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Cool Water Formation and Trout Habitat Use in a Deep Pool in the Sierra Nevada, California

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Abstract.—We documented temperature stratification in a deep bedrock pool in the North Fork of the American River, described the diel movement of rainbow trout *Oncorhynchus mykiss* and brown trout *Salmo trutta*, and determined whether these trout used cooler portions of the pool. From July 30 to October 10, 1992, the main study pool and an adjacent pool were stratified (temperature differences between surface and bottom were as great as 4.5°C) on all but two days. Six rainbow and one brown trout equipped with temperature-sensitive radio transmitters used water with temperatures ranging from 12 to 19.3°C. During the late afternoon, when the widest range of water temperature was available, trout were found in temperatures up to 19.3°C even though cooler (14.5°C) water was available. Radio tracking indicated that fish were significantly more active and had significantly larger home ranges at night; fish were least active during the day. Because we found no evidence of subsurface seepage into the pool and water flowing into the pool was warmer than the pool's maximum temperature, we concluded that the geometry and depth of deep pools may moderate elevated summer water temperatures that can stress trout populations.

Recent studies have documented the formation of cold water in stream pools and suggested its importance as a thermal refugium for fishes during periods of thermal stress (Bilby 1984; Berman and Quinn 1991; Nielsen et al. 1994, this issue). Because higher water temperatures increase their metabolic demands, many fishes, including salmonids, may detect and seek out cooler waters when ambient stream temperature is high (Bardach and Bjorklund 1957; Kaya et al. 1977; Berman and Quinn 1991; Nielsen et al. 1994).

Berman and Quinn (1991) documented that chinook salmon *Oncorhynchus tshawytscha* tagged with temperature-sensitive radio transmitters maintained a body temperature that averaged 2.5°C cooler than ambient. They concluded that salmon use cool areas to reduce metabolic demand and optimize energy conservation during their spawning migrations. However, they did not measure the full suite of temperatures available near the tagged fish. Using visual observation and population estimates, Nielsen et al. (1994) found that adult steelhead (anadromous rainbow trout *Oncorhynchus mykiss*) were more commonly found in stream sections with cold pools. They also observed that juvenile steelhead used warmer portions of pools (with temperatures up to 24°C) even when cooler areas were available. This suggests that ontogenetically determined thermal preferences may play a role in the use of coolwater areas.

Zones of cool water in pools are apparently caused by at least two mechanisms: influx of cool seepage water; and retention of cool, dense water at lower levels (Nielsen et al. 1994). Cool seepage water originates from intragravel, groundwater, hill slope, or tributary surface inflow that is physically isolated by a barrier such as a gravel bar or organic debris that slows mixing with warmer stream water (Keller and Hofstra 1983; Bilby 1984; Ozaki 1988; Nielsen et al. 1994). The second mechanism, stratification and retention of cool, dense water at the lower levels of deep pools, is thought to be enhanced by increased pool depth (Ozaki 1988). Cooler water at depth is isolated from turbulent mixing with the warmer surface waters and originates at night or other periods of lower air temperature or reduced solar energy inputs. Temperature stratification in these deep pools is most noticeable during the summer in the afternoon and early evening hours. The stratification may be enhanced by pool geometries that allow water to flow in with low turbulence and by the location of the pool's deeper areas in zones of low turbulent exchange (e.g., away from waterfalls or areas of high water velocity).

We know of no previous field studies that have documented in detail the range of available water

temperatures in cold pools in California streams in relation to the temperatures selected by resident rainbow trout and brown trout *Salmo trutta*. It is important to understand thermal habitat requirements and use in order to maintain and preserve all attributes of critical habitats. We monitored deep-pool habitat use by implanting rainbow trout and brown trout with temperature-sensitive transmitters. The deep study pool in the central Sierra Nevada was also monitored by temperature probes to measure the complete range of available temperatures. The objectives of our study were to document the stratification phenomenon in a pool during the period of summer peak temperatures, to describe the diel movements and habitat use by trout in relation to temperature, and to determine whether trout select cooler water from the complete range of available temperatures.

Study Site

We studied two pools in a section of the North Fork of the American River, one of several major tributaries to the Sacramento River on the west slope of the central Sierra Nevada of California. These relatively pristine pools (no logging or grazing has occurred nearby) are on privately owned land at an elevation of 1,603 m (39°15′14″N, 120°15′20″W); the watershed area is about 46 km^2. Two fish species, rainbow and brown trout, were present in the main study pool (there were no nonsalmonids in the pool). The North Fork of the American River has a 4% gradient in the site vicinity (measured 1 km upstream and downstream).

The main study pool was chosen because of its potential for thermal stratification and its populations of rainbow and brown trout, limited fishing pressure, an upstream barrier to fish migration, and accessibility for study. A 4-m waterfall at the head of the pool blocks most upstream migration; there was no downstream barrier to fish movement. Fish movement, water temperature, and other physical characteristics were monitored at this pool. To determine if stratification also occurred in nearby pools, we monitored water temperatures in a similar pool 400 m downstream from the main pool.

Both pools are in a metamorphic rock basin characterized by bedrock pools with 1–10-m, near-vertical walls. Substrate consisted of bedrock or large boulders in the upstream portion of the pool and bedrock, boulders, and smaller cobbles in the shallower, downstream end. Bank vegetation at the site was dominated by old-growth incense cedar *Libocedrus decurrens*, Jeffrey pine *Pinus ponderosa* var. *jeffreyi*, and some deciduous riparian vegetation (willows *Salix* spp.).

Our study was conducted from July 30 to October 10, 1992. In the central Sierra Nevada, this period is dry except for occasional afternoon thunderstorms. Mean annual precipitation is 1,340 mm, and mean annual snowfall is 5–6 m. Two thunderstorms during our study resulted in 3.4 mm of precipitation (measured at the U.S. Forest Service's Central Sierra Snow Laboratory in Soda Springs, elevation 2,100 m, 14 km away). Air temperatures ranged from 8.1 to 22.6°C; pool water temperatures (measured throughout the study pool) ranged from 6 to 19.5°C.

Methods

Pool mapping.—We mapped the main study pool to pinpoint trout locations relative to water temperatures and to document trout habitat use (Figure 1). We made approximately 330 depth soundings with a weighted meter tape over a 1-m (length) by 0.5-m (width) grid pattern covering the 24.2-m-long by 17-m-wide pool. The two deepest points were 4.57 m and 4.7 m, and they were 0.5 m apart. Using scuba we thoroughly inspected the pool, especially the coolwater area, for signs of incoming cool seeps (e.g., signs of incoming flow on the bottom or bubbling water).

