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Rainbow trout responses to water temperature and dissolved oxygen stress in two southern California stream pools

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Habitat use by rainbow trout *Oncorhynchus mykiss* is described for a southern California stream where the summer water temperatures typically exceed the lethal limits for trout (>25° C). During August 1994, water temperature, dissolved oxygen (DO), and trout distribution were monitored in two adjacent pools in Sespe Creek, Ventura County, where summer water temperature reached 28·9° C. Water temperature was an important factor in trout distribution in the two pools. During 1–11 August 1994, water temperatures in pool 1 ranged from 21·5° C at the bottom (4·1 m) to 28·9° C at the surface. After 5 August, trout were no longer found in this pool, suggesting that trout had moved out of the high temperature water or died. In the adjacent, shallower (1·5 m) pool 2, surface water temperatures were as high as 27·9° C, but temperatures on the bottom remained cooler (17·5–21° C) than pool 1, presumably due to groundwater seeps. Consistent aggregations of trout were observed in pool 2 throughout the study period. During the day when water temperature was highest, most trout were found in a region of the pool with the lowest water temperature (mean = 18·3° C). Conversely, regions with the highest water temperatures had the fewest trout during the day. The seeps may have introduced water with low dissolved oxygen into pool 2, as the DO in many locations on the bottom ranged from <1 mg l^{-1} to 5 mg l^{-1} over 24 h, while the surface DO ranged from 4·1 to 10·0 mg l^{-1}. Lowest DO occurred from 2400 to 0600 hours. During August, water temperature and DO were positively related. Thus, rainbow trout faced a trade-off between the relatively cool water temperature with low, possibly lethal levels of DO (e.g. 1·7 to 3·4 mg l^{-1} in region 3), and lethally high water temperature but high DO. Seeps may serve as important thermal refugia for trout, and an increased understanding of their role as potential critical refugia in southern California is necessary.

Key words: rainbow trout; *Oncorhynchus mykiss*; dissolved oxygen; water temperature; environmental stresses; southern California; habitat; abiotic factors.

INTRODUCTION

Rainbow trout *Oncorhynchus mykiss* (Walbaum) are near the southern extent of their range in southern California, and inhabit streams that reach temperatures reported to exceed the upper lethal limits for trout (>25° C) (Hokanson *et al.*, 1977; Jobling, 1981; Bjornn & Reiser, 1991). Many studies have reported on the importance of cool water refugia for salmonids during summer periods with high water temperatures (King, 1937; Gibson, 1966; Keller & Hofstra, 1983; Berman & Quinn, 1991; Matthews *et al.*, 1994; Nielsen *et al.*, 1994*a*). Although little information is available on trout habitat use in southern California, recent stream surveys (Sara Chubb, Los Padres National Forest, unpublished data) and anecdotal information indicate that when summer water temperatures are high

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(i.e. >25° C) in some parts of the stream, trout are often located in cooler water areas near seeps or in thermally stratified pools. These cooler water areas may be critical for trout survival in southern California. However, because groundwater seeps may bring in cooler water that is oxygen depleted (Todd, 1976), these fish may face a trade-off between lethal temperature or low dissolved oxygen (DO). The incipient lethal level of dissolved oxygen for adult and juvenile rainbow trout is about 3 mg l^{-1} or less, depending on environmental conditions, particularly temperature (Gutsell, 1929; Doudoroff & Shumway, 1970; Raleigh *et al.*, 1984).

This study examined the range of water temperatures and DO available to and used by trout during periods of elevated water temperatures (summer) common to southern California streams. Because both resident (rainbow) and anadromous (steelhead) populations of *O. mykiss* range into southern California and Mexico (Shapovalov & Taft, 1954; Behnke, 1992), information on habitat use during periods of thermal stress has geographically broad implications. After an 8-year drought in California and years of severe population decline, steelhead trout were observed in several southern California streams with the onset of a wet winter in 1992–1993 (Nielsen *et al.*, 1994*b*). Although steelhead may have different habitat requirements from rainbow trout, in many areas they are sympatric and genetically indistinguishable. Currently, because interest in restoring habitat and runs of the southern California steelhead is considerable (Nehlsen *et al.*, 1991; Titus *et al.*, 1996; Douglas, 1996), information on their habitat requirements is critical.

This paper describes a study in Sespe Creek, Ventura County, California which (1) identifies the diel range of available water temperatures and DO, and possible sources of cool water; and (2) determines whether steelhead/rainbow trout use the cool water zones.

MATERIALS AND METHODS

STUDY SITE

Sespe Creek is about 112 km north-west of Los Angeles, California in the Coast Range and is the last remaining free-flowing (undammed) major steelhead drainage in southern California. The stream originates at about 1500 m elevation near Reyes Peak and flows east and south for 88 km where it joins the Santa Clara River near the City of Fillmore at 122 m elevation. It drains a catchment of approximately 690 km^2 (Sasaki, unpublished). The study site (34°33′34″ N, 119°11′29″ W, 945 m long) was in the middle third of Sespe Creek approximately 3·4 km upstream of the Sespe Creek/Piedra Blanca Creek confluence. The stream channel in this section (channel type C_{1-5}, *sensu* Rosgen, 1994) is broad and rocky, displaying layered sediments, exposed bedrock, large cobbles, and fine-sand point bars. Arroyo willow *Salix lasiolepis*, white alder *Alnus rhombifolia*, and Fremont cottonwood *Populus fremontii* line many of the meanders; large pools are common. The study site is typical of the middle portion of the mainstem Sespe Creek. The channel gradient of this reach is 0·5%, with a flood plain ranging in width from 2 to 10 m. Like most of southern California, the climate of the Sespe drainage is hot and dry during the summer and mildly cool and wet during the winter. The average annual precipitation for the Sespe drainage is 635 mm (Sasaki, unpublished).

The U.S. Geological Survey maintains two stream-level gauging stations on the Sespe: one in Sespe Gorge, 8 km upstream of the study pools; and another 9·5 km upstream of the Sespe Creek/Santa Clara River confluence. The 45-year record from the Sespe Gorge station shows an average monthly discharge low of 0·02 m^3 s^{-1} for August and an average monthly discharge high of 1·84 m^3 s^{-1} for February (U.S. Geological Survey, 1994). Wide fluctuation in monthly, seasonal, and annual flows are typical of the Sespe and southern California drainages (U.S. Geological Survey, 1984).

