

Assessment of thermal stratification within stream pools as a mechanism to provide refugia for native trout in hot, arid rangelands

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Abstract Native trout species, such as the redband trout (*Oncorhynchus mykiss*), occupy thermally harsh stream habitats in hot, arid rangeland basins of the western United States. Declines in the distribution and abundance of these species has generated interest in understanding how these cold water species survive in these systems, as well as in identifying opportunities to restore these species to their former ranges. The purpose of this study was to assess the potential for thermal stratification to provide thermal refuge for redband trout in stream pools characterized by warm intermittent flow conditions on arid rangelands. We studied vertical thermal stratification in two pools during three summers on Boles Creek located on the Modoc Plateau in extreme northeastern California. Water and air temperature data were collected on a 0.5 h time step from 15-Jun through 15-Sep during 1996, 1997, and 2000 using commercial temperature data-loggers.

Water temperature was measured at the top (0.3 m below pool surface) and bottom (0.3 m above pool substrates) of each pool. Vertical thermal stratification occurred within these pools creating conditions as much as 7.6 °C cooler and consistently more constant at the bottom of pools compared to pool surface waters. Thermal stratification was dependent upon air temperature with the magnitude of stratification increasing as air temperature increased. The magnitude of thermal stratification varied significantly from year to year, likely reflecting variation in annual weather conditions. The thermal regime in the study pools was often near the upper lethal limit reported for redband trout, but temperatures at the bottom of these pools did offer refuge from lethal temperatures realized near the pool surface. Temperatures at pool bottom were consistently above optimal levels published for redbands.

Keywords Stream temperature · Cold water refugia · Redband trout · *Oncorhynchus mykiss*

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1. Introduction

Stream temperature is an important limiting factor affecting the distribution of aquatic vertebrate and invertebrate species (Baltz *et al.*, 1987; Lyons, 1996; Jacobsen *et al.*, 1997; Hawkins *et al.*, 1997; Isaak and Hubert, 2004). The distribution and abundance of native coldwater fisheries in the western United States has been reduced since European settlement (Nehlsen

et al., 1991; Hunington *et al.*, 1996; Thurow *et al.*, 1997), and land and water management practices that impact stream temperature are considered to be in part responsible for these reductions (Li *et al.*, 1994; Isaak and Hubert, 2001; Poole and Berman, 2001; Zoellick, 2004). Water temperature is a particularly important habitat determinant for trout species in arid rangeland basins of the western United States.

Arid rangeland streams are often characterized by maximum temperatures, temperature fluctuations, and intermittent streamflow conditions generally unsuitable as cold water fish habitat. However, certain native trout species are able to occupy these thermally harsh habitats. For example, the redband trout (*Oncorhynchus mykiss*) is native to high desert streams characterized by extreme variations in water temperature and streamflow conditions where water temperatures exceed 25 °C, generally considered the lethal limit for trout (Hokanson *et al.*, 1977; Jobling, 1981; Bjornn and Reiser, 1991; Thurow *et al.*, 1997; Behnke, 1992; Moyle, 2002). In southwestern Idaho, Zoellick (1999) found redband trout in streams with maximum daily water temperatures up to 29 °C and diurnal fluctuations up to 11 °C. Vinson and Levesque (1994) observed redband trout in pools in an intermittent southwest Idaho stream and reported persistence under static flow conditions and dissolved oxygen levels as low as 2 mg/L with temperatures ranging from 2 to 17 °C.

In 1991, Nehlsen *et al.* reported that 11 populations of redband trout had become extinct and that 10 populations were at risk. The mechanisms responsible for the occurrence and persistence of redband trout in high desert streams are of interest to scientists, regulators, and natural resource managers concerned with the conservation and recovery of these species throughout their original habitat. Physiological adaptation of desert trout to warm temperatures and the occurrence of thermal refuges in desert streams are two mechanisms potentially sustaining native trout populations in high desert basins. Redband trout have significant tolerance for high stream temperatures, with a reported critical thermal maxima of approximately 29 °C (Bowers *et al.*, 1979; Rodnick *et al.*, 2004). While redband are tolerant of harsh thermal regimes and low flow conditions, Zoellick (2004) found that redband density and biomass were both negatively correlated with stream temperature in two streams in southwestern Idaho. At stream temperatures ranging from 24

to 28 °C, Rodnick *et al.* (2004) found that large redband trout (400 to 1400 g) incurred higher metabolic costs and were more thermally sensitive than smaller fish (40 to 140 g). Gamperl *et al.* (2002) reported preferred water temperatures of ~13 °C for redband trout from two southeastern Oregon streams studied under laboratory conditions. Bowers *et al.* (1979) estimate that optimal water temperature for redbands is below 21 °C.