Water temperatures.—Water temperature data were collected at both pools, their inlets, and a point 25 m upstream of the main study pool. In the main study pool, two adjacent, vertically distributed probe arrays (in place from July 29 through October 10, 1992) measured the temperature profile of the deepest waters (Figure 1). Five thermistors were attached to each vertical array, one at the bottom of the pool, one 3 cm below the surface, and the other three spaced at even intervals (array 1, 4.57 m deep; array 2, 4.7 m deep). The upper four probes in each array were assumed to be in a zone of turbulent mixing. Because we suspected that vertical array 1 was moved during our hook-and-line fishing on August 6, we analyzed three vertical array periods: vertical array 1 (July 29–August 6), vertical array 1A (August 7–September 11, September 23–October 10), and vertical array 2 (July 29–August 19). No data were collected between September 12 and 22 from the vertical arrays in the main study pool. Eight horizontally distributed single probes (in place from July 30 through October 13, 1992) measured water temperature in the shallow, southwest end of the pool anticipated to be a zone of low turbulence

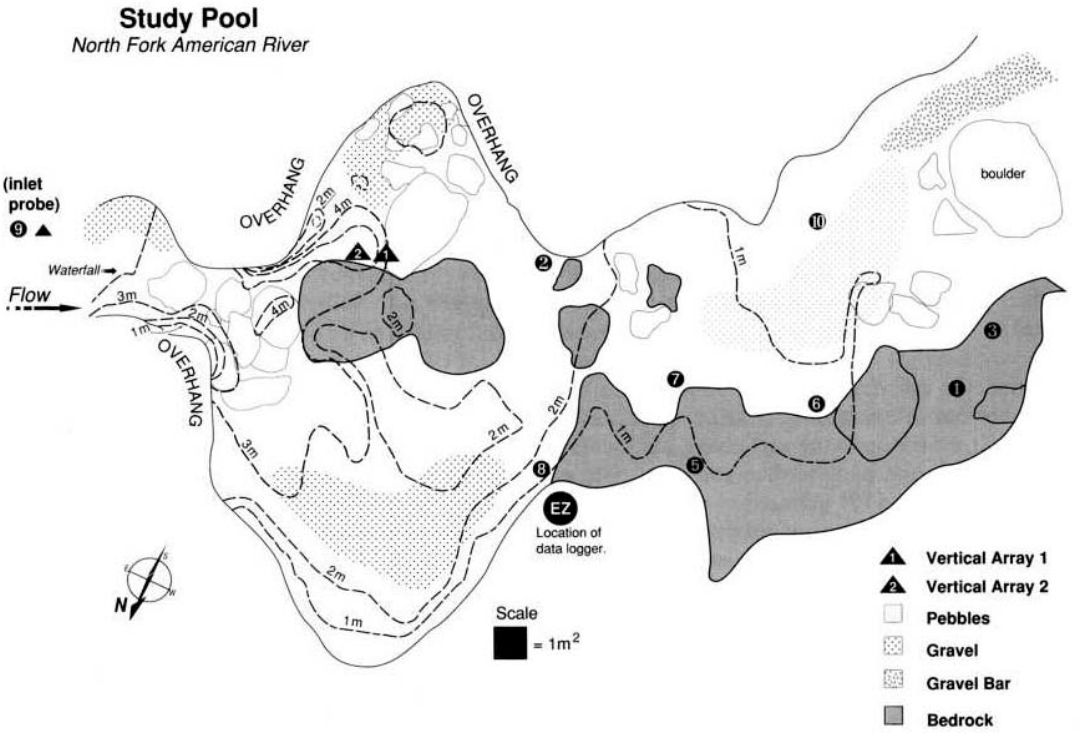

FIGURE 1.—Bathymetric map of the main study pool showing depth contours and locations of horizontal and vertical probe arrays. Total length of the pool is 24.2 m. Circled numbers 1–10 denote bottom temperature probes; probe 4 was not used.

(Figure 1). These probes were placed on the pool bottom. All probes in the main study pool were left in place after intensive documentation of fish location ceased to determine longer-term water temperature dynamics.

At the main study pool, inlet temperatures were measured at the top of the waterfall and about 25 m upstream. At the top of the waterfall, a single probe (in place from August 19 to October 13, 1992) was placed at the stream bottom. At the upstream point, two probes (in place from July 30 to October 10, 1992) were placed 0.5 m below the water's surface and 0.06 m above the bedrock pool bottom, in well-mixed water.

The downstream pool was also instrumented (from August 25 through October 10, 1992) with two vertically distributed temperature arrays placed at the deepest point in the pool. The maximum depth in this pool was 7.5 m. One vertical temperature array consisted of four thermistor probes and the other of five probes. In the four-probe array, probes were located 7.5 m, 5 m, 2.5 m, and 0.3 m from the water's surface. In the five-probe array, probes were distributed at 7.5 m, 6.25 m, 5 m, 2.5 m, and 0.3 m from the water's surface. An additional temperature probe was placed directly above the pool's inlet waterfall.

Except for the temperature-sensing installation 25 m upstream from the main pool, all thermistor probes (Omnidata International, Inc., model ES-606)[1] were connected by 30-m cables to portable dataloggers (Omnidata Easyloggers, model EL824-GP). Temperatures were scanned every 5 min and averaged and recorded for 15-min spans. At the upstream location, temperatures were scanned every 15 min and averaged and recorded for 60-min spans (Omnidata International, Inc., model DP212, two-channel temperature–volt recorder). Probes, nominally accurate to 0.25°C, were tested before installation and after removal with a precision mercury-in-glass thermometer accurate to 0.1°C.

To characterize water temperature differences

[1] Trade names and commercial enterprises are mentioned solely for information. No endorsement by the U.S. Forest Service is implied.

within the main study pool, temperatures from the horizontal array probes were compared by analysis of variance with temperatures averaged over eight of the vertical array probes (exclusive of the bottom two). These comparisons were of probes expected to be in the water column zone of the high turbulent mixing with probes in the bottom zone of little or no mixing.

Thermal stratification.—Stratification was operationally defined as a difference between pool surface and bottom temperatures greater than or equal to 0.5°C. Stratification was characterized as three indices: (1) time—the length of time each day that the difference between pool surface and pool bottom temperatures equaled or exceeded 0.5°C; (2) maximum—the maximum daily difference between the pool surface and pool bottom temperatures; and (3) cumulative—the daily cumulative water temperature difference between the pool surface and pool bottom over the period identified in (1). Although the value of each of these indices depended somewhat upon the previous day's value, we assume the dependencies were very weak from one day to the next. We calculated six sets of correlation coefficients to evaluate the hypothesis that each index correlated positively with both the daily maximum surface water temperature and the daily range in surface water temperature.