Two adjacent pools were chosen for their size, potential for temperature stratification, presence of fish, and because much of the bedrock surrounding nearby area showed evidence of groundwater seepage through cracks in horizontally stratified layers. Pool 1, 40×60 m, had a maximum depth of 4·17 m and a volume of 2230 m^3. Pool 2, the smaller and shallower of the two pools, 17×48 m, had a maximum depth of 1·42 m and a volume of 232 m^3. The substratum in pool 1 consisted of bedrock and small cobbles overlaid with fine sands. Pool 2's substratum was mostly large boulders to cobbles and gravels; two sand bars were also present. During our study, surface water flow was continuous and the two pools remained connected by a short riffle.

Rainbow trout (approximately 10–50 cm T_L) were observed in both pools during preliminary surveys and they were in pool 2 throughout our 1–11 August study period but they were not observed in pool 1 after 4 August. Historically, steelhead runs were common in Sespe Creek, but access was eliminated in the 1950s (Titus *et al.*, 1996). Thus, in Sespe Creek, steelhead populations may have become landlocked; if so, they are indistinguishable from resident rainbow trout. Rainbow trout (20–30 cm T_L) are stocked about 3 km downstream in Sespe Creek during winter and spring (Steve Parmenter, personal communication, California Department of Fish and Game, Bishop). We observed rainbow trout in both pools. Other fish in pool 1 included aggregations of three-spined stickleback *Gasterosteus aculeatus microcephalus* (L.), green sunfish *Lepomis cyanellus* (Rafinesque), arroyo chub *Gila orcutti* (Eigenmann & Eigenmann), and black bullhead *Ictalurus melas* (Rafinesque). In pool 2, three-spined stickleback and arroyo chub were also common, green sunfish were observed only twice. Dead trout and sticklebacks were found in the study pools and in areas upstream and downstream of the study site during 1–11 August.

PHYSICAL MEASUREMENTS

Pool mapping

We mapped both study pools to be able to identify trout locations relative to water temperatures and DO concentrations, to document trout habitat use, and to pinpoint cool water zones. Soundings were made at 0·5-m intervals on transects spaced every 2 m along the longitudinal axis of each pool. These data were used to calculate pool volume, Richardson number (R_i), and residence time.

Inflow discharge

Flow into the pools was calculated by the velocity-area of discharge method (U.S. Geological Survey, 1977), using a pygmy (Gurley*) current meter and the 0·6 depth method for velocity determination (U.S. Geological Survey, 1977). Four measurements were made at inflow locations to both pools during the main 10-day study period.

Water temperature

Water temperatures were measured at both pools to (1) quantify vertical temperature gradients; (2) identify cool seeps; (3) compare temperatures at locations where trout were present and absent; (4) quantify temperature differences in several regions across the horizontal extent of the pools; (5) determine ambient inflow temperature; and (6) relate water temperature to DO. For objectives 1–5, thermistor probes were positioned at fixed locations. To relate DO and water temperature, we lowered probes manually into pool 2 at fixed time intervals.

*Trade names and commercial enterprises are mentioned solely for information. No endorsement by the U.S.D.A. Forest Service is implied.

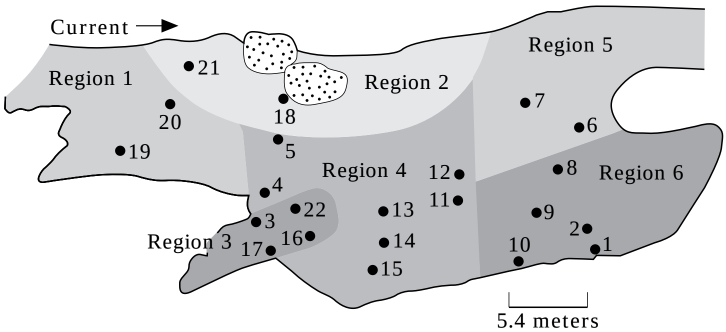

FIG. 1. Plan view of study pool 2, with location of water temperature probes and the pool's six regions. (● = water temperature probe.)

From earlier habitat surveys on Sespe Creek (Sara Chubb, pers. comm., fish biologist Los Padres National Forest), two sources of cool water were anticipated: vertical stratification with cooler water at depth, and cool water inflows through seeps. Thus, in reconnaissance surveys, we used temperature probes to find vertical stratification and possible seeps. Suspected seeps were found by walking in the pools or paddling a small boat, and temperatures were measured specifically to identify differences between adjacent areas. An attempt was made to measure the flow around the suspected seeps at the site of the coolest water by injecting dye from syringes.

Water temperature was measured ($\pm 0{\cdot}1^\circ$ C) by using thermistor probes connected to portable dataloggers. Temperatures were measured every 5 min, and averaged and recorded at 15-min intervals (an average of three 5-min measurements).

In pool 1, two vertically distributed arrays were placed from the deepest waters (4·1 and 3·01 m) to the surface. Each array incorporated two thermistors at the bottom of the pool, two 0·5 m from the bottom, one each at 1, 1·5, and 2 m from the bottom, and two 0·05 m below the surface. The 4·1 m location also had a thermistor 1 m below the surface. In pool 2, thermistors were arrayed vertically at the deepest location in the pool (1·4 m, location 12; Fig. 1), with two at the bottom, two each 0·5 and 1 m up from the bottom, and two 0·05 m below the surface.

Of the eight pairings of replicated probes on the vertical arrays in both pools, data from six were always within $\leq 0{\cdot}1^\circ$ C of each other. Temperatures differed by up to $0{\cdot}3^\circ$ C in the other pairings (the bottom probes on both vertical arrays at pool 1). The mean value from these two probes was used in all analyses.

The vertical array at pool 2 and at the 4·1-m depth location in pool 1 functioned for 10 days, from the morning of 1 August to the morning of 11 August. Trout apparently left pool 1 (or died) during the course of the August study period. After no longer observing trout in pool 1 and because we wanted to measure temperatures where fish aggregated in pool 2, the thermistors were moved to pool 2 on 4 August.