Based upon fish surveys and habitat use analysis at multiple spatial scales in tributaries to the Columbia River in Montana and Idaho, Muhlfeld *et al.* (2001) identified pools as preferential summer habitat for juvenile and adult redband trout. Cold water refuge created by thermal stratification in stream pools has been shown to serve as critical habitat for trout. Matthews *et al.* (1994) report that water temperatures at the bottom of a deep bedrock pool on the American River in the Sierra Nevada Mountains of California were as much as 4.5 °C cooler than surface temperatures, but that rainbow (*Oncorhynchus mykiss*) and brown trout (*Salmo trutta*) use of cold water refuge at the bottom of pools was potentially muted due to low dissolved oxygen levels in these locations. During periods of highest ambient stream temperature trout were found at locations averaging 19.3 °C even though colder water (14.5 °C) was available in the pool. On three north coast rivers in California, Neilson *et al.* (1994) report surface water temperatures 3.5 to 9.0 °C higher than temperatures at the bottom of pools when surface flows decreased to less than 1 m³/s. They observed preferential use of thermally stratified pools by anadromous steelhead/rainbow trout (*Oncorhynchus mykiss*) over other stream areas during periods of high ambient stream temperature (23 to 29 °C). Matthews and Berg (1997) examined pool thermal and dissolved oxygen stratification as well as location of rainbow trout during August in two pools on a southern California stream where water temperatures reached 28.9 °C. They reported water temperatures and dissolved oxygen levels at the top and bottom of a pool consistently occupied by trout to be 27.9 and 17.5–21.0 °C, and <1.0–5.0 and 4.0–10.0 mg/L, respectively. During the warmest period of the study most trout were found in the coldest region of the pool (18.3 °C) where dissolved oxygen levels ranged from 1.7 to 3.1 mg/L.

The importance of in-stream cold water refuge to redband trout in arid rangeland streams has received

limited research attention. Cold water refuges can be created by processes such as the influx of cool water from tributary streams and surface springs, influx of cool subsurface water from the floodplain, riparian zone, and/or hyperheic zone, and thermal stratification in pools, backwaters, or side channels during low or intermittent flow conditions (Constantz, 1998; Ebersole *et al.*, 2001; Ebersole *et al.*, 2003). Several studies demonstrate the preferential selection of wild salmonids for cold water refuge during periods of high ambient stream temperature. Torgersen *et al.* (1999) report that 78% of adult spring-run Chinook salmon (*Oncorhynchus tshawytscha*) surveyed during August on the middle fork of the John Day River in north-central Oregon were found in cold water refuges generated by influxes of water from tributaries and subsurface flow. The authors concluded that these thermal refuges were important habitat for species existing at the margin of their environmental tolerances. Ebersole *et al.* (2001) identified cold water refuges created by influx of subsurface water in 12 streams in northeastern Oregon in which temperatures were 3 to 8 °C below ambient stream temperatures. While the authors determined that these refuges were too small and infrequent to support high densities of rainbow trout (*Oncorhynchus mykiss*), they did conclude that these thermal refuges could allow persistence and survival of low densities of the species streams during warm water conditions.

We studied vertical thermal stratification in two pools during three summers on Boles Creek located on the Modoc Plateau in extreme northeastern California. The purpose of this study was to assess the potential for pool thermal stratification to provide thermal refuge for redband trout in streams characterized by intermittent flow conditions and isolated pool formation in the arid rangeland watersheds of northeastern California and southcentral Oregon. Several redband populations exist within in the region. Recovery and restoration efforts are on-going in the region in an attempt to maintain and enhance existing populations, addressing issues such as modification of instream flow regimes and fish migration due to dams and instream diversions. Uncertainty exists about the potential for various streams, including the study stream, in the region to support redband trout given inherently harsh summer maximum water temperatures and intermittent streamflow. Our specific objectives were to: (1) determine if thermal stratification occurs within intermittent pools

in this system and relate observed thermal conditions to published estimates of redband response to thermal gradients, and (2) examine relationships between thermal stratification and air temperature over the course of the summer (15-Jun through 15-Sep) and across years.

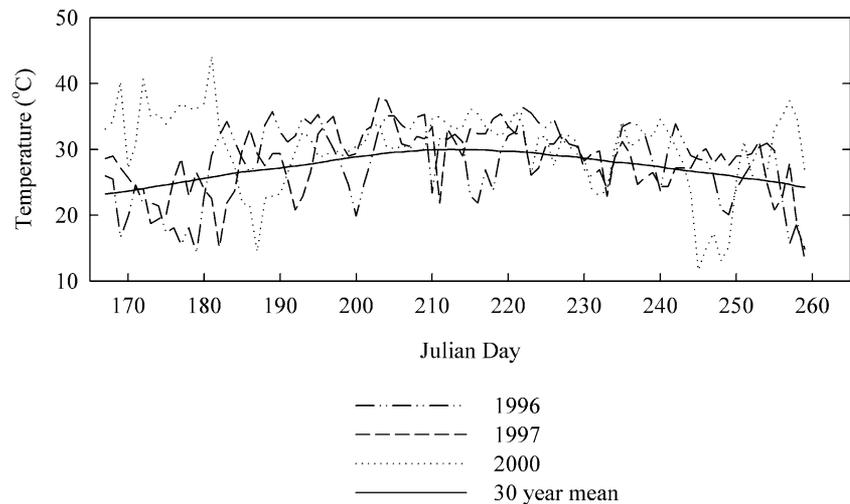
2. Methods

2.1. Study site

The study was conducted in 2 pools in the lower reaches of Boles Creek which is a major tributary to Clear Lake within the upper Lost River Watershed in northwest Modoc County, Calif. (41°51'5"N, 121°00'6"W). The Lost River is a tributary to the Klamath River. Boles Creek watershed is approximately 85,500 ha in area. Study pools were located 8 to 16 km upstream of Clear Lake on the Double Head Ranger District of the Modoc National Forest at an elevation of 1400 m. Climate is dry with precipitation falling predominantly November through May. A distinct dry season occurs from mid-May through October. Forty-six year mean annual precipitation (1-Oct through 30-Sep, 1949 through 2004) at the closest representative long term weather station, Lava Bed National Monument, 45 km west of the study site, is 37.8 cm. Figure 1 displays mean maximum daily air temperature at Lava Bed National Monument for the period 15-Jun through 15-Sep, based upon 30 years of maximum daily air temperature observations.

