout.

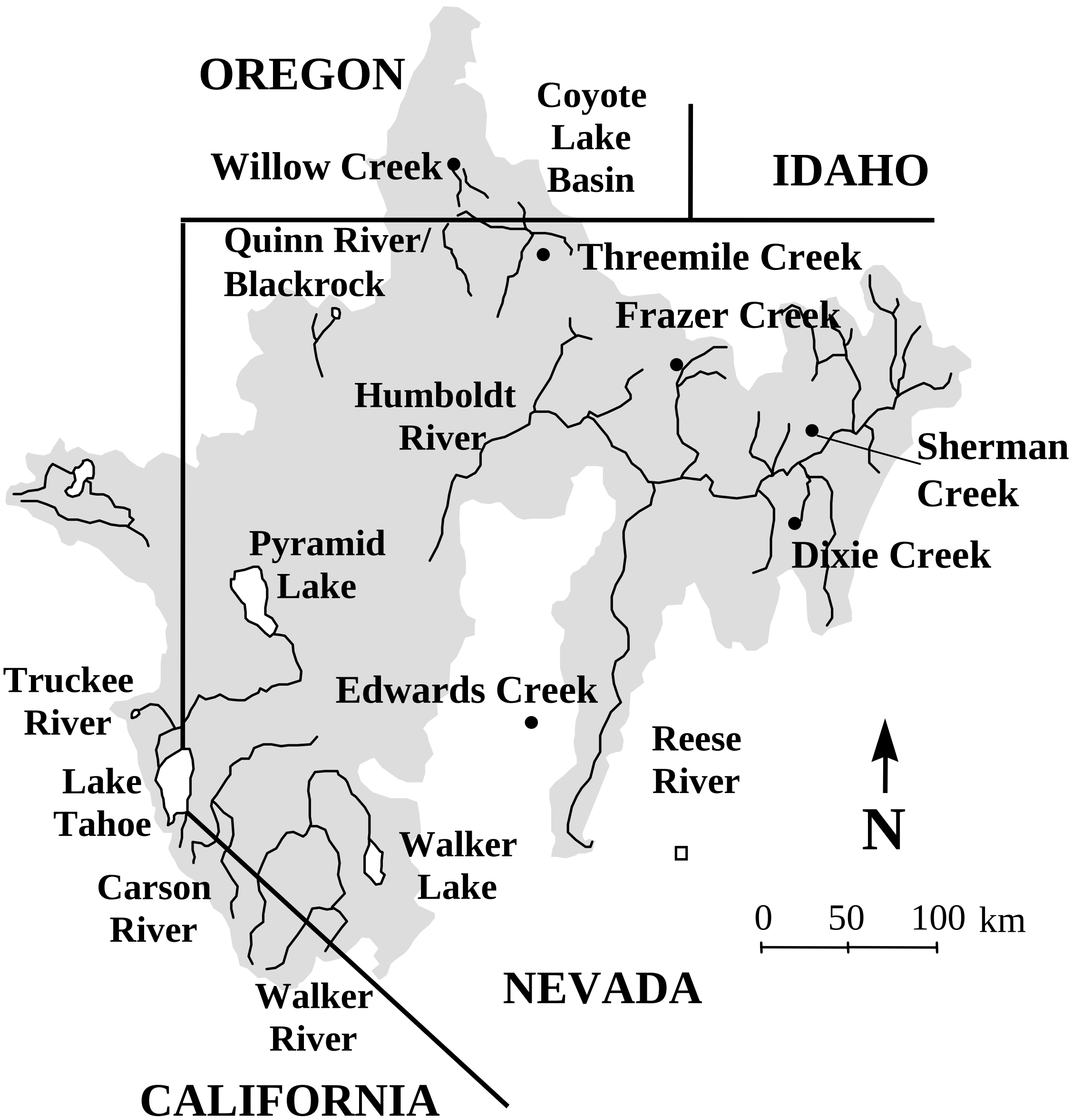
Dunham et al., unpublished data. Following the distribution limits study of 1997, a study to monitor stream temperatures and fish distributions within streams was initiated in 1998. The stream temperature project utilizes inexpensive temperature dataloggers to continuously monitor thermal variability. In 1998, dataloggers were arrayed longitudinally along stream habitats occupied by Lahontan cutthroat trout and in unoccupied habitat downstream. Both air and water temperatures were monitored every ½ hour using a paired (air and water) sampling design. Streams were sampled throughout the eastern Lahontan basin (Fig. 2).

This is an ongoing study with the following objectives:

1) Characterize temperature regimes that discriminate occupied and unoccupied habitat.
2) Describe patterns of stream heating.
3) Initiate development of a long-term monitoring program to track changes in thermal characteristics of stream habitats in the region.

At this point data and analyses must be considered to be work in progress. Data from 1998 and 1999 will be combined in a more comprehensive analysis at a later date. The following analysis is focused on patterns in Willow Creek, Oregon, but data from streams to the south in Nevada are included to provide a broader perspective.

Figure 2. Map of Lahontan basin. Circles indicate locations of streams with both temperature and fish distribution data.



1) Thermal regimes and Lahontan cutthroat trout occurrence

In 1998, thermal regimes of stream habitats and corresponding distribution limits of Lahontan cutthroat trout were quantified in six streams. Other streams were sampled for temperature and/or fish distributions, but sampling of these streams did not span over both occupied and unoccupied habitat, or fish distributions were not quantified. Therefore, data from these streams were not informative for the purposes of this analysis and omitted. Temperature data from all streams are potentially useful for many other purposes, such as analyzing thermal regimes and patterns of heating, however (see item 2 below).

A potential problem with the 1998 dataset is lack of temporal concordance between fish distribution and temperature data. Lahontan cutthroat trout do make well-known seasonal migrations or forays into downstream habitats that are presumably unsuitable during warmest times of the year. The potential for seasonal migrations may add some noise to the data relating fish distributions directly to thermal regimes since sampling of fish distributions did not correspond exactly in time with maximum summer temperatures. This lack of concordance would be expected to bias the data in a way to suggest that fish occurred in warmer than actual temperatures in the field. Even if concordance is exact, potential time lags in responses may still produce some bias.

Other local factors may also affect the correspondence between fish distributions and temperature within streams, including variability in other components of habitat quality, disease, prey availability, migration barriers, and water quality and quantity. With these well-known caveats in mind, I summarized data on several measures of thermal variation to qualitatively examine concordance between stream temperature and distribution of Lahontan cutthroat trout.

In Figure 3, occurrence of Lahontan cutthroat trout (filled symbol = "present," unfilled symbol = "absent") is plotted in relation to MDAT and MDMT. "Site" is a number that corresponds to the relative location sampled within a stream (Site #1 is the downstream-most sample and distance between consecutively numbered sites is 600 m). Several patterns were obvious.

First, it was clear that air temperature was a poor indicator of fish occurrence at this spatial scale (data not shown). Recall at a larger scale, distribution limits *did* correspond closely to air temperatures (Dunham et al. 1999). In other words, variation in air temperature along the length of streams did not explain occurrence of Lahontan cutthroat trout, but at the larger (among-stream) scale, variation in air temperature was large enough to show important patterns.