At the bottom of pool 2, five cool spots (suspected seeps) were identified (locations 1, 3, 11, 14, 22; Fig. 1) and probes were set at depths between 0·63 and 1·45 m during 4–11 August. Many trout were observed at these five locations. The probes were paired with probes located nearby (typically within 1 m horizontal distance, locations 2, 17, 12, 13, 16; Fig. 1) but presumably outside the cool water zones. A three-probe vertical array was positioned at the largest cool water zone in pool 2 (location 3; Fig. 1). In this array, probes were placed at the bottom (0·87 m), midway up the water column, and 0·05 m below the surface.

To quantify spatial differences better in pool 2, and to segregate the pool into horizontal regions, 30 additional probes were dispersed throughout pool 2. The temperature of water entering pool 2 was also gauged by two probes located at the pool's inlet throughout the August measurement period.

Table I. Concurrent DO (mg l^{-1}) measurements made on 2 and 3 August at pools 1 and 2 showing mean DO and range (in parentheses) for water column, surface, and bottom of pools

Pool	Mean water column	Surface	Bottom
1 Depth (m)	2·0	0	3·6
Measurement	7·0 (5·9–7·9)	7·7 (6·9–8·5)	6·2 (3·9–7·3)
2 Depth (m)	1·0	0	1·1
Measurement	7·0 (4·9–8·3)	7·1 (4·9–9·3)	5·1 (4·3–6·7)

Cool water zones

Measures of stratification include estimates of residence time of water in pools (quantified as pool volume divided by discharge), and the Richardson number, a dimensionless ratio of buoyancy forces to mixing forces (Nielsen *et al.*, 1994*a*). Both residence time and R_i index the relative strength of mixing cool and warm water. As residence time and R_i increase, the likelihood of stratification increases (Fisher *et al.*, 1979; cited by Nielsen *et al.*, 1994*a*). Values of R_i >1 imply stratification. Residence times and R_i were calculated for both pools. To characterize thermal stratification further, two other indices were calculated: (a) the maximum daily difference between the pool surface and pool bottom temperatures; and (b) the vertical temperature gradient in each pool's near-surface mixing zone.

Dissolved oxygen

From 6 to 10 August, DO and water temperatures were recorded approximately every 2 h at five locations in pool 2 (total of 96 h) (locations 1–5; Fig. 1). The locations were selected based on two suspected seep sites (locations 1 and 3) where trout were observed commonly and three adjacent (within 1–2 m) non-seep sites (locations 2, 4 and 5; Fig. 1) where trout were observed rarely. From these locations DO and water temperature were compared for areas fish did and did not use. Location 1, a possible seep, was located along a ledge at a depression in the bedrock and had cooler water temperatures than adjacent areas; location 3 was along a bedrock crease and also had detectably lower water temperature than adjacent areas. Trout consistently aggregated in these two locations. At all five locations, DO, water temperature, and depth were recorded at the surface and bottom. In addition, DO was measured from 2 to 3 August in both pools at the surface, middle of the water column, and at the bottom (Table I).

DO was measured throughout both pools with a Yellow Springs Instrument (YSI) 3800 water quality logger (accurate to $\pm 0{\cdot}03$ mg l^{-1}) and two hand-held meters: an Orion 820 DO meter (accurate to $\pm 0{\cdot}1$% of measured value) and a YSI 55 (accurate $\pm 0{\cdot}3$ mg l^{-1}). All meters gave similar DO measurements ($\pm 0{\cdot}3$ mg l^{-1}).

To determine the range of DO and water temperatures throughout pool 2, concurrent measurements were made at locations 1–22 (Fig. 1) starting at 2000 hours on 6 August to 1400 hours on 10 August. These values were plotted to determine the relationship between water temperature and DO. Because of the difficulty in relocating all 22 locations in the dark and so as not to disturb the temperature probe cables, DO and temperature were measured at night only at locations 1–5.

On 12–14 October, DO and water temperature were remeasured at the same 22 locations monitored in pool 2 in August. To define the vertical and horizontal range of these values further, measurements were taken every 10 cm at locations 1–5 from the bottom to the surface. Also, on 13–15 October, temperature and DO measurements were taken at a new suspected seep.

To determine if water temperature and DO were related significantly, the August and October temperature and DO readings were analysed by linear regression. The August data were examined for both the surface and bottom using three spatial stratifiers: the 22 individual locations, the 22 individual locations clumped into six regions (Fig. 1), and all locations together. A regression including all locations together, stratified by surface/bottom, was computed from the October data set. Means of all the locations within each region were calculated for each DO/temperature observation.

Hydrologic condition

The representativeness of water temperatures and cool water zonation during the study period was assessed by comparing these data to the long-term flow discharge rates and water temperatures at the Sespe Gorge gauging station 8 km upstream from the study site (U.S. Geological Survey, 1994). The U.S. Geological Survey recorded daily maximum and minimum water temperatures at this station from February 1962 to September 1978. We compared our temperature and discharge rates from August 1994 to those mean measurements from 1962 to 1978.

ANALYSES OF FISH DISTRIBUTION

To relate trout distribution throughout pool 2 to time of day, water temperature, and DO, we conducted 52 fish counts (rainbow trout only) every 2 h before the DO and water temperature recordings. We recorded fish distribution on a map of pool 2, by walking around the bank, and recording fish numbers and locations directly on a map. Recorders held a dive light above the pool to aid in night-time measurements. Trout did not appear to be startled or affected by the light, and recorders were careful not to move abruptly or startle the fish. From the maps, we constructed a time series of the 5-day fish counts and physical measures, and graphed simultaneous time, fish numbers, water temperatures, DO, and depth for the six main regions.