The Boles Creek watershed is located on the Modoc Plateau which is capped by slightly weathered basalt flood flows estimated to be 100–300 m thick and created by volcanic activity over the past 60 million years (United States Department of Agriculture Soil Conservation Service 1980). Dominant plant species in the watershed are western juniper (*Juniperus occidentalis* Hook.), mountain big sagebrush (*Artemisia tridentata vaseyana* Nutt. (Rydb.) Beetele), and Idaho fescue (*Festuca idahonesis* Elmer). Like many streams in the region, Boles Creek has down-cut into the basalt flows, resulting in 2–5 m vertical entrenchment of the stream channel relative to the surrounding basalt plain. Boles Creek is intermittent during summer months creating large, isolated stream reaches or pools characterized by massive bedrock – basalt substrate. Pool size can range from 25–150 m long, 5–15 m wide, and 1 – 3 m deep during summer. The 2 pools enrolled in this

Fig. 1 Daily maximum air temperatures observed from 15-Jun through 15-Sep in 1996, 1997, and 2000 at study pools on Boles Creek, Modoc National Forest, Calif., and the 30 year mean daily maximum air temperature at Lava Bed National Monument, Calif



study were approximately 75 m long, 10 m wide, and mean depth ranged from 1.5 to 2.5 m during the study period.

2.2. Data collection

Water and air temperature data were collected on a 0.5 hour time step ($n = 48$ per day) from 15-Jun through 15-Sep during 1996, 1997, and 2000 using commercially available temperature data-loggers (Onset Computer Corporation, Pocasset, MA, USA). Air temperature was collected adjacent to each pool by paired data-loggers placed in solar radiation – heat shields and suspended 1.5 m above the soil surface in western juniper trees. Air temperature data-loggers were placed in locations reflective of ambient air movement and mixing. Water temperature was measured at the top (0.3 m below pool surface) and bottom (0.3 m above pool substrates) of each pool in 2 locations. A system of weights and floats was used to maintain data-loggers at these depths throughout the course of each study year. Water temperature data-loggers were placed in the channel thalweg at the longitudinal one third and two third position of each pool, such that top of pool data-loggers were immediately above bottom of pool data-loggers. The same sampling locations were used each year. Mean water depth of each pool was determined at data logger deployment (15-Jun) and retrieval (15-Sep).

2.3. Data analysis

Daily maximum and mean temperature ($^{\circ}\text{C}$) was calculated from the 0.5 h time series collected by each paired air ($n = 4$ per year) and water temperature data-logger ($n = 8$ per year, 2 pools * 2 sample locations per pool * 2 depths at each sample location) for each day of each study year ($n = 92$ per sample location per depth per year). Linear mixed effects analysis (Pinheiro and Bates 2000) was utilized to: (1) determine if temperatures at the top and bottom of pools are significantly different, (2) account for possible relationships between water temperature, air temperature and season, and (3) determine if the temperature difference between top and bottom of pools was dependent upon air temperature, season or pool. Season was handled as a continuous variable (julian day 167 through 259). A separate analysis was conducted for each dependent variable (daily maximum, mean). Independent variables in each model were pool (A, B), location in pool (top, bottom), year (1996, 1997, 2000), air temperature (including quadratic form), julian day (including quadratic form), and all two way interactions. A backwards stepping approach was used to arrive at a final significant model with a criterion for inclusion in the model of $p < 0.05$. Final model coefficients were estimated using restricted maximum likelihood, and the P -value for each coefficient was estimated using the conditional t -test (Pinheiro and Bates, 2000). Repeated measures inherent in the dataset were addressed by setting sample location – depth identity (1-top, 1-bottom,

2-top, 2-bottom, etc.) as a random group effect during analysis. Analysis of standard residual plots indicated that assumptions of linearity, normality and constant variance were met for each analysis.

3. Results and discussion

3.1. Weather and water conditions

Overall, maximum daily air temperatures observed during the 3 year study period were above average. Figure 1 compares daily maximum air temperatures for 15-Jun through 15-Sep at the study site in 1996, 1997, and 2000 to the 30 year mean recorded at Lava Bed National Monument. Daily maximum air temperature was on average 0.6, 0.8, and 2.7 °C higher in 1996, 1997, and 2000 than the 30 year mean maximum daily air temperature. Median differences between daily maximum air temperatures in 1996, 1997 and 2000 and the 30 year term mean daily maximum air temperatures were 2.0, 1.5, and 2.6 °C, respectively. Total precipitation for the 1995–1996, 1996–1997, and 1999–2000 water year (1-Oct through 30-Sep) was 47.1 (125% of normal), 39.9 (105% of normal), and 31.9 cm (84% of normal), respectively. Both study pools were intermittent by 15-Jun of each study year. Mean pool depth on 15-Jun was 2.3, 2.1, and 1.8 m for 1996, 1997, and 2000, respectively. Mean pool depth on 15-Sep were 1.9, 1.6, and 1.4 m for 1996, 1997, and 2000, respectively.

For the purpose of illustrating the raw data structure, Fig. 2 displays a complete 0.5 hour time series of water and associate air temperature data collected from a representative sample location during 1996. Figs. 3 and 4 report daily maximum and mean water temperatures at the top and bottom of pools as well as maximum and mean daily air temperature averaged across all sample locations for each year. Overall, water temperatures at both depths were highest in 1996 and lowest in 2000 (Figs. 3 and 4). Peak observed daily maximum temperatures at pool top consistently ranged between 25 and 29 °C, while maximum temperatures at pool bottom tended to stay below 25 °C (Fig. 3). Peak daily mean temperatures at both pool top and bottom were consistently between 20 and 25 °C (Fig. 4).