Dissolved oxygen.—Because dissolved oxygen can be limiting to fish populations, it was measured twice daily on four days (August 4, 7, 10, and 12) during the study period. Water samples were taken at the surface and 3.2–3.5 m below the surface of the study pool with a Van Dorn bottle, which was lowered by line near the two vertical thermistor probe lines. Following collection, samples were transferred to 300-mL BOD (biochemical oxygen demand) glass bottles, immediately fixed with reagents, and titrated within 24 h by the azide modification of the standard Winkler method (APHA et al. 1985).

Fish tagging.—We used radio tracking to determine each trout's position in the pool relative to water temperature and other habitat characteristics. Representative rainbow and brown trout were captured on hook and line and immediately anesthetized in tricaine methanesulphonate (13 mg/L). Once the fish appeared sufficiently immobilized, the transmitters were surgically implanted because in our preliminary laboratory trials trout regurgitated ingested dummy transmitters within a few days. The radio transmitter was inserted through an incision in the abdominal cavity just anterior to the pelvic girdle and the incision was sutured (Supramid HS 23). To identify individual tagged fish during our visual observations (snorkeling and scuba), each trout was measured (total length, TL) and marked with a unique tattoo made with a Pan-Jet inoculator. After surgery and prior to release, the fish were allowed to recover for approximately 5 min in a water-filled cooler containing no anesthetic. We had no reason to believe that tagged fish behaved differently from untagged fish. Subsequent observations of tagged trout indicated no apparent adverse effects of the tag; the fish swam and fed normally.

Two types of temperature-sensitive radio tags were used. Model SM-1 by AVM of Livermore, California, with an encapsulated internal antenna was 35 × 8 × 7 mm and weighed 2.75 g in air. Model BD-2AT by Holohil of Woodlawn, Ontario, with an external nylon-coated, stainless steel antenna was 16 × 8 × 5 mm and weighed 1.0 g in air. The 20-cm external antenna trailed from the closed incision. Each transmitter was outfitted with an internal thermistor that changed pulse rate corresponding to the fish's body temperature. The thermal transmitters were calibrated and were accurate to 0.5°C. The life expectancy of the transmitters was 14–21 d depending upon the temperature.

During August 2–12, 1992, six rainbow and one brown trout were implanted with transmitters each with a different frequency (e.g., 151.548 or 151.963 MHz) (Table 1). To locate the tags, we used an AVM LA12-DSE receiver and a hand-held three-element collapsible Yagi antenna at the edge of the study pool. Fish could be detected up to 500 m away. We could determine the position of the transmitter to within a 10-m^2 area. We verified this accuracy by visually observing the tagged fish. Temperatures were calculated from a pulse interval timer that displayed the milliseconds between the transmitters' pulses. Occasionally, the timer malfunctioned and the pulses were counted per 15 s. After release, the temperature and approximate location of each tagged fish within the pool were recorded and mapped at 15-min intervals in four sessions: 1210 hours (Pacific Standard Time) on August 3 through 1900 hours on August 8, 0700 hours on August 10 through 1630 hours on August 15, 1200–1800 hours on August 18, and 1400–1630 hours on August 19: 264.9 h of tracking altogether.

We occasionally snorkeled the pool to observe the behavior of tagged and untagged fish. On September 23, after the tracking study ended, we used

TABLE 1.—Summary of species tagged, tag used (AVM or Holohil, HH), tag frequency (151.110–151.963 MHz), trout length (cm), and tracking hours for individual fish, 1992.

Fish number, tag type, and pulse frequency	Trout species	Fish length (cm)	Tracking start	Tracking end	Total hours tracked
1 AVM 548	Rainbow	26.0	1210 hours, Aug 3	1400 hours, Aug 10	134
2 AVM 963	Brown	33.5	1210 hours, Aug 3	0300 hours, Aug 12	171
3 HH 150	Rainbow	22.0	1905 hours, Aug 6	1630 hours, Aug 19	186
4 HH 169	Rainbow	22.0	1930 hours, Aug 6	Tag failed	
5 HH 190	Rainbow	30.0	2000 hours Aug 11	1630 hours, Aug 19	117
6 HH 129	Rainbow	21.5	0540 hours, Aug 12	1630 hours, Aug 19	91
7 HH 110	Rainbow	24.0	0710 hours, Aug 12	1630 hours, Aug 19	90

scuba and searched throughout the pool for tagged fish to determine their condition. Tagged fish were identified by either their tattoos or external antennas.

Analysis of fish data.—We compared body temperatures of individual trout with the full array of simultaneously measured water temperatures to determine whether trout used the coolest portions of the pool and what their temperature preferences were within the ranges of available temperatures. We determined whether trout used different portions of the pool during the day and night. The 24-h horizontal location data were digitized onto an x–y coordinate system (Data General model 4437) and overlain onto the pool maps. We divided location points into four time categories determined by the availability of light: dawn (0430–0600 hours), day (0600–2000 hours), dusk (2000–2130 hours), and night (2130–0430 hours). We used the data points from each time category to construct contours depicting 90% of the location points for individual fish during that time category using the "adaptive kernel" method (Silverman 1986; Worton 1989). Each contour represented the area (m^2) where 90% of the location data points were found; we did not collect depth information that would have yielded a three-dimensional home range (m^3). From the contour plots, we compared habitat use for the different time periods, testing the null hypothesis that there was no difference in the area (m^2) used in the four time periods dawn, day, dusk, and night (multivariate analysis of variance; SAS Institute 1985).

Results

Water Temperature

Diel temperature cycles.—Temperatures were the same at depths from 0.3 to 3.5 m along the vertical temperature probe arrays in the main study pool, suggesting that turbulent mixing occurred throughout this depth range. Temperatures at these depths differed from temperatures near and at the bottom (measured at 4.6 and 4.7 m; Figure 2). All temperatures decreased in the early morning (0000–0900 hours). Minimum temperatures, ranging from 7.3°C (October 6) to 14.7°C (August 15), occurred in midmorning, at about 0900 hours. In the late morning and through the afternoon (0900–1700 hours), temperatures increased, bottom temperatures increasing least. All four vertical temperature arrays in the two deep pools (two arrays in each pool) indicated zones of cooler water at the bottom of the pool. The deepest water temperatures remained constant and cool until late afternoon. Maximum vertical array temperatures, ranging from 9.3°C (October 7) to 19.2°C (July 29), occurred in late afternoon, at about 1600–1700 hours. From late afternoon until midnight (1700–2400 hours), surface temperatures became cooler; bottom temperatures first warmed rapidly then started cooling in concert with the other temperatures at about 2000 hours (Figure 2).