If trout were restricted during the day to the coolest water locations then it could be predicted that: (1) during the day, fish numbers would be greatest in the regions of the pool with the coolest water; and (2) once water temperatures cooled in the pool at night, then fish would be more evenly distributed throughout the pool. From fish counts in each of the six regions, we tested (ANOVA) whether the mean number of trout observed in the day counts (six counts at approximately 0800, 1000, 1200, 1400, 1600, and 1800 hours on five consecutive days 6–10 August) was the same as the mean number of trout observed in the night counts (six counts at approximately 2000, 2200, 2400, 0200, 0400, and 0600 hours on four consecutive nights 6–9 August). Also, to determine whether the mean number of fish was higher in any of the six regions, the means were analysed by ANOVA. If differences were shown, a Tukey or Student–Newman–Keuls (SNK) multiple comparison analysis was made to determine which regions in the pool had the highest mean number of fish. Regressions were used to determine if a relationship existed between the mean number of trout per region and mean water temperature or DO. To show the diel change in trout distribution throughout pool 2, we mapped the trout locations for the 4-day time series and, as an example, show seven separate fish counts from 8 August. To determine whether trout numbers were related to temperature and DO, we used linear regression using daytime (0800–2000 hours) counts only.

RESULTS

WATER TEMPERATURES

In August, near-surface (0·05 m depth) temperatures in both pools exceeded reported lethal temperatures for trout (Fig. 2). The mean 10-day maximum water temperature near the surface in pool 1 temperature was 27·9° C and daily maxima ranged from 26·9 to 28·9° C. In the smaller and shallower pool 2, daily

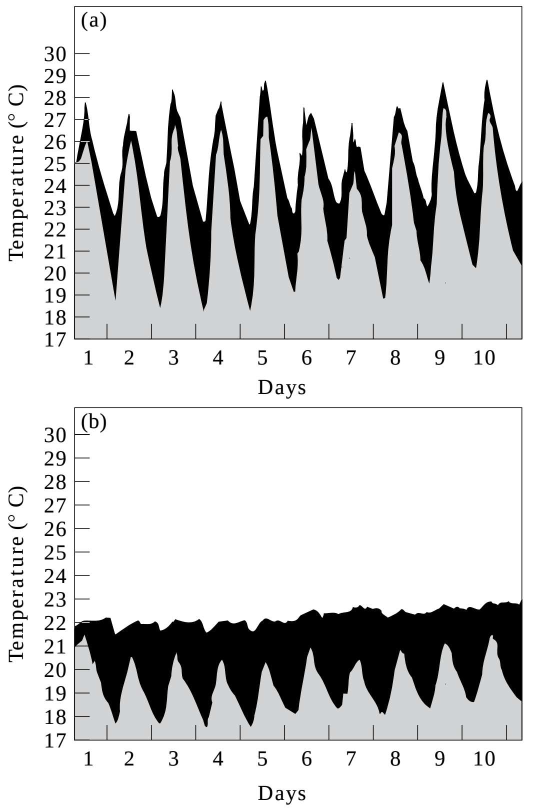

FIG. 2. (a) Surface and (b) bottom temperatures of pools 1 (■, 4·1 m deep) and 2 (□, 1·4 m deep) measured on 1–11 August 1994.

maximum near-surface temperatures were slightly lower, with a mean of 26·2° C and range of 24·7–27·9° C. Near-surface temperatures $\geq$25° C persisted for an average of 12 h and 5 h in pool 1 and 2, respectively, each day. Temperatures at the deepest locations in both pools were cooler and ranged between 17·4 and 23° C (Fig. 2). Pool 1 bottom temperatures (4·1 m array) fluctuated <1·3° C over the 10-day study period, and daily variations were not consistent; early morning lows were not always evident. Pool 2 bottom temperatures (1·4 m array) were more variable (fluctuating 4·1° C during the 10-day study period) and showed a consistent diel variation, with low temperatures always occurring between 0700 and 0830 hours and high temperatures between 1500 and 1800 hours. Both near-surface water temperatures were greater in pool 1 (mean 25·1° C and standard deviation 1·7° C) than in pool 2 (mean 22·5° C, standard deviation 2·5° C) and bottom temperatures were higher in pool 1 (mean 22·3° C, standard deviation 0·3° C) than in pool 2 (mean 19·3° C, standard deviation 1·0° C). Localized zones of cooler water were identified in pool 2, but not in pool 1.

Vertical stratification

Vertical stratification was well developed in both pools. Residence times for pools 1 and 2 were 96·9 and 10·1 h, respectively. The calculated value of R_i was substantially higher in pool 1 (600 000) compared to pool 2 (4200); but both R_i values imply stratification. Moreover, at the primary vertical array in pool 1 (4·1 m maximum depth) and at the vertical array in pool 2 (1·5 m maximum depth), the near-surface water was always warmer than water on the pool bottom. Minimum daily differences between concurrently-measured near-surface and bottom temperatures averaged 0·6 and 0·7° C (pool 1 and 2, respectively), and ranged from 0·4 to 1·0° C in pool 1 and 0·4 to 1·1° C for pool 2. The minimum difference, and the minimum daily temperatures, occurred slightly later in pool 2 (0630–0810 hours) than in pool 1 (0450–0715 hours). Maximum daily differences between concurrently measured near-surface and bottom temperatures were similar in both pools (5·6° C for pool 1 and 5·9° C for pool 2), as were the range in the surface-bottom temperatures (4·3–6·5° C in pool 1 and 4·5–6·8° C in pool 2). The maximum difference, and the maximum daily temperatures, occurred between 1200 and 1500 hours in pool 1 and slightly later (1400–1650 hours) in pool 2. Presumably, because either pool 2 received cool seep inflow, or it was smaller and therefore had quicker flow-through of incoming surface water than pool 1, the daily near-surface minimum temperatures in pool 2 (between 18·1 and 20·2° C) were appreciably lower than the daily near-surface minima in pool 1 (22·2–23·7° C). Lastly, temperatures in the lower one-third of pool 1 were near-constant with depth, in contrast to the upper metre of pool 1 where vertical thermal gradients ranged to above 3° C m^{-1}.

Between 2–10 August, inflow discharges to the pools ranged between 0·004–0·008 $m^3 s^{-1}$, and averaged 0·006 $m^3 s^{-1}$.

Regional temperatures

Hourly temperatures were averaged over all fixed-sensors in each region in pool 2 and overlapped with the 52 2-h fish count observation periods in regions 1–5. The two regions with suspected seeps had the lowest mean temperatures (18·0° C in region 3 and 19·5° C in region 6). The lowest minima in every period were also found in either region 6 or region 3. Region 3 had the lowest maximum temperature for all time periods. Temperatures were higher in region 1 than in any other region and the mean temperature in region 1 (21·8° C) was 1·5° C higher than in the next warmest region (region 4).