3.2. Linear mixed effects models

Tables 1 and 2 report final linear mixed effects models developed for daily maximum and mean water tem-

perature, respectively. Year, location (top or bottom of pool), air temperature, julian day, year by location interaction, and air temperature by location interaction were significant ($p < 0.05$) predictors of maximum (Table 1) and mean (Table 2) water temperature. Pool was not a significant predictor of water temperature ($p = 0.54$). Due to the significance of interactions in each model the results are most easily interpreted by calculating and plotting the products of this additive linear model, thus displaying the direction and magnitude of coefficients for significant variables (Figs. 5–7).

3.3. Relationships between air and water temperature

A positive relationship between air temperature and water temperature at both pool depths was evident in the observed data, with diurnal fluctuations in water temperature at the top of pools most closely matching air temperature (Fig. 2). Linear mixed effects analysis confirmed that maximum and mean water temperature was positively, significantly ($p < 0.001$) correlated to air temperature (Tables 1 and 2, Figs. 5 and 6). The significance and negative coefficient for air temperature² reported in Table 1 indicates that the positive effect of maximum daily air temperature on maximum daily water temperature was reduced as air temperature increased (Table 1, Fig. 5). The positive relationship between air temperature and water temperature observed in Boles Creek is not surprising given that air temperature has been recognized as a strong predictor of water temperature in numerous studies (Stefan and Preudhomme, 1993; Mohseni and Stefan, 1999; Larson and Larson, 2001; Webb *et al.*, 2003; Tate *et al.*, 2005). A more interesting aspect of the results of this study is the significant air temperature by location in pool (top, bottom) interaction which indicates that the magnitude of vertical thermal stratification in pools was dependent upon air temperature (Tables 1 and 2). This relationship is discussed below in the thermal stratification section.

3.4. Thermal stratification

Raw water temperature data (Fig. 2) as well as daily maximum and mean temperatures (Figs. 3 and 4) indicate thermal stratification with appreciably cooler and more consistent temperatures at the bottoms of the study pools. Linear mixed effects analysis confirms

Fig. 2 Stream pool water and associated air temperature data collected on a 0.5 hr time step at one of four sample locations from 15-Jun through 15-Sep during 1996. Water temperatures were measured 0.3 m below pool water surface (top) and 0.3 m above pool substrates (bottom). The two study pools were located on Boles Creek, Modoc National Forest, Calif

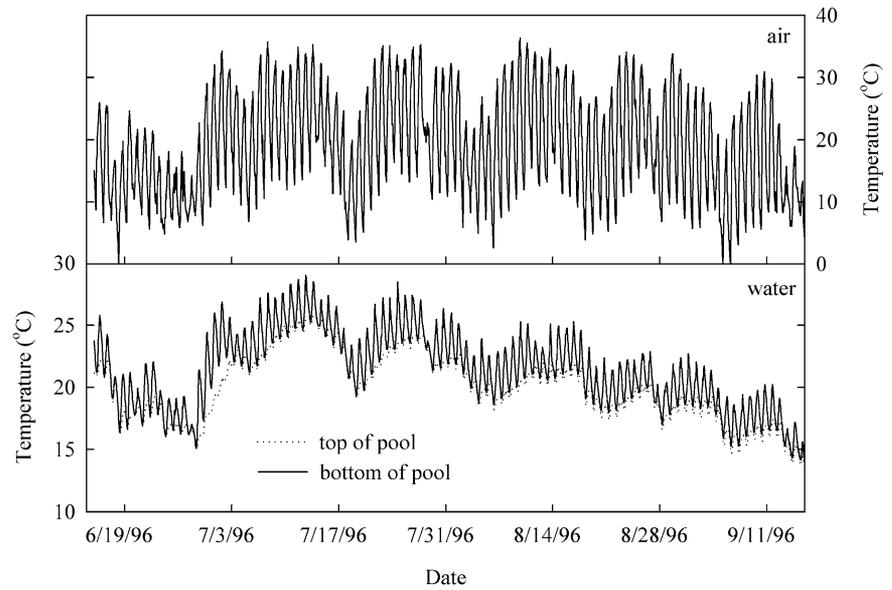


Fig. 3 Mean daily maximum stream pool water and associated air temperature calculated from 0.5 hr time step data from four sample locations from 15-Jun through 15-Sep during 1996, 1997, ad 2000. Water temperatures were measured 0.3 m below pool water surface (top) and 0.3 m above pool substrates (bottom). The two study pools were located on Boles Creek, Modoc National Forest, Calif