The temperature of the study pool's inlet water exhibited more diel variation than did the vertical array temperatures (Figure 3). Ambient incoming water was warmer than pool water at any depth in the afternoon but cooler than these areas at night. Specifically, from late afternoon to midnight (1700–1000 hours), water entering the study pool was as much as 1°C colder than pool surface temperatures. From early morning through afternoon (1000–1700 hours), inlet temperatures were as much as 1.25°C warmer than surface temperatures.

Trends over the entire study period.—Over the 62 d in July–October that the various temperature arrays were operational, temperatures of the pool inlet, surface, and bottom waters gradually decreased (Figure 4). Daily mean temperatures at the pool bottom ranged from 18.6°C (July 29; 1700 hours) to 6.6°C (October 7; 0900 hours); surface

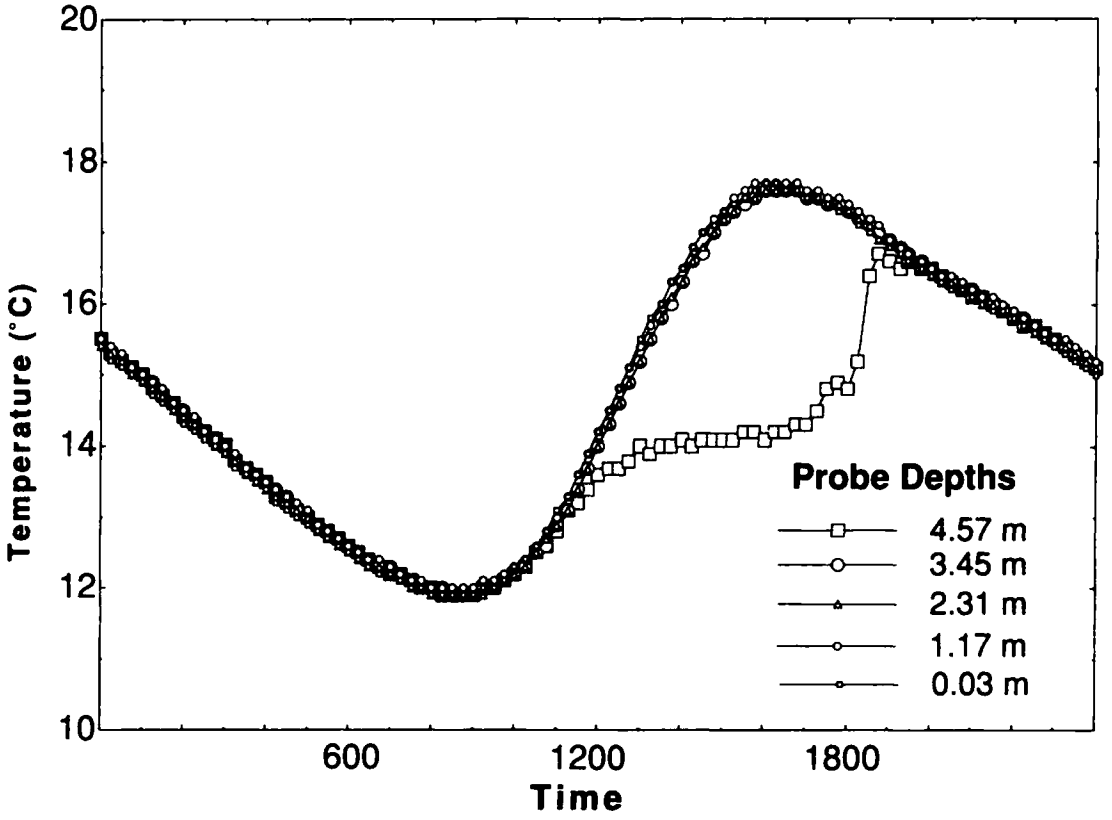

FIGURE 2.—Typical diel temperature pattern measured by vertical probe array 1 in the study pool. The temperatures shown were recorded on August 3, 1992.

temperature declined from 19.1 to 6.8°C, and inlet temperature declined from 19.4 to 6.1°C.

Stratification.—Stratification (vertical temperature differences of 0.5°C or more) changed over the study period. Vertical array 2 showed the maximum amount of stratification in terms of both duration and magnitude of difference between the surface and bottom probes. The maximum durations of stratification were 15 h for vertical array 2 (August 12), 8.75 h for vertical array 1 (August 5), and 8.0 h for vertical array 1A (August 19). The maximum diel temperature difference between the bottom and surface ranged from 0.1°C (October 2) to 3.9°C (August 4) along vertical array 1. Along vertical array 2, this difference ranged from 2.7°C (August 14 and 15) to 4.5°C (August 12). On September 3 and October 2, no stratification was detected by vertical array 1A (Figure 3 includes data from October 2).

Time, magnitude, and cumulative degree of stratification did not generally correlate significantly with daily maximum temperature or with range in surface water temperatures. Correlation coefficients were significant for variable pairs in only 2 of the 18 possible pairings: (a) array 1, cumulative stratification versus maximum daily surface temperature; (b) array 2, maximum daily difference between the pool surface and bottom temperatures versus range of daily surface temperature (Table 2). Eleven of 18 correlation coefficients were less than 0.4 in absolute magnitude.

Comparisons within the study pool.—Temperatures varied within the main study pool between the upper zone of mixing and the bottom zone of nonmixing. Mean water column temperatures (averages of the eight "upper" vertical array probe values) often differed significantly (t-tests, $P < 0.05$) from bottom temperatures (measured by horizontal array probes) during both day (0900–1745 hours) and night (1800–0845 hours; Table 3).

The warmest areas in the study pool were in shallow (<1 m deep), sunny parts of the pool; bottom probes 1, 5, and 6 were warmer than mean