Average water temperatures (expressed as MDAT) did seem to weakly discriminate occupied and unoccupied habitat, but maximum water temperature (MDMT) showed more obvious and consistent differences (Fig. 3). A more quantitative analysis of these and other temperature metrics is planned after more intensive surveys of fish distributions and temperature are completed in 1999.

The correspondence between thermal regimes and fish distributions appeared to vary strongly among streams, but most populations appeared to have a distribution limit that corresponded closely to maximum summer water temperature of 26^{o} C (e.g. Frazer, Threemile, Sherman, and Dixie Creeks; Fig. 3). This pattern of occurrence was similar to results of laboratory experiments on thermal tolerance (Dickerson and Vinyard 1999).

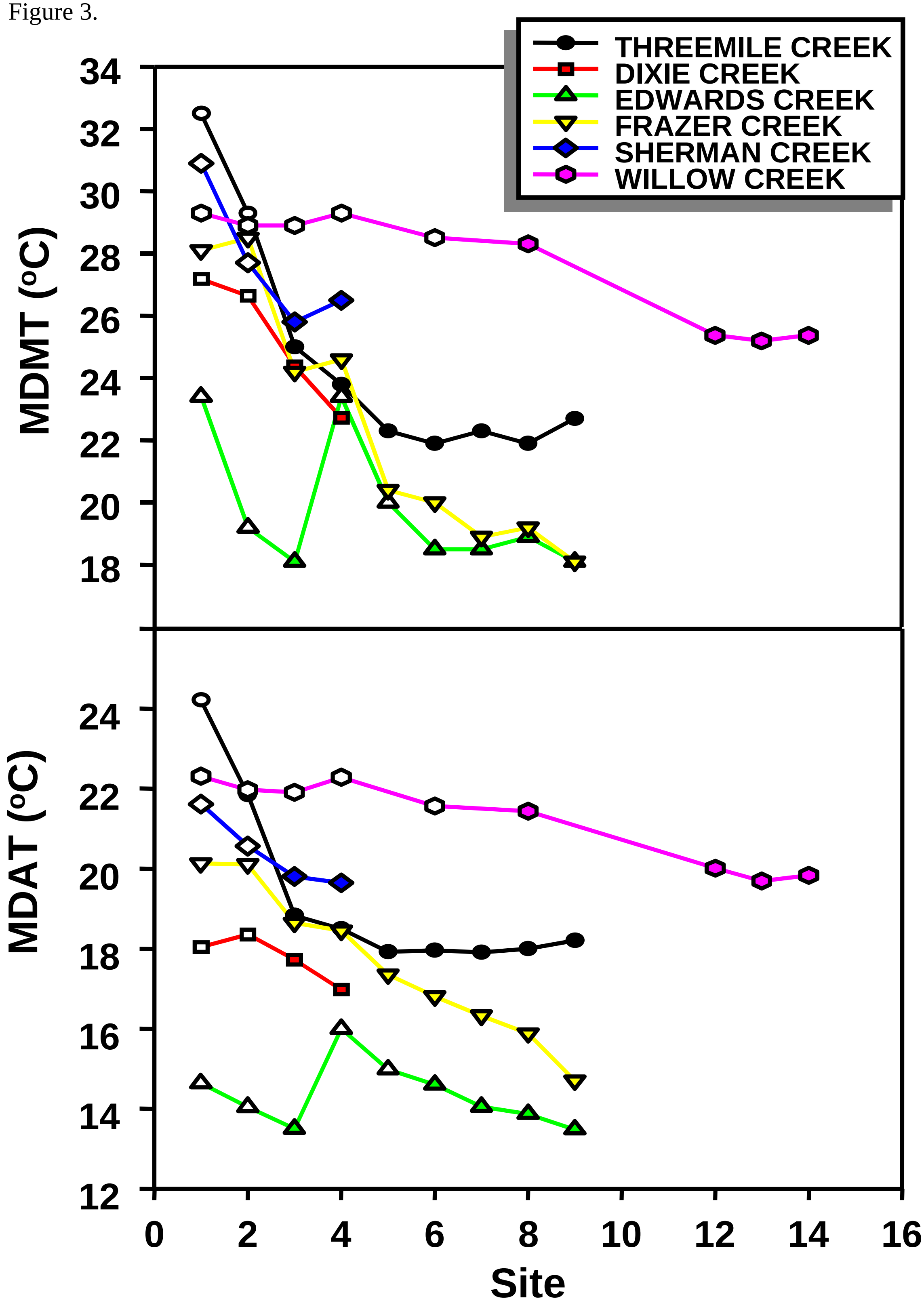
Among-stream variation in correspondence between thermal regimes and fish distributions was obvious, however. This may suggest important spatial or ecological variation, or perhaps local adaptation in thermal relations. Lahontan cutthroat trout in Edwards Creek occurred in much cooler water, about 6-7^{o} C cooler for maximum temperatures. In Willow Creek, Lahontan cutthroat trout occurred in warmer (daily maximum of 28.4^{o} C) waters than observed in other streams. Distribution of Lahontan cutthroat trout was determined on 30 July 1998 (A. Talabere, Oregon State University, personal communication), within two weeks of the warmest recorded water temperatures, so an upward bias temperature correspondence (see above) would not be expected.

Field observations of patterns of density in relation to migration barriers (beaver dams) in lower Willow Creek suggested many fish were trapped in downstream areas and unable to migrate upstream to avoid unsuitably warm temperatures (A. Talabere, personal communication). The effect of migration barriers may therefore have biased the pattern of thermal habitat selection by Lahontan cutthroat trout in Willow Creek. Additional information on the effect of these barriers and thermal exposure on rates of growth and mortality in the field are needed to better understand the thermal response of Lahontan cutthroat trout in Willow Creek.

Overall, correspondence between fish distributions within streams and water temperature suggests a strong response of populations to unsuitably warm maximum summer water temperatures. While many factors potentially interact to affect patterns of correspondence in the field, these patterns do reflect a more realistic thermal response, in comparison to controlled laboratory experiments.

In conclusion, Lahontan cutthroat trout appear to avoid water temperatures of 26^{o} C MDMT. Maximum daily average temperatures (MDAT) were less consistent in terms of discriminating occupied versus unoccupied habitat. This implies that fish respond more strongly to maximum, rather than mean temperatures, as may be expected. The potential for among-stream variation in thermal response merits further research to provide potential improvements in temperature criteria for populations with specific requirements.

Figure 3.



THREEMILE CREEK
DIXIE CREEK
EDWARDS CREEK
FRAZER CREEK
SHERMAN CREEK
WILLOW CREEK
MDMT (ºC)
34
32
30
28
26
24
22
20
18
MDAT (ºC)
24
22
20
18
16
14
12
0
2
4
6
8
10
12
14
16
Site

2) Thermal regimes and AWMT: probability modeling of Willow Creek data

Existing temperature criteria for salmonid habitat in Oregon are based on values of MWMT. The MWMT criterion has been criticized in part because it is possible for single-day maximum temperatures to exceed critical thresholds that may impair growth or survival (ORDEQ 1995; Berman 1998). A related concern is that MWMT may not adequately account for variance in temperature, which may affect fish growth.