Seep flows

Water temperature at the bottom of the bedrock crease in pool 2 varied less than at a nearby location outside the crease (Fig. 3). Water temperature was also nearly constant at the depression (averaged 16·2–16·4° C) in the bedrock joint through much of the observation period (Fig. 3). We expected seep outflow at these locations, and although dye injected into water at the base of the crease and at the depression did not move, the seep outflow hypothesis is bolstered by the near-constancy in water temperatures, particularly relative to the diel fluctuations in both bottom and surface temperatures in the remainder of pool 2. Water of subsurface origin typically has a constant or near-constant temperature (Todd, 1976; White *et al.*, 1990). Moreover, the near-constant seep temperature was cooler than the inlet water temperature that averaged 17·8° C (minimum) and 27·9° C (maximum).

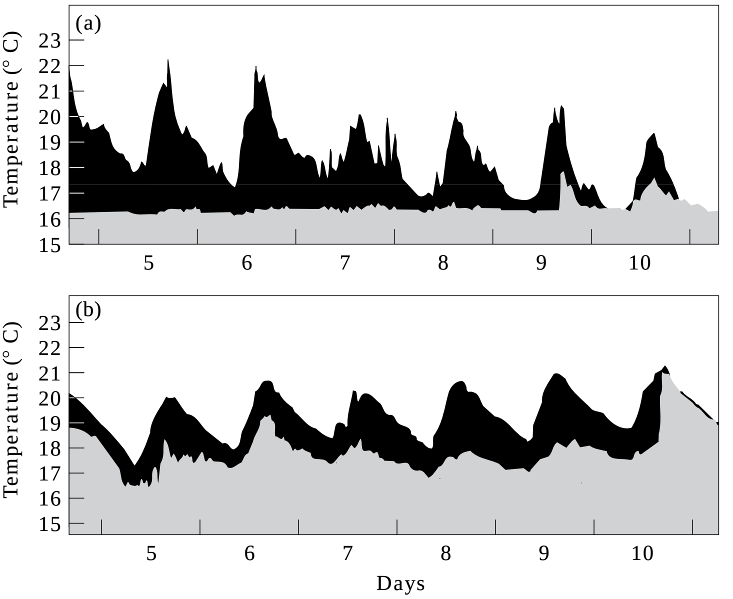

FIG. 3. Pool 2: water temperature measured at (a) bedrock depression (■, depression, 0·63 m deep; ▒, ' warm ' pair to depression, 0·52 m deep) and (b) bottom of bedrock crease (■, ' warm ' pair to bottom of crease, 1·15 m deep; ▒, bottom of crease, 1·25 m deep) paired with temperatures measured 1 m away.

DISSOLVED OXYGEN CONCENTRATIONS

During the August study period, DO in pool 2 was higher at the surface (e.g. Figs 4 and 5) than at the bottom. Also, concurrent measurements on 2 and 3 August at both pools showed that mean DO (mg l^{-1}) was lower in pool 2 than in pool 1 (Table I). The mean bottom DO was significantly lower ($P \leq 0{\cdot}05$) in pool 2 than in pool 1. At the surface DO was lowest in the early morning (0400–0800 hours) and highest in the late afternoon (1500–1800 hours). Diel fluctuations at the surface ranged from 4·1 to 10 mg l^{-1} in pool 2.

At the bottom of pool 2, DO levels underwent diel fluctuations and ranged from 0·2 to 8·8 mg l^{-1}. DO levels were lowest from 2400 to 0400 hours and highest in the late afternoon. Location 5 underwent the greatest diel fluctuations in DO ranging from 0·2–8·8 mg l^{-1} in a 24-h period. Location 3 underwent the least diel DO change ranging from 1·7–3·4 mg l^{-1} over the intensive 4-day recording period. The low diel variation in DO at location 3 suggests a groundwater seep of deoxygenated water.

Dissolved oxygen and water temperature

DO levels were lowest on the bottom (minimum 0·2 mg l^{-1}) in pool 2 (Figs 4 and 5) and were positively related to water temperature: slope coefficients were non-zero for each of the six regions at both the surface and bottom of pool 2 (Fig. 6).

October water temperature and DO measurements and hydrodynamics

Heavy rainfall ending on 4 October increased streamflow into pool 2, and on 5 October measured flow was 0·34 m^3 s^{-1}, 50 times the August rate, and

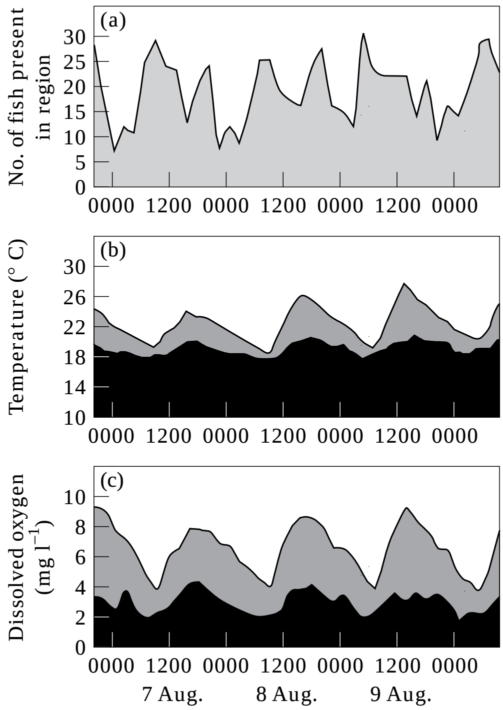

FIG. 4. (a) Fish frequency; (b) water temperature; and (c) dissolved oxygen measurements from surface (▨) and bottom (■) of region 3 in pool 2 on 7–9 August 1994.

pool levels were about 40 cm above the August levels. By 12 October, pool 2 had cooled and no temperatures >18° C were observed. From 12 to 15 October, water temperature at the 22 locations ranged from 11·3 to 17·7° C at the surface, and 11·3–16° C on the bottom. DO was also higher than in August, and ranged from 7·6–14·4 mg l^{-1} at the surface to 2–5·7 mg l^{-1} on the bottom.