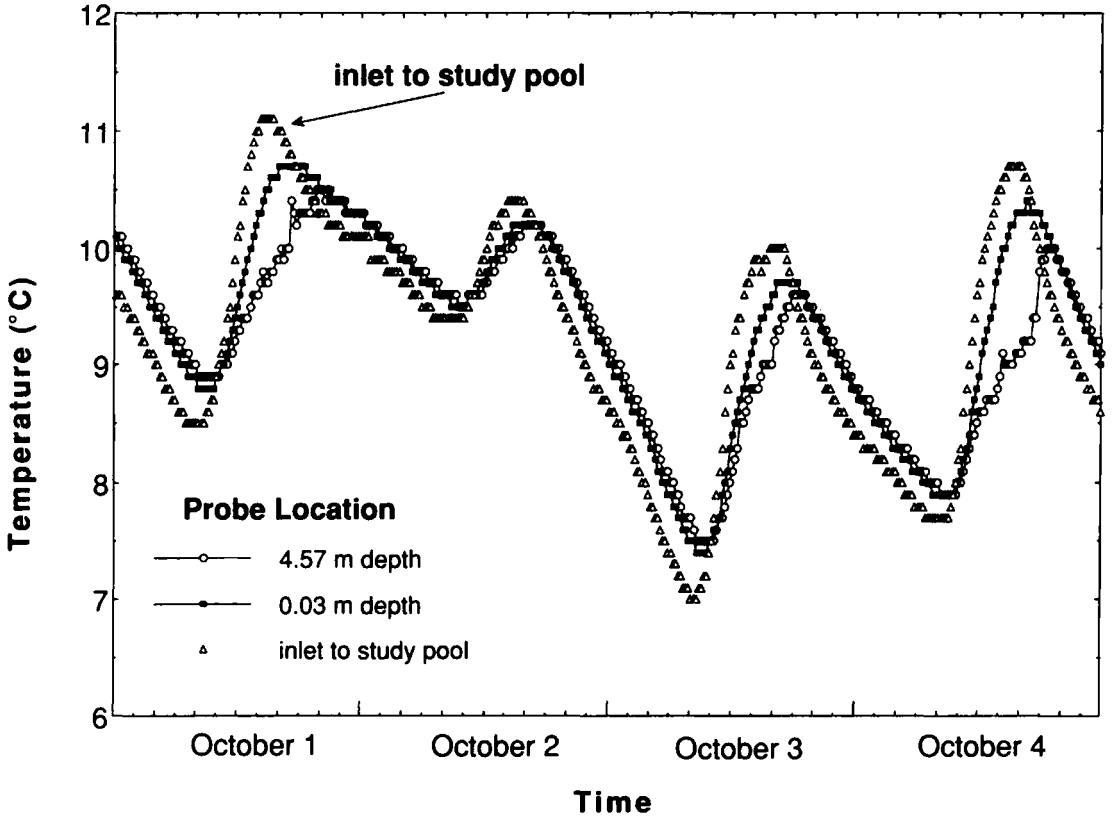

FIGURE 3.—Study pool inlet temperature in relation to surface and bottom temperature, October 1–4, 1992.

water column temperatures in more than 75% of the observations (Table 3). Horizontal probe 5 was located above dark grey metamorph rock, which may have absorbed and reradiated heat even after sunset. For 60% of the observations over the diel period, horizontal probes 3, 7, and 10 were warmer than the average of higher probes. In the late afternoon when the sun no longer shone directly on the study pool (1500–1900 hours), horizontal probes 3, 6, and 7 were colder than mean upper pool waters.

Inlet temperatures (probe 9) were mostly warmer than mean vertical array temperatures during the day and colder at night (Table 3).

Comparison with the downstream pool.—Stratification was compared between the downstream and study pools from August 24 to September 10 and from September 23 to October 11 with a two-sample t-test ($\alpha = 0.05$). The downstream pool had greater depths of cool water on the bottom (2.5 m) than the main study pool (0.5 m). Over the comparison periods, the mean daily duration of stratification was greater in the downstream pool ($P < 0.05$, 10.6 h versus 5.0 h). The downstream pool also stratified earlier in the morning than the main study pool ($P < 0.05$, 1148 versus 1436 hours). For all days combined, maximum temperatures did not differ significantly between pools.

Dissolved Oxygen

Dissolved oxygen concentrations did not appear to decline to stressful levels. Surface dissolved oxygen measurements ranged from 7.4 mg/L (August 7, 1550 hours) to 9.2 mg/L (August 7, 0904 hours). At a depth of 3.5 m, dissolved oxygen ranged from 8.0 mg/L (August 12, 0835 and 1715 hours) to 9.1 mg/L (August 4, 0756 hours). Samples from the study pool fell within the range preferred by rainbow trout (7–11 mg/L: Nikolsky 1963). Saturation throughout the sampling period exceeded 75%, which is not limiting to trout (Moyle 1976).

Trout Home Range and Temperature Selection

Six rainbow and one brown trout (21.5–33.5 cm) were successfully tagged and released (Table

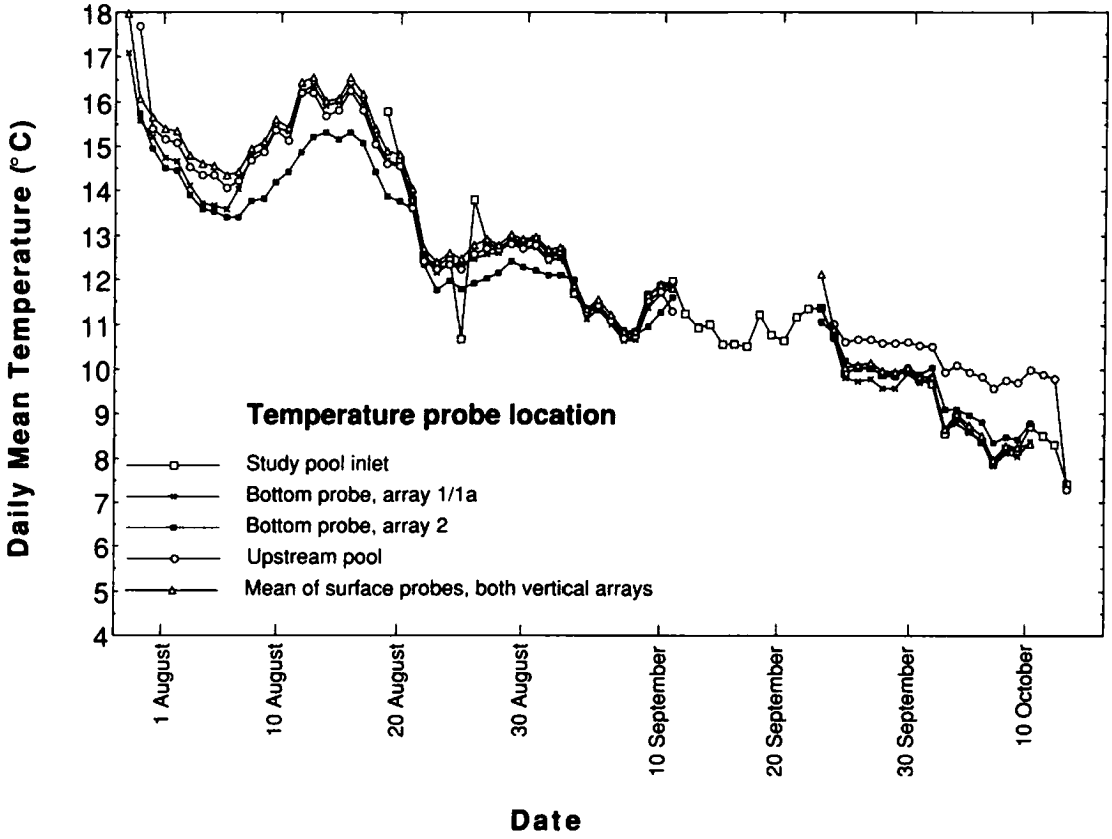

FIGURE 4.—Mean daily water temperatures upstream, at the pool inlet, and at the pool surface and bottom, July 30–October 13, 1992 (August 19–October 13, 1992 for the inlet).