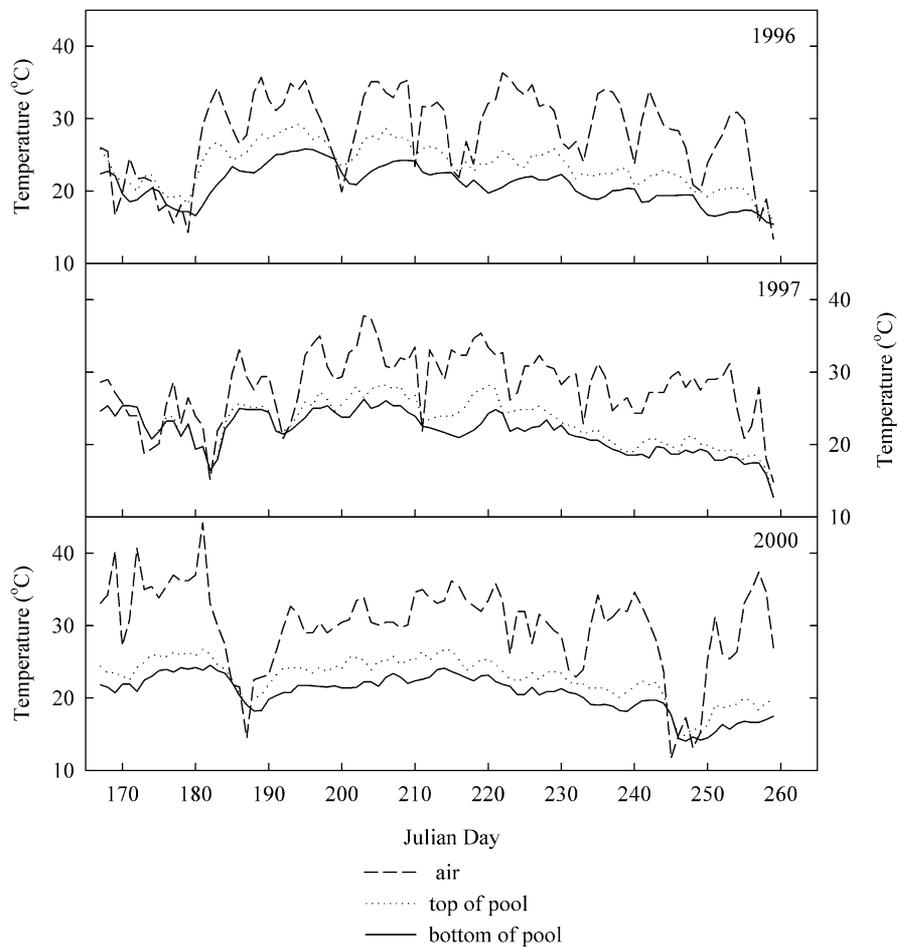


Fig. 4 Mean daily mean stream pool water and associated air temperature calculated from 0.5 hr time step data from four sample locations from 15-Jun through 15-Sep during 1996, 1997, and 2000. Water temperatures were measured 0.3 m below pool water surface (top) and 0.3 m above pool substrates (bottom). The two study pools were located on Boles Creek, Modoc National Forest, Calif

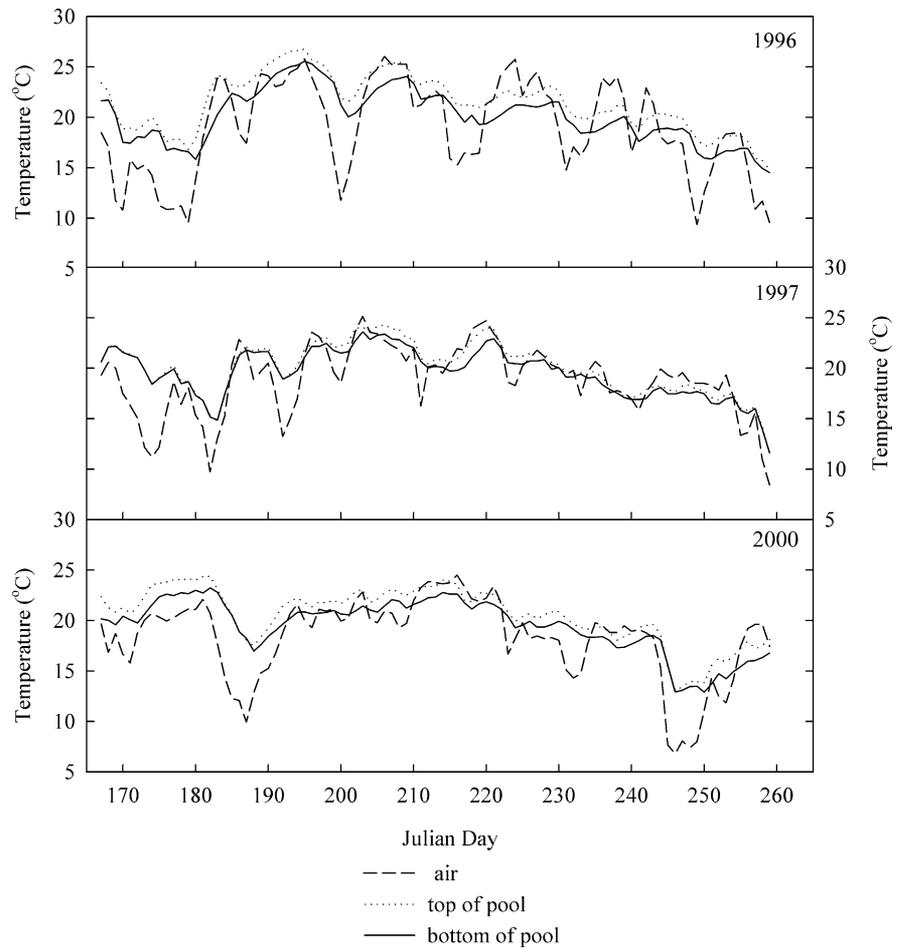


Table 1 Final linear mixed effects model predicting maximum daily water temperature (°C) as a function of location in pool (0.3 m from top or 0.3 m from bottom), maximum daily air temperature (°C), day of year, and year. Data collected from 15-Jun through 15-Sep 1996, 1997, and 2000 from 2 pools in Boles Creek on the Modoc National Forest, Calif