In mid-October, two low DO sites (3 and 5) identified in August no longer had low DO. An extensive search of the pool revealed only one suspected seep where, at 1220 hours on 13 August, a localized area about 5 cm along the bottom (30 cm deep) was 17° C with a DO of 1·5 mg l^{-1}. In October, however, within 5–30 cm of this spot, water temperature ranged from 13·9 to 14·8° C and DO ranged from 6·2 to 6·7 mg l^{-1}, similar to the pool's ambient temperature and DO. Thus, in October when the overall water temperature was cooler, the seep water temperature was slightly warmer than ambient. In the early mornings of 14–15 October, the seep water temperature was again around 16–17° C while the adjacent (5–30 cm away) water temperatures were 12–13° C; DO at the seep was 3·0 mg l^{-1}. These seep water temperature and DO measurements were similar to those observed during August. The relative stability of the water temperature and DO suggest a subsurface water source. The high correlation of DO with temperature evident in August was not observed in October, when DO appeared to be distributed randomly with temperature (Fig. 7). Higher, more turbulent flows would presumably entrain

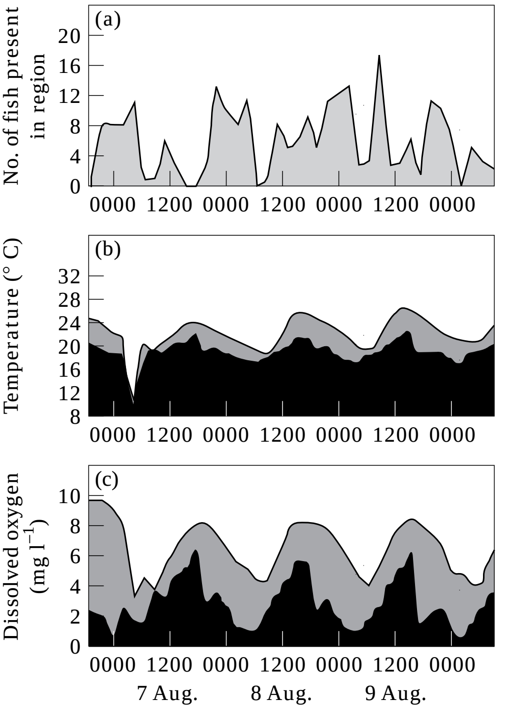

FIG. 5. (a) Fish frequency; (b) water temperature; and (c) dissolved oxygen measurements from surface (▨) and bottom (■) of region 6 in pool 2 on 7–9 August 1994.

atmospheric oxygen and serve to oxygenate water, thereby causing changes in water temperatures and DO.

HYDROLOGIC CONDITION

The mean daily maximum water temperature from 1–10 August during the 17 years of USGS records (1962–1978) was 24·2° C. The mean yearly water temperature maximum during the same period was 26·3° C and ranged from 22·2–29·5° C. During 4 of the 17 years of record, the maximum temperature for the year occurred during the first 10 days in August. During the other 13 years, the maximum temperature during the first 10 days each August was usually no more than 1 or 2° C below the maximum daily temperature recorded for each year. This condition suggests that surface water temperatures in the study pools during the first 2 weeks in August 1994 were at or near the annual maximum temperatures.

Mean daily discharge at the U.S. Geological Survey gauge during the first 2 weeks of August 1994 was 0·0082 $m^3 s^{-1}$ (U.S. Geological Survey, 1994). This value is similar to the median value 0·009 $m^3 s^{-1}$ for the 34-year analysis period. Fifteen years had discharges lower than 1994, and 18 years had discharges higher than 1994. The first 2 weeks of August 1994 appear to be representative of average discharge conditions at the USGS gauge, and presumably also at the study site.

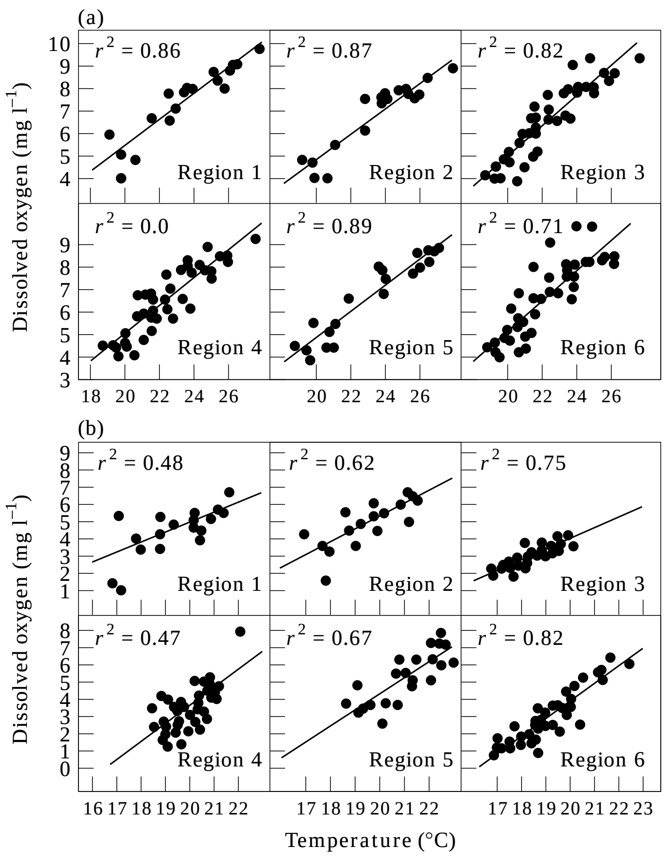

FIG. 6. August dissolved oxygen–temperature relationships for (a) surface and (b) bottom locations in six regions of pool 2.

FISH COUNTS

August fish observations

During the day, highest fish counts were observed in regions 2–4 (Table II). Trout numbers changed from day to night in these three regions and significantly higher numbers ($P<0{\cdot}05$, square root transformation, ANOVA) were observed during the day. Throughout the diel period, low numbers (means ranged from 0·3 to 6·7 trout) were observed in regions 1, 5, and 6. Moreover, diel differences were also evident in fish distributions as seen in the pool maps of seven fish counts on 8 August (Fig. 1). Fish appeared to redistribute themselves spatially throughout the diel period. During the day trout aggregated in regions 2–4 and during the night in regions 1 and 6 ($P<0{\cdot}05$ ANOVA; Fig. 8).