TABLE 2.—Correlation coefficients between surface water temperature variables and three indices of temperature stratification, North Fork of the American River, summer 1992.

Vertical probe array number	Output variable (index of stratification)	*r*-value for correlation of output variable with: Maximum daily surface temperature	Difference between maximum and minimum daily surface temperature
1	Duration of stratification	−0.797	−0.299
	Magnitude of stratification	−0.640	0.159
	Cumulative stratification	0.812	0.219
1A	Duration of stratification	0.019	0.346
	Magnitude of stratification	0.277	0.541
	Cumulative stratification	0.047	−0.274
2	Duration of stratification	0.158	−0.573
	Magnitude of stratification	0.446	0.694
	Cumulative stratification	−0.328	−0.116

1). One transmitter (number 169) failed soon after the fish was released. Searches in adjacent pools were unsuccessful in locating the signal. Transmitter 548 produced a signal, but evidently the thermistor was defective. Thus, locational data were collected for only six trout (transmitters 548, 963, 150, 190, 129, and 110); temperature data were collected for all of these fish except the one with transmitter 548. The six individual fish were tracked for 8–13 d (89–185 h/fish) during August 3–19 (Table 1).

The trout did not appear to be adversely affected by the transmitters. Throughout the study period, we visually observed tagged fish. On the basis of comparisons with untagged fish in the study pool, we saw no signs that the transmitters altered swimming performance, feeding, or behavior. Thus, we had no reason to believe that tagged fish behaved differently from untagged trout in the study pool. After the study was completed, we observed three tagged fish (two with external

TABLE 3.—Numbers and percentages of observations when horizontal probes 1–10 were significantly (t-test, $P \leq 0.05$) warmer than, not different from, or cooler than the mean of the uppermost vertical probes, July 30–October 9, 1992.

Probe number	Number (%) of observations		
	Warmer	No difference	Cooler
	Day (0900–1745 hours)		
1	337 (72.9%)	125 (27.1%)	0 (0.0%)
2	45 (9.7%)	417 (90.3%)	0 (0.0%)
3	270 (56.8%)	140 (29.5%)	65 (13.7%)
5	400 (84.2%)	63 (13.3%)	12 (2.5%)
6	313 (65.9%)	99 (20.8%)	63 (13.3%)
7	264 (55.6%)	121 (25.5%)	90 (18.9%)
8	229 (42.8%)	306 (57.2%)	0 (0.0%)
9	227 (66.4%)	106 (31.0%)	9 (2.6%)
10	306 (64.4%)	167 (35.2%)	2 (0.4%)
	Night (1800–0845 hours)		
1	645 (83.7%)	126 (16.3%)	0 (0.0%)
2	41 (5.3%)	730 (94.7%)	0 (0.0%)
3	562 (70.3%)	232 (29.0%)	6 (0.8%)
5	775 (96.9%)	25 (3.1%)	0 (0.0%)
6	700 (87.5%)	78 (9.8%)	22 (2.8%)
7	540 (67.5%)	235 (29.4%)	25 (3.1%)
8	263 (29.5%)	628 (70.5%)	0 (0.0%)
9	0 (0.0%)	5 (0.9%)	571 (99.1%)
10	525 (65.6%)	275 (34.4%)	0 (0.0%)

Holohil antennas) in the study pool swimming and feeding normally.

Home ranges.—Most tagged trout used significantly larger areas of the pool at night (mean of six trout home range contours, 89.7 m^2) and smaller areas during the day (mean, 58.6 m^2; Table 4). One rainbow trout, number 6, did not follow the pattern; it was located over large areas during dawn, day, and night and over a smaller area during dusk, when other fish were most active. We excluded this fish from statistical comparisons of home range size among time periods (mean home range sizes in Table 4 are for all six fish). Home range areas were not significantly different when dawn, day, dusk, and night were compared together (multivariate analysis of variance, $P > 0.05$) because of the small sample size (five fish in each of four time periods). The night home range areas were larger than day areas when compared separately, however (paired t-tests, $P < 0.05$). The differences in home ranges between day and dusk are especially dramatic considering the relatively low number of observations during dusk (Table 4).

During the day, transmitter signals were often difficult to locate because, as our snorkeling ob-

TABLE 4.—Mean home range sizes (from contours enclosing 90% of locations in each time period) for six tagged trout during dawn, day, dusk, and night.

Fish number and tag frequency	Trout species	Home range size, m^2 (number of data points)			
		Dawn, 0430–0600 hours	Day, 0600–2000 hours	Dusk, 2000–2130 hours	Night, 2130–0430 hours
1 AVM 548	Rainbow	71.9 (24)	47.8 (228)	130.3 (28)	66.4 (116)
2 AVM 963	Brown	43.8 (31)	30.4 (248)	123.0 (36)	85.5 (121)
3 HH 150	Rainbow	60.9 (38)	54.5 (363)	85.6 (41)	110.2 (180)
5 HH 190	Rainbow	43.6 (27)	37.3 (195)	127.6 (27)	80.3 (112)
6 HH 129	Rainbow	157.5 (23)	92.4 (214)	62.2 (18)	109.4 (81)
7 HH 110	Rainbow	56.2 (26)	89.4 (217)	83.4 (21)	86.5 (83)
Mean		72.3[a]	58.6[a]	102.0[b]	89.7[b]

[a] Combined mean, dawn and day: 65.5 m^2.
[b] Combined mean, dusk and night: 95.9 m^2.