Factor	Coefficient	95% CI ^a	P-value
Year			
1996 ^b	0.00	–	–
1997	–0.09	–0.47, 0.30	0.660
2000	–1.08	–1.37, –0.78	<0.001
Location			
Top ^b	0.00	–	–
Bottom	0.48	–0.37, 1.32	0.269
Max. Air temperature	0.50	0.40, 0.60	<0.001
Max. Air temperature ²	–0.004	–0.005, –0.002	<0.001
Julian Day	0.63	0.57, 0.68	<0.001
Julian Day ²	–0.0016	–0.0017, –0.0015	< 0.001
Year*location			
1996*bottom ^b	0.00	–	–
1997*bottom	1.48	1.04, 1.92	<0.001
2000*bottom	0.82	0.43, 1.20	<0.001
Max. Air temperature*location			
Max. Air*top ^b	0.00	–	–
Max. Air*bottom	–0.11	–0.14, –0.09	<0.001
Intercept	–47.36	–52.95, –41.77	<0.001

^aReference category for each categorical variable to which other levels of the categorical variable are compared

^b95 % confidence interval for coefficient (lower, upper)

Table 2 Final linear mixed effects model predicting mean daily water temperature (°C) as a function of location in pool (0.3 m from top or 0.3 m from bottom), mean daily air temperature (°C), day of year, and year. Data collected from 15-Jun through 15-Sep 1996, 1997, and 2000 from 2 pools in Boles Creek on the Modoc National Forest, Calif

Factor	Coefficient	95% CI ^a	P-value
Year			
1996 ^b	0.00	–	–
1997	–0.73	–1.01, –0.44	<0.001
2000	–0.34	–0.56, –0.11	0.003
Location			
Top ^b	0.00	–	–
Bottom	–0.15	–0.76, 0.46	0.628
Mean air temperature	0.42	0.40, 0.44	<0.001
Julian Day	0.35	0.31, 0.40	<0.001
Julian Day ²	–0.0009	–0.0010, –0.0008	<0.001
Year*location			
1996*bottom ^b	0.00	–	–
1997*bottom	0.88	0.54, 1.22	<0.001
2000*bottom	0.27	–0.02, 0.56	<0.072
Mean air temperature*location			
Max. Air*top ^b	0.00	–	–
Max. Air*bottom	–0.06	–0.09, –0.03	<0.001
Intercept	–18.63	–23.32, –13.95	<0.001

^aReference category for each categorical variable to which other levels of the categorical variable are compared

^b95 % confidence interval for coefficient (lower, upper)

that maximum and mean water temperatures were significantly ($p < 0.001$) cooler at pool bottom compared to pool top for all three years of the study (Tables 1 and 2, Figs. 5 and 6). Maximum daily thermal stratification observed across all sample locations during 1996, 1997, and 2000 was 6.1, 5.3, and 7.6 °C, respectively. Minimum daily thermal stratification observed across all sample locations during 1996, 1997, and 2000 was 0.2, 0.1, and 0.2 °C, respectively. Mean daily maximum water temperature at the top of pools was 2.8, 1.3, and 2.2 °C warmer than at the bottom of pools in 1996, 1997, and 2000, respectively. Mean daily mean water temperatures at the top of pools were 1.3, 0.5, and 1.0 °C warmer than at the bottom of pools in 1996, 1997, and 2000, respectively. Mean daily range in water temperature at the top of pools for 1996, 1997, and 2000 was 2.5, 1.3, and 2.1 °C greater than at the bottom of pools, respectively.

Examination of Figs. 3 and 4 indicates that the magnitude of daily thermal stratification was dependent upon air temperature, with the greatest differences between top and bottom of pool water temperature occurring on days with the warmest air temperatures (e.g., Fig. 3 day 190 compared to day 200, 1996). This is confirmed by the significant ($p < 0.001$) air temperature by location in pool (top, bottom) interaction for both daily maximum and mean water temperatures (Tables 1 and 2). As daily air temperature increased, water temperature at the top of the pools increased at

a greater rate than at the bottom of pools (Figs. 5 and 6). This resulted in increased thermal stratification between top and bottom of pools as daily air temperature increased. For instance, the difference in daily maximum water temperature between top and bottom of pool location in 1996 increased from a 2.1 to 3.9 °C as daily maximum air temperature increased from 22 to 38 °C (Fig. 5, Table 1).

There was significant year to year variation in the magnitude of thermal stratification. The significant year ($p < 0.001$) by location (top, bottom) interaction in the model for daily maximum temperature indicates that the magnitude of vertical thermal stratification in 1997 and 2000 was statistically less than in 1996 (Table 1, Fig. 5). Daily mean water temperature stratification in 2000 was marginally ($p = 0.072$) lower than 1996. These differences are most likely attributable to year to year variation in weather conditions (temperature, precipitation) as well as pool volume and depth. Stratification was greatest in 1996 which had the greatest precipitation and pool depths of the 3 season study, and had moderate air temperatures. The magnitude of thermal stratification was least during 1997, the year with average precipitation conditions and the coolest air and water temperatures of the study period.