Fish numbers also differed between regions both day and night (H_o=median number of fish is the same for each region when day or night are compared, $P<0{\cdot}05$, Kruskal–Wallis, SNK multiple comparison). Region 3 had higher median number than all other regions both day and night. The results of the SNK indicated that regions 3>2>4>6>5=1 during the day, and regions 3>4>6>2>1>5 at night.

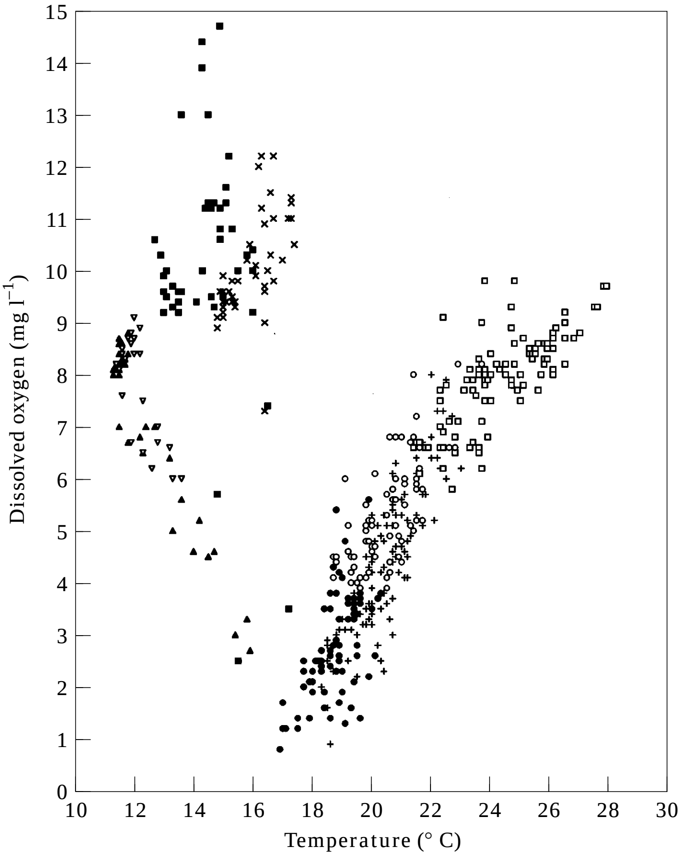

FIG. 7. August and October dissolved oxygen and temperature relationships in pool 2. ○, August surface AM; □, August surface PM; ●, August bottom AM; +, August bottom PM; ▽, October surface AM; ×, October surface PM; ▲, October bottom AM; ■, October bottom PM.

TABLE II. Mean temperature (° C), dissolved oxygen (DO) (mg l^{-1}) (both measured with YSI 3800), and mean number of trout from each region of pool 2 for counts made every 2 hours on 6–10 August, 1994

Region	Day			Night		
	Temperature	DO	Trout	Temperature	DO	Trout
1	20·0	4·7	1·4			3·4
2	20·4	4·8	8·4	19·5	2·1	5·7
3	19·4	3·5	22·4	18·8	2·9	17·0
4	19·8	4·0	14·9	20·7	4·5	12·9
5	20·7	5·2	1·0			0·3
6	20·4	4·2	4·9	18·4	2·0	6·7

Counts are separated into day (0800–2000 hours) and night (2000–0800 hours).

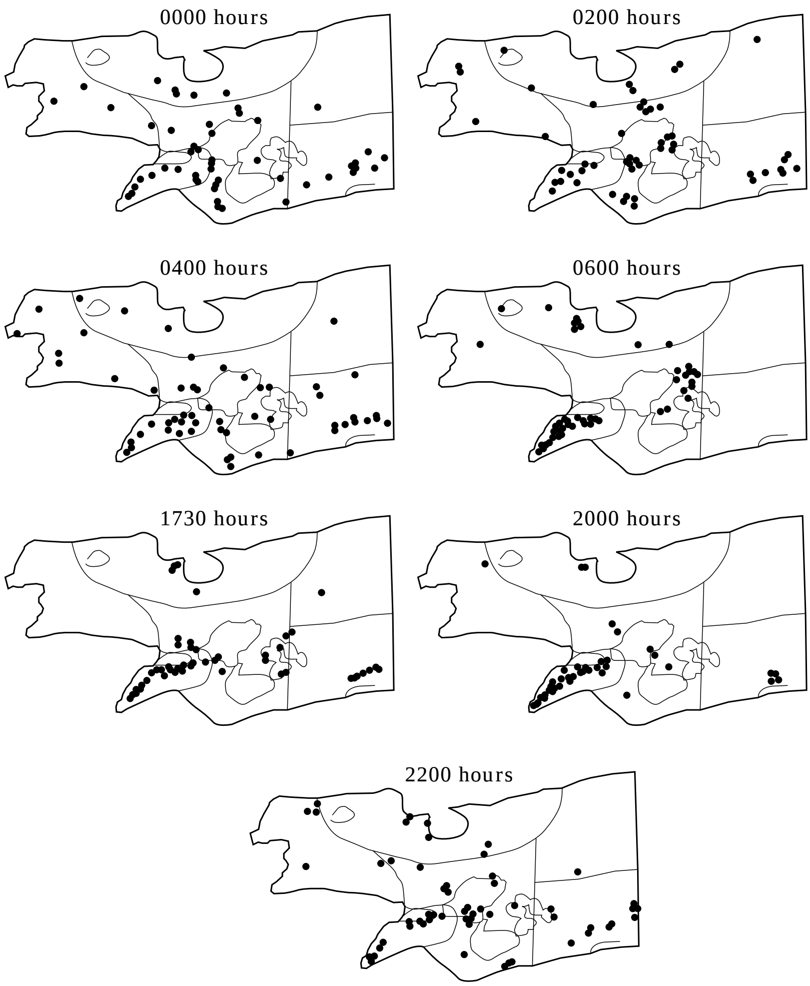

FIG. 8. Fish distribution in pool 2 at 0000, 0200, 0400, 0600, 1730, 2000, and 2200 hours on 8 August 1994.