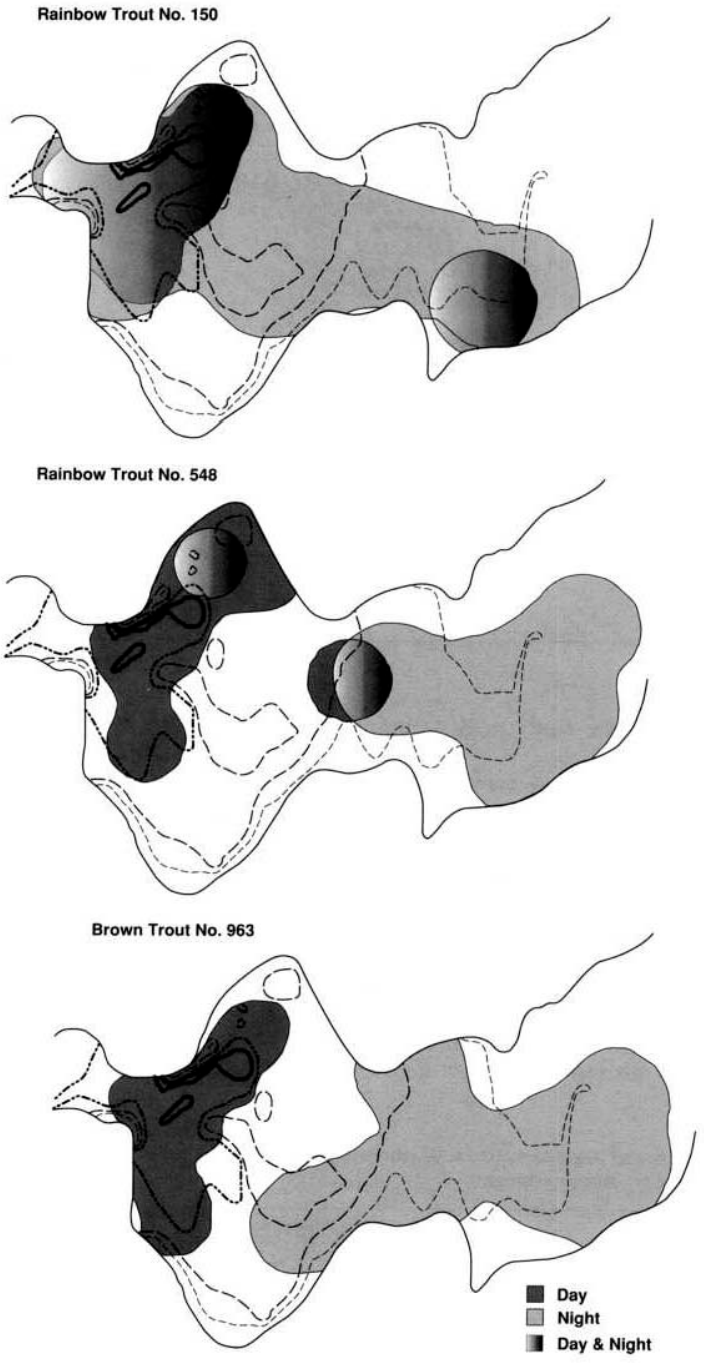

FIGURE 5.—Home range plots for two rainbow and one brown trout during day (0430–2000 hours) and night (2000–0430 hours). Range areas encompass 90% of the location points for the respective time periods. Identification numbers are transmitter frequencies (Tables 1, 4).

servations revealed, many fish were under rocks or ledges. Activity (and signal clarity) picked up markedly at dusk, when fish were out in the open and often visible to observers on the bank. At night, fish also were active and used most of the pool, especially the downstream end (Figure 5). The only occasions when fish were actively moving during radio tracking were at dusk or night. At dawn, activity and area used decreased. No tagged fish left the study pool during tracking operations.

The brown trout was the only tagged fish with no range overlap between day (here, dawn plus day, 0430–2000 hours) and night (2000–0430 hours; Figure 5). During the day, the brown trout used a 39.9-m^2 area of the upstream, deeper end of the pool. At night, the area used by the brown trout increased to 106.8 m^2 in the downstream, shallower portion of the pool.

Rainbow trout 1, 3, and 5 (transmitters 548, 150, 190) were typically found in the deeper, upstream portion of the pool during the day. At night, they were found either in the downstream, shallower portion of the pool or in the entire pool. For example, rainbow trout 3 (transmitter 150) was primarily found in the deep end during the day, although about 10% of its daytime positions were in the shallow end (Figure 5). At night, this fish used the entire pool.

Habitat use and activity varied from one sampling day to the next, particularly during dusk and night. For example, rainbow trout 3's activities over several days demonstrated its tendency to remain in the deeper upstream portion of the pool during the day and to have variable movements at night. This fish primarily stayed in the upstream area during the dawn, day, and dusk on days 2 and 4 (Figure 6). At night, the fish ranged over much of the pool on sampling day 2, but it was primarily located in the upstream portion of the pool, and was never located in the downstream portion, on day 4 (Figure 6).

Temperatures selected.—Tagged fish were recorded in water up to 19.3°C even when cooler stratified water (14.5°C) was available (Figure 7). Fish were found in water with temperatures that matched the daily fluctuations in the upstream portion of the pool (August 12–14: Figure 7). Trout were never found in the cool water on the bottom. The four rainbow and one brown trout selected temperatures similarly (within the 0.5°C accuracy range); these temperatures ranged from 12.5 to 19.3°C throughout the study period.

We found no evidence that trout selected the coolest water available. Fish did not use cooler water during the late afternoon and evening when stratification occurred even though cooler water was readily available. They occupied areas that experienced a wider range of water temperatures than were found in just the deeper part of the stratified pool. For example, from August 12 to 19 the temperature in the coolest portion of the pool (probe at the bottom of array 2) ranged from 12.7 to 16.4°C (3.7°C span), whereas the temperatures of the water that trout occupied ranged from 12.8 to 19.1°C (6.3°C span). At night, when fish were sometimes located in the shallower end of the pool, the temperatures of the water there were either warmer than or similar to those in the deep end (Table 3). Thus, we found no evidence that water temperature influenced trout behavior.

Discussion

Pool Temperature and Thermal Stratification

The strength of our study lies in the simultaneous detailed mapping of thermal patterns and trout positions in a deep pool of a headwater mountain stream. However, the general magnitude of the temperature differentials between surface and deep water (1–3°C) was smaller than the mean differential of 4°C or more reported by Bilby (1984) for a fifth-order river in coastal Washington, and the 3–9°C differential reported by Ozaki (1988) for coastal pools in northern California. Our operational definition of thermal stratification (a difference of more than 0.5°C between the pool surface and bottom) contrasts with the 3.0°C differential used by other researchers (e.g., Ozaki 1988). We believe that the less restrictive 0.5°C threshold is appropriate because the almost identical temperatures (within 0.1°C) throughout the upper layers of the main study pool implied that a 0.5°C differential was real, and not an artifact of the instrumentation. In our central Sierra study pools, coolwater zones persisted throughout the observation period from late July to mid-October, appearing to be long-term features of pool hydraulics.