The results from Boles Creek agree with published studies conducted on intermittent or low summer flow streams from several climatic zones in California. In coastal mountain streams of northern California,

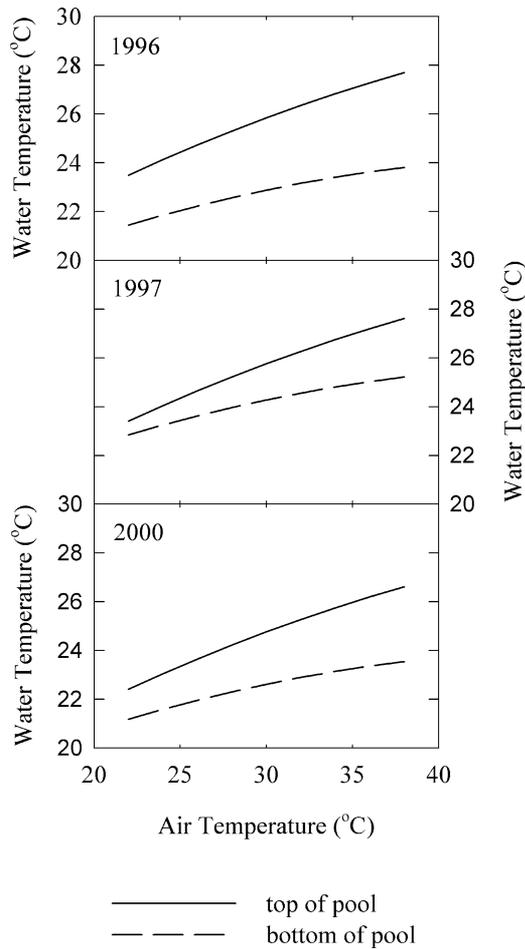


Fig. 5 Relationship between maximum daily air temperature and maximum daily stream pool water temperatures predicted by a linear mixed effects model containing pool location (0.3 m below pool surface, 0.3 m above pool substrate), year (1996, 1997, 2000), air temperature, julian day, a year by pool location interaction, and a air temperature by pool location interaction. Prediction was calculated for julian day 196 (15-Jul). Linear mixed effects model was developed from data collected 15-Jun to 15-Sep from two study pools in Boles Creek, Modoc National Forest, Calif

Neilson *et al.* (1994) report summer surface water temperatures 3.5 to 9.0°C higher than temperatures at the bottom of pools greater than 3 m deep when surface flows decreased to less than 1 m/s. Matthews *et al.* (1994) report as much as 4.5°C stratification in a 4.5 m deep pool the central west-slope Sierra Nevada Mountains. Matthews and Berg (1997) report maximum thermal stratifications of 5.6 to 5.9°C in 4.1 and 1.5 m deep pools in a southern California coastal stream. As Neilson *et al.* (1994) discuss, vertical thermal stratification occurs due to a lack of mixing when

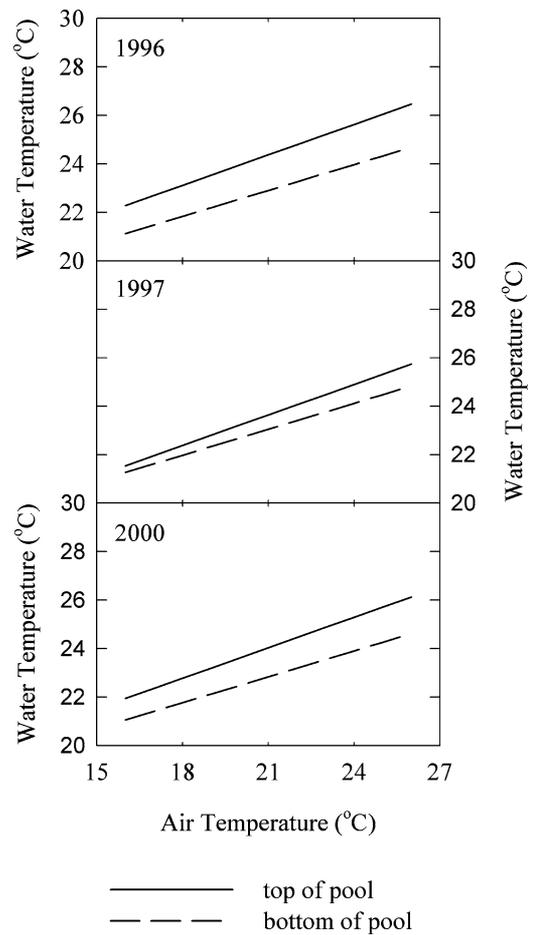


Fig. 6 Relationship between mean daily air temperature and mean daily stream pool water temperatures predicted by a linear mixed effects model containing pool location (0.3 m below pool surface, 0.3 m above pool substrate), year (1996, 1997, 2000), air temperature, julian day, a year by pool location interaction, and a air temperature by pool location interaction. Prediction was calculated for julian day 196 (15-Jul). Linear mixed effects model was developed from data collected 15-Jun to 15-Sep from two study pools in Boles Creek, Modoc National Forest, Calif

stream pools are either isolated from main channel flows and/or streamflow levels fall below some threshold. Neilson *et al.* (1994) also reported pool stratification due to non-mixing influx of cool subsurface water from porous gravel substrates. We lack data to identify the specific mechanism leading to pool thermal stratification observed in Boles Creek. We hypothesize that minimal subsurface water input occurred through the massive bedrock substrate in these study pools. It is most probable that stratification occurred due to a lack of mixing due to intermittent streamflow conditions.