To address this issue, I conducted an analysis of values of seven-day average maximum temperatures from stream temperature data collected from 15 July to 15 September 1998 in lower Willow Creek, Oregon. Temperature sampling was conducted at stations ranging from 4570 to 4360 elevation in lower Willow Creek (see Fig. 3).

Here it is crucial to note the difference between AWMT, which refers to the average maximum weekly temperature during any seven-day period within a specified time frame, and the special case of MWMT, which is the maximum of AWMT during a one year period. Both MWMT and AWMT are comparable in the sense that both are a average of maximum daily temperatures recorded over a seven-day period (see Table 1).

I used logistic regression and correlation analysis to analyze the relationship between various temperature metrics and AWMT. Objectives of the analyses were to 1) address the probability of exceeding critical daily maximum temperatures in relation to AWMT; and 2) to define the relationship between maximum weekly temperatures, AWMT, and daily variation (range) in temperature.

Logistic regression is a convenient analytical tool because it is robust to assumptions that typically constrain other parametric statistical methods (Tabachnik and Fidell 1997), and produces an easily interpreted probabilistic prediction of events.

Data were arranged to define relationships between AWMT (average weekly maximum temperature) and the probability of exceeding maximum daily temperatures of 21, 22, 23, 24, and 26^{o} C. In all cases, AWMT was an excellent predictor of maximum daily temperatures, with jackknifed classification rates of 92% or greater at the 0.50 probability level. Results of the analysis are displayed in Table 2, and graphically in Figure 4. In Table 2, selected values of AWMT and predicted probabilities of attaining temperatures of 21, 22, 23, 24, and 26^{o} C are shown.

Table 2. Values of AWMT and associated probabilities of attaining maximum daily water temperatures of 21, 22, 23, 24, and 26^o C.

	DAILY MAXIMUM TEMPERATURES				
AWMT	21	22	23	24	26
16	0	0	0	0	0
16.5	0	0	0	0	0
17	0	0	0	0	0
17.5	0	0	0	0	0
18	0	0.00001	0.00001	0.00001	0
18.5	0.00004	0.0001	0.00008	0.00003	0
19	0.00272	0.0008	0.00048	0.00012	0
19.5	0.16864	0.00624	0.00274	0.00047	0.00001
20	0.93793	0.04701	0.0156	0.00191	0.00004
20.5	0.99911	0.27932	0.0837	0.00773	0.00013
21	0.99999	0.75278	0.34488	0.0308	0.00045
21.5	1	0.95988	0.7521	0.11468	0.0015
22	1	0.99471	0.9459	0.34557	0.00502
22.5	1	0.99932	0.99017	0.6828	0.01667
23	1	0.99991	0.99828	0.8977	0.05383
23.5	1	0.99999	0.9997	0.9728	0.16036
24	1	1	0.99995	0.99319	0.39068

I selected a probability cutoff of 5% (0.05) to define "likely" (>5% chance) and "unlikely" (<5% chance) to exceed a certain maximum daily temperature. For example, predictions from the logistic regression analysis (Table 2) indicated that daily maximum temperatures of 21^o C were likely to be exceeded when AWMT exceeded about 19.0^o C. Daily maximum temperatures of 22^o C were likely to be exceeded when AWMT equaled about 20.0^o C, and so on (see Table 2).

Maximum daily range in temperature (maximum-minimum) within a 7-day period generally increased as a function of AWMT (Fig. 4, bottom graph). Temperature varied widely at higher AWMT, often exceeding a daily range of 10^o C. Daily water temperatures never ranged within ± 4^o C (the USFWS criterion), though this value was approached at lower values AWMT observed in Willow Creek (17.7^o C).

Data are available from several other stream habitats in the Lahontan basin in Nevada, and there may be significant spatial and/or temporal variability in the relationships explored herein. Here, I considered only data from Willow Creek in 1998. Further analysis is beyond the scope of this work, and will be needed to extend these analyses and produce a more robust and general understanding of stream temperatures in the region.

Key points to be made from this analysis are:

1) Selection of thermal habitat by Lahontan cutthroat trout appears to be most strongly related to maximum daily maximum temperatures (MDMT), not maximum daily average temperatures (MDAT).

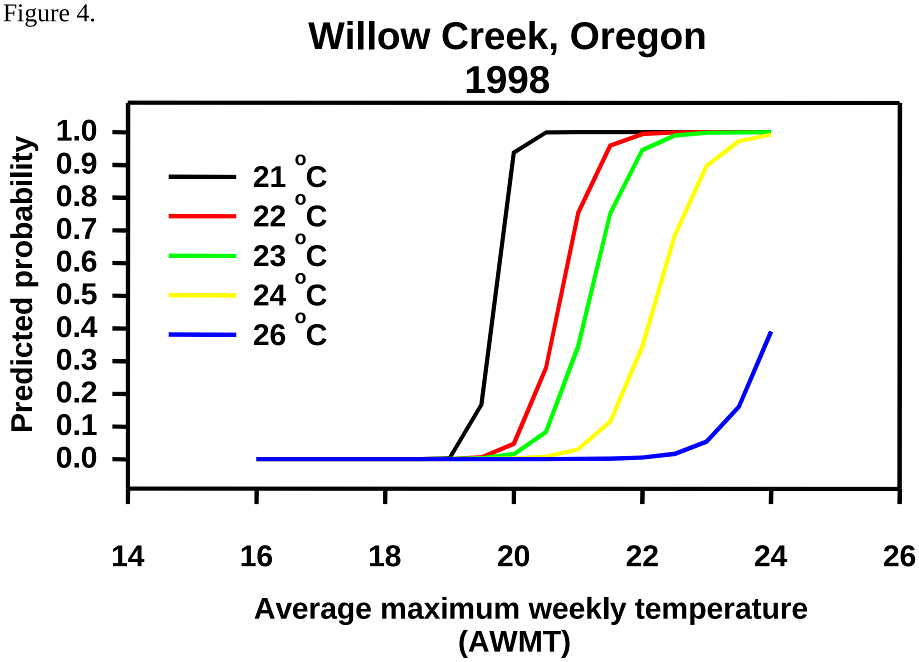
2) Values of AWMT that allow for a low (<5%) chance of exceeding a particular maximum daily temperature are about 2-3^o C lower than MDMT. This suggests that an MWMT to protect from unacceptably high maximum daily temperatures must be at least 2-3^o C cooler than the unacceptable maximum temperature. For example, if it is undesirable to have daily maximum temperatures of 22.0^o C or greater, then MWMT should be set at 20.0^o C (see Table 2).