Fish numbers relative to DO and water temperature

During the day when water temperature peaked, most trout (mean = 22·4 fish region^{-1}) were found in region 3 with the lowest mean water temperature (mean = 19·4° C from concurrent fish counts and DO and water temperature measurements with YSI 3800). Conversely, during the day, regions 1 and 5 had the highest average water temperature in the pool, and the fewest trout (Table II). Regression analysis also revealed that mean fish numbers per region were inversely related to water temperature and DO: the mean number of trout per region decreased as DO and temperature increased (significant regression coefficients, $P < 0·05$).

October fish observations

Only five trout were observed in pool 2 on 12 and 13 October (compared to 50–60 in August). No groups of fish were observed near the previous seeps. Also in October, four trout were observed in a downstream pool where none were observed in August.

DISCUSSION

During the August 1994 study in two Sespe Creek pools, ambient water temperature often exceeded reported lethal levels for rainbow trout (i.e. >25° C). In the warmer pool 1, maximum water temperatures reached 28·9° C, and surface temperature averaged 27·9° C; trout either left this pool or died during the study period. It is unknown whether acclimation is an important mechanism that enables trout to tolerate these extreme temperatures. Similar to results of other studies (Baltz *et al.*, 1987; Cech *et al.*, 1990), water temperature in Sespe Creek was an important determinant of trout distribution during periods of stressfully high water temperatures: during the day when temperatures were warmest, trout were found in regions of the pool having the coolest water temperatures. Trout often aggregated along the suspected seep in region 3 of pool 2, and these fish remained stationary near the seep throughout the warmest periods of the day. Such aggregating behaviour has been observed regularly in other southern California streams (S. Chubb, unpublished data). King (1937) also observed over 100 rainbow trout aggregated near a cool temperature spring source in a stream where ambient temperature was 29° C.

Because water temperature was related to DO during August, rainbow trout faced a trade-off between the coolest water temperatures with low, possibly lethal levels of DO (e.g. 1·7–3·4 mg l^{-1} in region 3), and high DO combined with lethally high water temperature. At any time of day, rainbow trout could find higher DO at the surface of the pool, but would have been subjected to the highest water temperature. Although rainbow trout can survive at DO levels just above 3 mg l^{-1}, low DO has a negative effect on feeding rate (Gutsell, 1929; Doudoroff & Shumway, 1970; Davis, 1975). Indeed, during the study, trout appeared stressed and were never observed feeding. Some studies have indicated that fish will avoid oxygen concentrations below 5 mg l^{-1} and will move to find higher oxygen concentrations if available (Reynolds & Thompson, 1974; Kramer, 1987; Spoor, 1990). However, our study indicated that, when faced with the choice between high temperature and low DO, trout were distributed closest to the water with the lowest temperature despite its associated low oxygen.

Other studies have reported fish venturing into oxygen depleted waters for foraging (Luecke & Teuscher, 1994; Rahel & Nutzman, 1994); use of these potentially lethal environments may be a trade-off when fish are subjected to low food abundance or, as in the current study, high water temperature. Conversely, hypoxia tolerance has been reported as a more important influence on fish distribution than hyperthermia (Smale & Rabeni, 1995). Other biotic and abiotic factors (e.g. predation, physical habitat availability) could potentially explain the trout behaviour we observed, but the close linkage between fish location and cool water temperature zones suggests that temperature and DO affected fish behaviour during the study period. Moreover, by associating near the suspected seeps, trout were out in the open and more susceptible to predators. The trade-off between water temperature and DO during the stressful warm summer period deserves additional study.

For trout in southern California, summer may represent the critical limiting period comparable to winter for salmonids in other regions (Cunjak & Power, 1986; Cunjak & Randall, 1993). Low water temperatures in winter (prolonged temperatures below 5° C) are thought to decrease habitat availability and reduce fish activity and winter survival (Bjornn & Reiser, 1991; Cunjak & Randall, 1993). Thus, the warm water temperatures experienced by southern California trout during the summer may represent an opposite, but equally stressful, critical period, and may contribute to low survival in extreme years or areas without groundwater inflow.

Because water temperatures near the bottom in the shallower pool 2 were actually lower than in pool 1, stratification may not be the dominant control of sub-surface temperature in pool 2. We believe localized seep sources of cool water were active in pool 2. Although similar localized sources of cool water were observed in pools elsewhere on Sespe Creek during August 1994, nothing is known about the longer-term spatial distribution or temperature dynamics of these seeps. Stream flow in 1994 appears representative of long-term conditions, and the residence time and Richardson number calculations suggest that vertical temperature stratification was very persistent during the first portion of August 1994. Therefore, we believe that stratification at the study pools is a common occurrence, and cool water zones should exist often in the deeper areas of the study pools during periods of thermal stress.

DO concentration in streams is a function of many biological, chemical, and physical variables. In the simplest case, with little or no biological activity, DO is controlled largely by water temperature (typically an inverse relationship) and pressure. In a stratified pool, DO concentrations theoretically should be greater where temperatures are lower although this relationship is influenced by water depth. Solely on the basis of greater maximum depth, DO should be lower at the bottom of pool 1 than at the bottom of the shallower pool 2. However, our findings showed that DO was lower at several locations at the bottom of pool 2 than at the bottom of pool 1 suggesting that other processes control DO at the bottom of pool 2.

Thus, low DO near suspected seeps suggests that seeps are the source of the low DO. The unexpected positive correlation of DO with temperature may be localized and be due to seep inflows during low flow periods in pools. Seeps may be of critical importance to trout during periods of thermal stress. Seeps may be most important as a source of cool water despite low DO during periods of low flow when mixing is minimized. To the extent that fish were not plentiful in the deeper pool that experienced thermal stratification, but were plentiful in the pool with lower temperature inflows from suspected seeps, stratification may be less important than seep flow during high temperatures. Apparently, increased flows perturb the hydrodynamics enough to disrupt the effect of the seeps, as we observed during our October measurements. On this basis, we believe seeps may serve as important refugia for trout, and increased understanding of the frequency of seeps, the magnitude of their flows, and their chemical and thermal characteristics is needed.

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