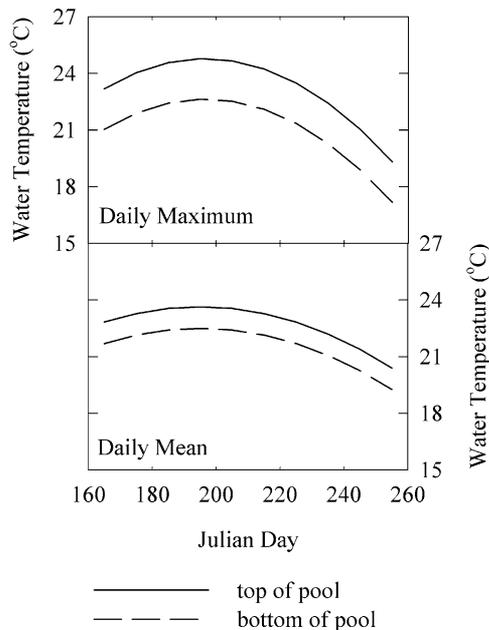


Fig. 7 Relationship between julian day and maximum and mean daily stream pool water temperatures predicted by a linear mixed effects model containing pool location (0.3 m below pool surface, 0.3 m above pool substrate), year (1996, 1997, 2000), air temperature, julian day, a year by pool location interaction, and a air temperature by pool location interaction. Prediction was calculated for a maximum daily air temperature of 30 °C, and a mean air temperature of 20 °C, respectively. Linear mixed effects model was developed from data collected 15-Jun to 15-Sep from two study pools in Boles Creek, Modoc National Forest, Calif

3.5. Seasonal temperature patterns

Water temperatures closely followed seasonal air temperature trends (Figs. 2–4). Regardless of depth or year, daily maximum and mean pool water temperature was significantly ($p < 0.001$) associated with julian day and julian day² (Tables 1 and 2). Figure 7 displays this relationship, illustrating that water temperature increased from 15-Jun to a peak on approximately 15-Jul (day 196) and then steadily decreased for the remainder of the season. We have observed similar seasonal water temperature patterns on other streams in the region (Tate *et al.*, 2005). The significance of julian day indicates that air temperature did not explain all the variation in water temperature due to seasonal patterns in weather conditions. Factors such as day length, daily solar input, and sun angle logically effect water temperature and vary across season. The insignificance of the interaction term for julian day and location in pool (top, bottom) indicates that the magnitude of pool strat-

ification was uniform across the season ($p = 0.47$ and $p = 0.63$ for daily maximum and mean, respectively).

3.6. Cold water refuge

Temperature stratification in the study pools did create potential refuge for redband trout from lethal maximum temperatures observed in surface waters in 1996. Figure 3 illustrates that with the exception of pool surface waters in 1996, maximum water temperatures observed in this study did not exceed the estimated 29 °C lethal maxima for redband trout (Bowers *et al.*, 1979; Rodnick *et al.*, 2004). Surface waters did exceed the 25 °C lethal limit generally accepted for trout in each year of the study (Hokanson *et al.*, 1977; Jobling, 1981; Bjornn and Reiser, 1991). However, with the exception of a brief period in 1996, temperatures at the bottom of pools were below 25 °C (Fig. 3). While it does appear that stratification provides refuge from lethal maximum temperatures for redband trout, temperature conditions above 21 °C still made these pools sub-optimal thermal habitat for redband trout during peak seasonal temperatures (Bowers *et al.*, 1979; Gamperl *et al.*, 2002). Maximum and mean daily water temperatures at both top and bottom of pools were certainly above the preferred 13 °C water conditions reported by Gamperl *et al.* (2002). During late June through August, maximum and mean water temperatures were consistently at or above levels shown to increase metabolic costs, and negatively impact redband trout density and biomass (Rodnick *et al.*, 2004; Zoellick, 2004).

While thermal refuge conditions created by pool stratification in this study were not always optimal for redband trout (<21 °C), temperatures were within the range which redbands have been observed to occur and persist in intermittent pools in arid rangeland streams (Zoellick, 1999). Thermal refuge due to vertical temperature stratification in the study pools has the potential to facilitate redband survival during periodic summer water temperature fluctuations above the lethal maximum level of 29 °C. The increased magnitude of stratification observed as air temperature increased is particularly fortuitous, creating maximum temperature differentials between top and bottom of pools at times when surface water temperature is approaching upper lethal limits. The potential for thermally stratified pools in the region to provide refugia from periodic ambient water temperature excursions above lethal limits seems feasible. However, additional research

involving simultaneous evaluation of water temperature, dissolved oxygen concentrations, food availability, and other important determinants of trout habitat quality is needed to fully determine the suitability of such pools for redband trout recovery.

4. Conclusions

Vertical thermal stratification did occur within intermittent pools typical of arid rangeland streams of the Modoc Plateau in northeastern California and south-central Oregon. This created cooler and more constant water temperatures at the bottom of pools compared to pool surface waters. Daily water temperature was significantly associated with daily air temperatures. Pool thermal stratification was dependent upon air temperature with the magnitude of stratification increasing as air temperature increased. The magnitude of thermal stratification varied significantly from year to year, likely reflecting variation in annual weather conditions. Stratification was uniform across the summer season. Overall, the thermal regime in the study pools was often near the upper lethal limit reported for redband trout. Although temperatures at the bottom of these thermally stratified pools could feasibly offer refuge from lethal temperatures near the pool surface, temperatures at pool bottom were consistently above optimal levels for redbands. Given the broad interest in recovery of this species into former habitat and the demonstrated potential for pool stratification to provide escape from lethal temperatures, a more robust evaluation of stratification generated thermal refuge is warranted for the region.

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