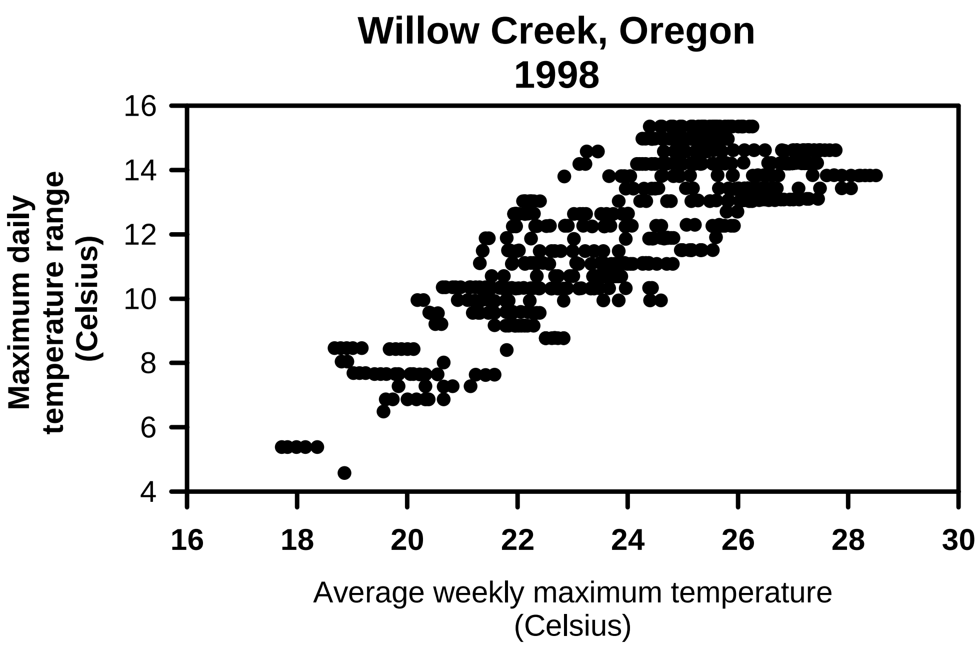
3) The relationship between daily maximum temperatures and MWMT will be driven in part by variance in temperature. Higher variance in temperature will mean that lower values of MWMT are needed to avoid unacceptable daily maximum temperatures. Acceptable values of MWMT may therefore depend on local thermal regimes, and possibly vary through time.

4) Variance in temperature increases strongly as a function of AWMT, and daily ranges do not fall within acceptable limits in lower Willow Creek, as specified by USFWS criteria.

5) Data from longer time series (i.e. additional years of data) may produce different relationships, so additional monitoring will be needed to validate modeling results.

Figure 4.


Willow Creek, Oregon
1998
Predicted probability
1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.0
21 °C
22 °C
23 °C
24 °C
26 °C
14
16
18
20
22
24
26
Average maximum weekly temperature
(AWMT)


Willow Creek, Oregon
1998
Maximum daily
temperature range
(Celsius)
16
14
12
10
8
6
4
16
18
20
22
24
26
28
30
Average weekly maximum temperature
(Celsius)

Temperature criteria for Lahontan cutthroat trout: synthesis and recommendations

Available evidence strongly points toward the importance of temperature to Lahontan cutthroat trout. At the level of individuals, laboratory experiments show that warm water temperatures can influence growth, survival, and physiological symptoms of stress. Within streams, fish distributions appear to be limited by unsuitably warm summer water temperatures in lower elevation habitats. Among streams, broad geographic patterns in distribution limits parallel climatic gradients. Among-stream variability in responses of populations to water temperature may reflect the influence of local environmental variation, local adaptation, or both.

Effects of temperature on Lahontan cutthroat trout at different spatial scales have different implications in terms of individual fitness, population viability, or ecological/genetic diversity within the species as a whole. Furthermore, the response of fish to thermal regimes will clearly depend on the total distribution of temperatures, including minimum, maximum, average, and variation in temperature. In the following discussion, I first provide interim recommendations for revised maximum temperature criteria for Lahontan cutthroat trout. Following these recommendations, I conclude with a discussion of critical uncertainties and information needs, with an emphasis on regulatory requirements of the CWA and ESA.

Recommended maximum temperature criteria: juveniles and resident adults

Thermal relationships described herein are limited in the sense that experiments and field studies have focused on juvenile and adult fish. Recommended temperature criteria are provided only for juveniles and resident adults because little is known about relationships between temperature and other specific life history requirements of Lahontan cutthroat trout.

Juveniles and resident adults are treated similarly because 1) in most streams their distributions overlap almost completely (Dunham et al. 1999); and 2) there is no evidence to suggest differences in thermal tolerance that may be related to body size in Lahontan cutthroat trout, and evidence of such effects for other salmonids is limited (Elliott 1981).

Maximum daily temperature. The best available data indicate Lahontan cutthroat trout begin to show signs of physiological stress under chronic exposure to temperatures above 22^{o} C (Vigg and Koch 1980; Dickerson and Vinyard 1999). This applies only to fish held under relatively optimal (e.g. high food availability, dissolved oxygen, low ammonia) laboratory conditions. Heat shock proteins are induced at detectable levels almost immediately when fish are exposed to chronic temperatures of 26^{o} C, and within 24 hours at 24^{o} C (L. Weber, personal communication).

While induction of heat shock proteins was not immediately detectable at 24^{o} C, this does not mean that fish exposed to temperatures equal to or greater than 24^{o} C were not immediately stressed (L. Weber, personal communication). There may be a time lag between occurrence of physiological stress (e.g. cell damage caused by high temperature) and the stress response (e.g. induction of detectable levels of heat shock proteins). Here it is critical to distinguish between occurrence of stress and the expression of detectable symptoms.

Nothing is known of response times of Lahontan cutthroat trout to potentially stressful temperatures, so it is impossible to define a critical short-term exposure time (e.g. number of seconds, minutes, or hours over a critical temperature). Until such data are available, I conservatively assume that stress occurs immediately at 24^{o} C. Another source of uncertainty is that heat-shock protein experiments were conducted at 2^{o} C intervals, so resolution of the temperature threshold for stress response is limited accordingly.

In summary the evidence suggests Lahontan cutthroat trout *may* experience stress when exposed either chronically or intermittently on a short-term basis to maximum daily temperatures equal to or greater than 23-24^{o} C.

Following the 2^{o} C measure of safety recommended by the National Academy of Sciences (NAS 1972), this means that maximum daily water temperatures of 21-22^{o} C should not be exceeded to minimize the potential for sublethal stress in Lahontan cutthroat trout. Furthermore, since neither growth depression or induction of heat shock proteins by Lahontan cutthroat trout has been observed at chronic exposure of temperatures less than or equal to 22^{o} C, I recommend the following:

> <u>To minimize risk of mortality and sublethal thermal stress for Lahontan cutthroat trout, water temperatures should not exceed a *daily* maximum of 22^{o} C.</u>

Of necessity, this recommendation is conservative, but until uncertainties regarding responses of fish to natural thermal regimes are resolved, a precautionary approach is warranted to avoid adverse effects.

Two critical assumptions are inherent in this recommendation:

1) Sublethal stress is elicited rapidly at 24^{o} C.

2) A 2^{o} C measure of safety is appropriate.

Daily variation in temperature. A second issue in determining suitable thermal regimes for salmonids is variability in temperature. Under a variable thermal regime, exposure to high water temperatures for several hours (e.g. 8 hours over 24^{o} C, peaking at 26^{o} C) within a day compromised growth (Dickerson and Vinyard 1999). Data from the field indicate that variability in daily temperatures increases as a function of MWMT.

In fact, temperatures in lower Willow Creek never attained the acceptable threshold of $\pm 4^{o}$ C specified by Coffin and Cowan (1995), nor did they often fall within acceptable limits specified by ORDEQ's criterion of 17.8^{o} C MWMT. It is unclear, however, if the $\pm 4^{o}$ C refers to a range (as assumed here), standard deviation, variance, or some other measure of the dispersion of temperatures (P. Coffin, USFWS-Reno, personal communication).

There is currently not enough information to set criteria for daily variability in temperatures. Laboratory studies to examine further aspects of this issue are in the process of completion (M. Meeuwig, University of Nevada-Reno, personal communication). Field research is needed as well to determine how fish response to daily, seasonal, and spatial variation in temperature (e.g. Berman and Quinn 1991; Ebersole 1994; Torgerson et al. 1999).

MWMT recommendations. Probability modeling of maximum daily temperatures within a week in relation to AWMT indicates maximum daily temperatures of 22^{o} C are unlikely to be exceeded when AWMT is equal to or less than 20.0^{o} C. Higher maximum daily temperatures of 23-24.0^{o} C also are very unlikely (estimated probabilities = 0.02-0.002, respectively; see Table 2). Therefore, for MWMT, the following is recommended:

> <u>To minimize risk of exposure to excessive daily maximum temperatures and cumulative weekly exposure to high and fluctuating temperatures an interim MWMT of 20.0^{o} C is recommended for Lahontan cutthroat trout.</u>

This revised criterion may be subject to change (either increase or decrease) as new information is available. The revised criterion is 2.2^{o} C warmer than the existing CWA criterion (17.8^{o} C) that ORDEQ applies to water bodies supporting Lahontan cutthroat trout.

Again, this revision may be viewed as conservative, but a conservative approach is warranted, because insufficient data are available to ensure that higher temperatures will not harm the productivity and viability of Lahontan cutthroat trout populations. Better information on the behavioral and physiological responses of fish in the field to varying thermal regimes would help to refine these criteria. In particular, it would be instructive to understand more about stress and exposure time to potentially stressful thermal conditions.

Recommended temperature criteria: other life history requirements

Spawning and spawning migration. Coffin and Cowan (1995) report that spawning migrations have been observed in water temperatures ranging from 5 to 16^{o} C. Vinyard and Winzeler (In press) observed similar temperatures during spawning migrations of Lahontan cutthroat trout in Mahogany Creek, a tributary to Summit Lake in northwest Nevada. Little is known about the range of water temperatures that may impair or block spawning migrations.

Egg incubation. Similarly, there are few data on specific thermal requirements for egg incubation. Most study has focused on juveniles and adult fish because it is more likely that unsuitably warm temperatures will occur in mid- to late summer. In lower elevation habitats, where unsuitably warm summer temperatures are more likely, young of year fish have typically attained average lengths of 30-50 mm by early to late summer, depending on the year (Dunham and Vinyard 1996). Spawning and egg incubation often occur in late spring or early summer, when water temperatures are much cooler in general (e.g. Vinyard and Winzeler, In press). In higher elevation habitats spawning may be delayed, or cooler water temperatures may prolong egg incubation, and young of year may emerge as late as October (Dunham and Vinyard 1996).

There is some evidence that variation in stream discharge may be important to early survival of Lahontan cutthroat trout. Because temperature and discharge may be related, this suggests a possible connection with temperature. Recent analysis of long-term data on populations of Lahontan cutthroat trout has shown that juvenile (age 1+) recruitment is a positive function of spring discharge in the natal year. This is possibly due to increased habitat quantity and/or quality in the form of a more favorable egg incubation environment (C. Ray, M. Peacock, and J. Dunham, unpublished data).

Specific studies will be needed to more clearly define the thermal requirements of different life history stages of Lahontan cutthroat trout. These studies should include controlled laboratory experiments and in situ studies of egg hatching success in relation to natural thermal regimes (e.g. capped natural redds and/or incubation boxes).

The existing ORDEQ criterion for salmonid spawning is 12.8° C MWMT. Bell (1986) reported a preferred range of 4.4-12.8° C for hatching of cutthroat trout eggs. Hickman and Raleigh (1982) suggested an optimum temperature of 10.0° C for egg incubation for cutthroat trout. Upper thermal limits for egg survival in other species of salmonids (excluding stenothermal charrs such as bull trout *Salvelinus confluentus,* Arctic charr *S. alpinus,* and lake trout *S. namaycush*) generally are reported to range between 11.0 and 20.0° C (e.g. Brungs and Jones 1977; Elliott 1981).

For spawning and egg incubation requirements, uncertainty regarding the spatial and temporal distribution of potentially suitable spawning habitat may be as relevant as determination of specific MWMT values within the potential range described above. The ORDEQ criterion for spawning applies to water bodies where cold-water fish spawning may occur, but it is unclear as to how potential (vs. actual or realized) spawning habitat should be defined.

The distribution of potential spawning and early rearing habitat may extend well outside that of occupied habitat, and even into habitats with extensive dewatering or reduced stream flow relative to historical conditions. In Oregon, it has been estimated that Lahontan cutthroat trout presently occupy "most" of the available habitat in the Coyote Lake basin, and about 15% of potential stream habitats in the Quinn River basin (Coffin and Cowan 1995). These estimates are assumed to refer to total occurrence of all life history stages of Lahontan cutthroat trout, so it is unclear where spawning and early rearing occurred historically.

Temporal changes in the availability of suitable thermal conditions for spawning and early rearing also must be considered. For example, changes in seasonal thermal regimes of streams may induce shifts in the timing and success of spawning, egg development, emergence, juvenile growth, and emigration, which may have important effects on populations (e.g. Holtby 1988).

Temperatures of all streams in the Lahontan basin fall within limits that are suitable for spawning and egg incubation at some time during the year. This may be particularly true of streams fed by melting snows in late spring and early summer. Many streams may heat up to exceed existing MWMT criteria (12.8° C) for spawning later in summer, yet remain suitable for juveniles and resident adults (MWMT = 20.0° C).

This is a complex issue that requires better information to define a natural range of potential spawning times for different populations (which may vary dramatically, see Dunham and Vinyard 1996), effects of different thermal regimes on fish populations, and what natural thermal regimes of streams should be (see also Holtby 1988, Berman 1998, and *Phase shifts and reference conditions* below).

In summary, three key issues remain in determining temperature criteria for spawning and egg incubation of Lahontan cutthroat trout:

1) Quantitative definition spawning and incubation requirements (numeric criteria).
2) Definition of actual and potential (historical) spawning sites or locations.
3) Definition of times when spawning and egg incubation are likely to occur.

Until these issues are addressed in more detail, I recommend the current ORDEQ (1995) standard for spawning, egg incubation, and fry emergence (MWMT = 12.8° C) be applied, with uncertainty regarding spawning sites and timing to be resolved through consultation with local biologists and external peer review.

Feeding migrations and migration corridors. There is virtually no information on relationships between temperature and feeding migrations or use of potential migration corridors by Lahontan cutthroat trout. Anecdotal information from seasonal changes in the distribution of Lahontan cutthroat trout within streams suggests the possibility for feeding migrations (Dunham, personal observations). Lahontan cutthroat trout will become piscivorous at a very small size (~150 mm; Dunham et al., In press), and may emigrate from headwater habitats downstream to feed on fishes or other prey when temperatures are suitable.

Feeding migrations under current habitat conditions are risky, however, as fish may become trapped by upstream dispersal barriers and suffer reduced growth or mortality when they are unable to escape unsuitably warm summer temperatures. In some situations, cold-water thermal refugia may play an important role for survival of migratory individuals. The role of refugia is poorly understood for Lahontan cutthroat trout, however.

Critical uncertainties, caveats, and information needs

Maximum temperature criteria recommended herein are simplifications of the actual thermal environment experienced by fishes. There are many sources of uncertainty, some of which are discussed in further detail below. A broader framework for understanding and managing key aspects of the thermal environment for fishes and other components of aquatic communities and ecosystems is clearly needed.

Individual vs. population-level effects. Quantitative temperature criteria are an essential part of monitoring for recovery of Lahontan cutthroat trout. A temperature criterion reflects management goals, considered here in the context of the CWA and ESA. In the interpretation of the author, goals of both of these regulatory statutes broadly overlap in the case of Lahontan cutthroat trout. In this review, the focus is on development of specific temperature criteria that apply to a thermal regime at a particular site. Attainment of required temperatures at a specific site does not guarantee the mandates of the CWA and ESA are satisfied, however.

In the case of Lahontan cutthroat trout, it is clear that effects of temperature on the amount and distribution of occupied habitat may affect risk of local extinctions, life history diversity, and habitat connectivity (Dunham and Vinyard 1996; Dunham et al. 1997, 1999).

Ultimately, temperature criteria should support beneficial uses, such as productive populations of native salmonids (CWA) and recovery of populations at risk of extinction (ESA). To be most effective, temperature criteria must have meaning at the population level. Protections at the individual level may apply in some cases, however, since Lahontan cutthroat trout are protected from "take" under section 9 of the ESA (see Rohlf 1989).

Modeling of suitable thermal habitat at broad scales can be used to define critical landscape features for persistence of fish populations (e.g. Rieman and McIntyre 1995; Dunham and Rieman 1999; Rieman and Dunham 1999), and should be incorporated into temperature criteria. Such an effort is underway for Lahontan cutthroat trout in the eastern Lahontan basin, including southeast Oregon (Dunham, unpublished data).

Measure of safety. Criteria in this review were developed with a measure of safety in mind. A measure of safety is necessary to avoid the risk of under-protecting an important beneficial use. I followed earlier recommendations (NAS 1972) and used a 2° C measure of safety. There are several sources of error or uncertainty that could produce bias in an assessment of temperature criteria, including the following:

1) Extrapolation from laboratory conditions to the field.
2) Temperature measurement error.
3) Sampling error.
4) Uncertainty in model prediction/model selection.
5) Spatial/temporal/ecological mismatch in fish and temperature data.

Extrapolation of laboratory results to the field obviously is problematic since many other factors may operate to determine a species' response to a given thermal environment (see next section). Temperature measurement error may result from lack of precision in the instrument (e.g. many dataloggers, such as those used in this study, measure temperature to within ±0.5^o C), error in calibration of the instrument, improper programming, or placement in the field. Sampling error may result because samples were collected only within a limited time frame or area, numbers of samples were small, or location of samples inappropriate for the study objectives. Uncertainty in model predictions (e.g. wide confidence intervals), selection of appropriate models (e.g. linear vs. curvilinear), or method of analysis also may be important. Finally, it is imperative to have a close match between fish (e.g. occurrence, density, behavior, physiology, or other responses) and temperature data.

These numerous sources of error can be minimized through careful attention to technique and experimental design, but they will never be completely eliminated. This, however, does not invalidate the practice of establishing numeric temperature criteria, so long as potential sources of error are explicitly identified and explained, and an appropriate measure of safety is applied. Furthermore, it is important to regard any temperature criterion as a "null hypothesis" to be rigorously tested and refined through future monitoring and/or research. This often is stated as the objective of "adaptive" management.

In this review, I have focused on sources of error from items 1 and 5 listed above. Potential issues with these sources of error are discussed above. A standardized sampling protocol was used (see Appendix), so instrument and sampling error was minimized. Models used in this analysis fit the data very well, so this source of uncertainty was likely minimal as well.

In keeping with a precautionary principle, I also have been conservative in evaluating the relative risks associated with exposure to maximum daily temperatures (e.g. assuming fish have a rapid stress response when exposed to temperatures greater than 24^o C).

Interactions with other factors. At this point, it is worth reiterating that temperature does not act independently to affect individual fish, and ultimately populations. For example, DeStaso and Rahel (1994) studied interactions between brook and Colorado cutthroat trout (*O. c. pleuriticus*) in experimental stream tanks at different water temperatures. At temperatures of 10^o C, brook and cutthroat trout were nearly equal competitors, but at 20^o C brook trout were dominant over cutthroat trout. Schroeter (1998) studied competitive interactions between brook and Lahontan cutthroat trout in experimental field tanks with a natural water supply (~15^o C), and found brook and cutthroat trout to be equal competitors, unless density of the former was high (2 brook: 1 cutthroat trout). In habitats where nonnative trout, such as brook trout, are present, different (cooler) temperature criteria may therefore be appropriate to benefit cutthroat trout.

Currently there is not enough information to provide clear guidance for thermal regimes that may benefit Lahontan cutthroat trout in habitats with nonnative salmonids. As a result, current management objectives and actions may be unintentionally ignoring important risks to cutthroat trout (Young 1995). In Oregon, nonnative salmonids pose a potential threat to Lahontan cutthroat trout in the Quinn River basin (Hanson et al. 1993). Research is needed to more clearly define the interaction between water temperature and effects of nonnative salmonids and other species on Lahontan cutthroat trout.

While nonnative salmonids are widespread, and potentially replacing Lahontan cutthroat trout in many habitats (Dunham et al. 1999) other less widespread or more localized factors, such as altered pH, sediment loads, reduced prey availability, concentrations of toxic metals, disease, and a host of other water quality factors also may interact with temperature. At this point it is difficult to imagine there will be sufficient resources to address all of these potentially important issues, but managers should be aware of and alert for these potentially interacting problems in Lahontan cutthroat trout habitats. Research to more clearly define the effects of these factors should be prioritized based on an assessment of risks posed by each.

Phase shifts and reference conditions. Our current view of Lahontan cutthroat trout and temperature is biased because aquatic habitats in the Lahontan basin have been tremendously altered by human activity over the past 150-200 years (Minshall et al. 1989). Alterations of the timing and magnitude of annual and seasonal changes in availability of thermal habitat may have important cumulative effects on salmonids (see Holtby 1988, Berman 1998). Determining the magnitude and direction of such "phase" shifts in annual, seasonal, and daily thermal regimes is complicated by the fact that historical data on unaltered systems are virtually nonexistent, and that virtually all extant aquatic habitats in the Great Basin have been dramatically altered. Research to more realistically define baseline or "reference" conditions for aquatic habitats would be useful in this regard.

Temperature criteria in a physical context. The potential for a stream to heat is a function of physical influences from both natural and human-related factors, the latter being the primary motivation for regulatory requirements. A simple example of the importance of the physical context is the relationship between stream temperature and elevation. Streams at higher elevations more likely receive cooler ground and surface water inputs, which may result in cooler overall stream temperatures and reduced rate of heating. Changes in these physical factors at lower elevations may increase the natural potential for a stream to heat. The natural potential for a stream to heat must be considered in developing realistic temperature criteria that apply to human-related influences. Further research is needed to understand the importance of natural variation in the physical setting of stream catchments at multiple spatial scales.

Thermal limits vs. optimal temperatures. Criteria proposed herein essentially define the maximum thermal limits to avoid adverse effects on individuals, and perhaps populations of Lahontan cutthroat trout. These criteria must therefore be considered to be "worst" case scenarios that represent cumulative effects of many natural and human-associated factors. Little is known about optimal thermal conditions that apply specifically to Lahontan cutthroat trout.

Hickman and Raleigh (1982) assumed an optimal temperature of 15^{o} C for cutthroat trout, the temperature at which Dwyer and Kramer (1975) found the greatest scope for activity (the difference between minimum or "standard" metabolism and maximum sustainable or "active" metabolism) in cutthroat trout. Improved criteria should incorporate some information on the minimal amount of optimal thermal habitat required to maintain healthy populations.

Thermal refugia. Thermal refugia have received much attention recently in the literature on inland salmonids (e.g. Ebersole 1994; Torgerson et al. 1999). The number and locations of thermal refugia play a potentially important role in population productivity and/or ability of salmonids to survive periods of thermal stress, and should therefore be identified and carefully managed (Berman and Quinn 1991, Berman 1998). Cooler headwater sections of streams may be considered to provide refuge from unsuitably warm temperatures, and serve as centers of production. Refugia also may be present further downstream as patches of suitable thermal habitat created by advection from cooler surface or groundwater sources (Bilby 1984). These refugia may be especially important for growth and survival of migratory fish when temperatues are otherwise unsuitable. It should also be recognized that such thermal refugia may be symptomatic of dysfunctional or degraded thermal regimes in aquatic ecosystems (Torgerson et al. 1999). In such cases, management should not be focused simply on maintenance of refugia, but also on restoration of a natural thermal regime with continuously suitable habitat.

Minimum temperatures. The focus in this document is on maximum temperature criteria, which certainly are important to Lahontan cutthroat trout, and many other salmonids near the southern limit of their natural distribution. Minimum temperatures during winter also may be important (reviewed by Cunjak 1996; also see Jakober et al. 1998), but little is known about the ecology of Lahontan cutthroat trout in winter. Factors related to thermal characteristics of over-wintering habitat include reduced temperatures and supercooling (<0^{o} C) of water, stream icing, de-watering, ice blockage, and oxygen depletion in ice-covered pools that may lead to winter kills of fish (Cunjak 1996; Jakober et al. 1998). All of these factors are potentially important, but there is little information upon which to base recommendations for minimum temperature criteria for Lahontan cutthroat trout.

Conclusion

To conclude, the findings of this report and temperature criteria for Lahontan cutthroat trout must be viewed as a part of an evolving process. Clearly, there are many uncertainties (see previous discussion), and new information may substantially change the temperature criteria recommended herein. Most of these concerns were acknowledged in technical reviews of water quality criteria for the state of Oregon (ORDEQ 1995). Continued thermal monitoring and study of the response of Lahontan cutthroat trout individuals and populations is needed to ensure important considerations are not overlooked. I have suggested specific information needs throughout to highlight potentially important issues. Findings of this report should be used as a basis for developing a prioritized list of information needs for research, monitoring, and management.

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Appendix: 1998 stream temperature monitoring protocol (to be revised for 1999)

Purpose

This stream temperature monitoring protocol is designed to provide information relevant to water and air temperatures of stream and riparian habitats, respectively, supporting Lahontan cutthroat trout and other coldwater organisms in Nevada (Dunham et al. 1998). Modifications of this protocol may be necessary for different applications. We refer the reader to references listed at the end of this document for general information. The protocol that follows is specific to monitoring water temperature. A brief note about air temperatures is included at the end.

Equipment Needed

- Electronic submersible temperature dataloggers or thermographs, such as the HOBO or StowAway models manufactured by Onset Corporation[1].
- Durable protective casings for dataloggers
- Ice, and a 2-5 gallon bucket
- Tags, labels, or other durable marking device
- Field notebook and pencils
- 1:25,000 topographical maps and/or aerial photographs of study sites
- Equipment for tethering, securing, and concealment of dataloggers or thermographs
- Camera and film
- Tape measure

Method

Site selection

For purposes of this study, dataloggers should be deployed at, above, and below predicted or observed downstream (lower) distribution limits (altitude, in meters) of Lahontan cutthroat trout (see Dunham et al. 1998b). A database of predicted distribution limits is being developed with a geographic information system at the Biological Resources Research Center, University of Nevada-Reno, and should be available by June of 1998 (contact J. B. Dunham 541-752-3683).

If you visually observe Lahontan cutthroat trout or have the opportunity to sample for distribution limits of Lahontan cutthroat trout following the survey protocol outlined in Dunham et al. 1998b, please do so to confirm the location of actual downstream (lower) distribution limits. This will permit a more precise determination of the relationships between thermal regimes and occurrence of Lahontan cutthroat trout.

[1]*Use of trade or firm names is for reader information only and does not constitute endorsement of any product or service by the University of Nevada-Reno.*

The total number of dataloggers to be used in a stream will vary according to availability. For research described in Dunham et al. 1998a, a minimum of 10 dataloggers will be deployed in each study stream. We therefore recommend using as many dataloggers as possible, up to 10 per stream, with at least 2-3 dataloggers placed downstream of the presumed lower distribution limit of Lahontan cutthroat trout. One objective of the proposed research (Dunham et al. 1998a) will be to evaluate the number and spacing of dataloggers needed to provide a reasonable characterization of thermal characteristics near downstream distribution limits of Lahontan cutthroat trout.

When at a site, take care to note potential sources of groundwater inflow, such as visible surface springs, seeps, tributary junctions (surface and subsurface). Inflows from groundwater may produce a thermal profile that is not representative of the stream in general and should be avoided when possible for the purposes of this work. While micro-refugia afforded by local groundwater flows may be locally important to small concentrations of trout, we do not view such habitats as being important to the population as a whole (except perhaps under very extreme conditions), especially if the population is to be considered viable over the long term.

Along these lines, it is a very good idea to use a hand-held thermometer to record a few temperatures in the vicinity of where you plan to place the datalogger - just to make sure there are no temperature anomalies at your site.

Dataloggers should be spaced at least 300-600 meters apart along the length of the stream to be sampled. According to Schuett-Hames et al. (1994) this is approximately the distance it should take for small streams to establish thermal equilibrium within a thermal reach. **UNR surveys: Space all dataloggers approximately 600 meters apart. Measure distance between dataloggers.**

Pick a site where the water column is well mixed, but not susceptible to excessive scour that may dislodge or damage the datalogger. Moderately turbulent flows at the downstream edge of lateral scour and plunge pools are good locations.

Pick locations with deep enough water so the datalogger is submerged throughout low-flow periods. This is critical as warmer water temperatures are of interest, and likely to occur during low-flow. Place the datalogger in the "thalweg" or deepest, well-mixed part of the channel when possible.

Take care to ensure dataloggers are not directly exposed to the sun. This can produced erroneous temperature "spikes" in the data, which are not reflective of actual water temperatures. Natural cover may be provided by turbulence produced by pool jets, overhanging banks and riparian vegetation, large wood, boulders, and large growths of macrophytes in the stream. If necessary, a lightweight piece of wood, or other shading material may be placed overhead to avoid exposing the datalogger to direct solar radiation.

Make sure also to keep the datalogger from contact with the stream bottom, as streambed material may serve as a heat sink/souce that may bias temperature readings.

Securing the datalogger

Suggested methods for tethering and securing temperature dataloggers in streams are provided in Onset Corporation's (1995) newsletter. In areas where human activity is an issue, be sure to use local materials to camouflage the datalogger, placing appropriate flagging, markers, etc., to mark the location. Make sure to keep an identification mark or tag on the datalogger itself to identify where it was placed (e.g. stream, year, site), and an address for returning it if found.

Photograph sites where dataloggers were deployed for future reference if needed. Mark the location of the datalogger on a 1:25,000 scale topographical map and record UTM coordinates (eastings and northings in meters); Township, range, section; latitude and longitude; or use a global positioning system. As always, written field notes are a safe way to record information, and should be used for later reference.

Marking sites and locations

UNR surveys: This is a *critical* step. Using calibrated altimeter and a 1:24,000 scale map, record altitude/elevation of location where each datalogger is located.

Mark location clearly on the map.

Record altitude/elevation at an upstream and downstream reference site. These sites are up- and downstream, respectively, of where dataloggers are located in streams. Reference sites are locations that you can easily locate on 1:24,000 maps. These include tributary junctions, road crossings, property boundaries, etc.

Calibration

The simplest and most inexpensive method for calibration is to use a large bucket or cooler of icewater. Be sure to use freshwater, which has a freezing point of 0^{o}C. Note: all temperature dataloggers should use international (metric, SI) units. Place a mixture of crushed ice and water in an insulated container. Launch the datalogger and place the external sensor or logger (if no external sensor) into the water bath, making sure to agitate the water gently every 2-3 minutes to avoid thermal stratification (it helps to have a larger container for this). After an hour, remove the probe and/or logger and download the data. If the logger is calibrated correctly, the temperature reading should level out at 0^{o}C (Fig. 1). It is a good idea to check calibration both before *and* after dataloggers are deployed and retrieved.

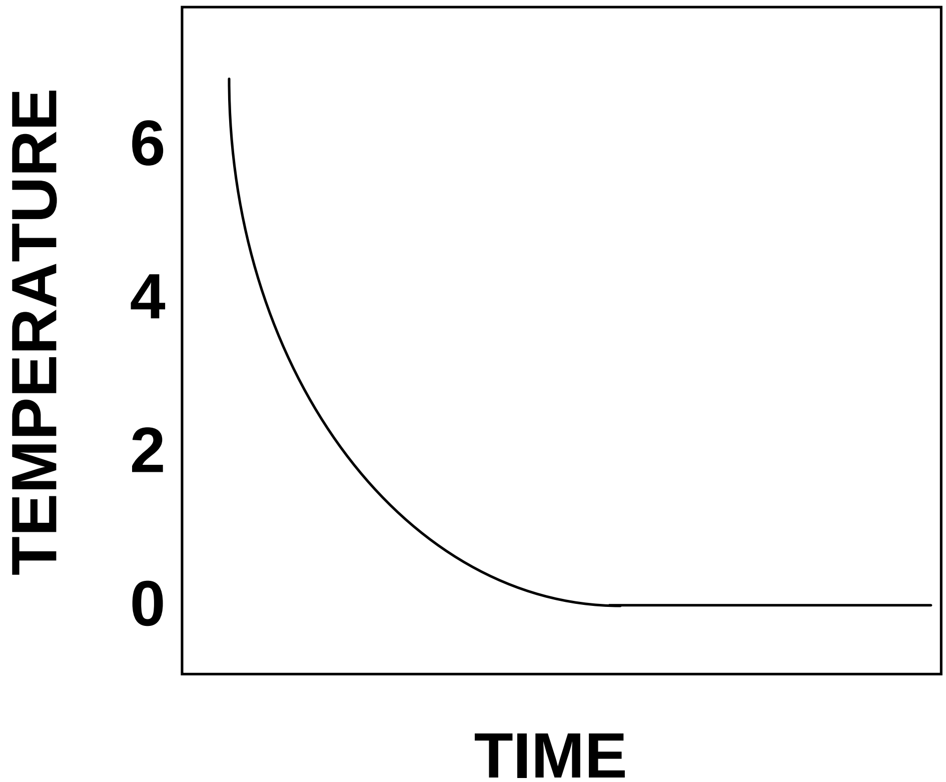

Figure 1. Illustration of datalogger calibration using the "ice bucket" method (from Onset Corporation 1995).

Monitoring period

For the purposes of this work, we ask that dataloggers be installed by 15 July 1998 at the very latest. If at all possible, dataloggers should be in place by 01 July. Dataloggers will be retrieved and downloaded after 30 September to permit analysis of summertime thermal regimes during winter of 1998-99, but some dataloggers will remain in the streams for at least one full year to characterize an entire year of temperatures.

Monitoring interval

Set your datalogger to monitor temperatures (Celsius) for at least <u>one hour intervals</u>. Continuous monitoring is strongly recommended for all situations.

Miscellaneous

Refer to the user instructions for your particular model/make of logger for launching instructions and other advice for improving the quality of information. Make sure to back up data downloaded from loggers and to be sure you have both graphic and numeric data downloaded and backed-up. If possible, enter the text from field notes to link to graph and numeric files. Otherwise, provide a paper copy of field notes and maps. If you plan to collect information other than temperature (e.g. canopy density, width of riparian zone, water depth, wetted channel width) that may be relevant, please note in data book and data files, so this may be accessed as needed.

Air temperatures

Use the same basic principles outlined above for placement of temperature dataloggers to measure air temperature. Obviously, many points (e.g. keeping the datalogger underwater) do not apply. Be especially careful to avoid exposing the datalogger to direct solar radiation (i.e. place the datalogger in a well-shaded area with good air circulation). Also, keep the datalogger far enough off of the ground to avoid the influence of heat radiating from the ground itself.

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