The hypothesized linkages between surface water temperature and stratification were not strongly supported in this study. The coincidence, however, of diel surface minimum water temperatures with diel minimum coolwater zone temperatures implied that the surface and coolwater zones mixed and that surface water minimums partially con-

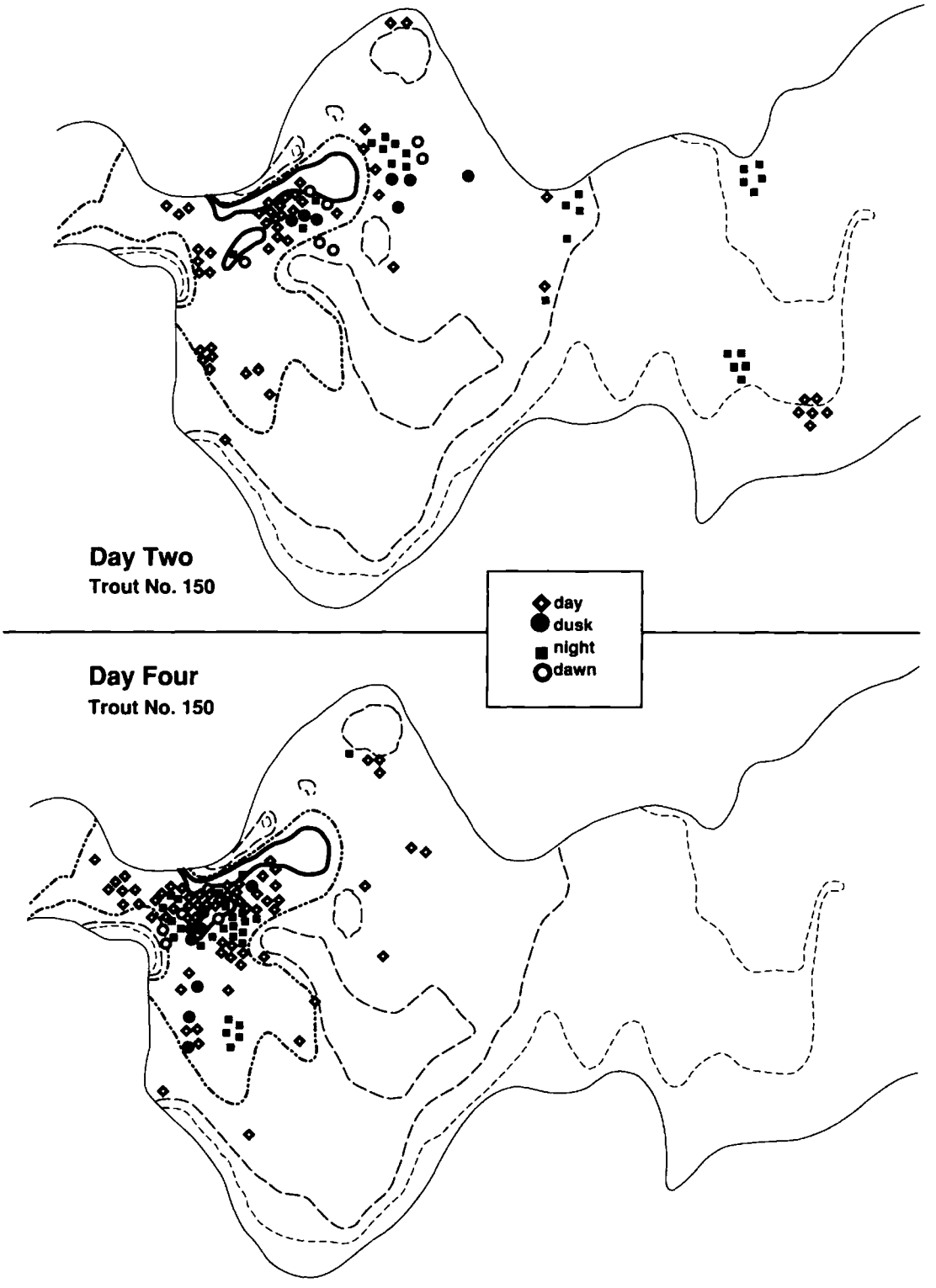

FIGURE 6.—Individual location points for rainbow trout 3 (transmitter 150) on sampling days 2 and 4 during day, dusk, night and dawn.

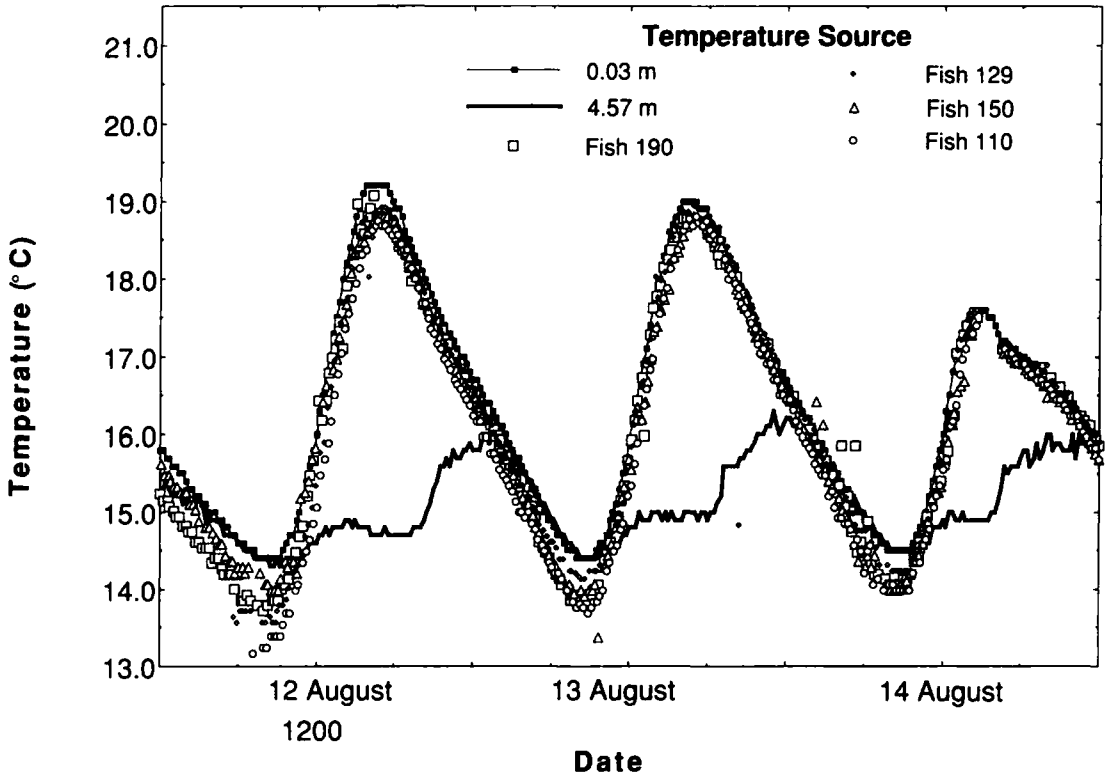

FIGURE 7.—Water temperatures at depths of 0.03 and 4.57 m along vertical probe array 2, and temperatures of water occupied by rainbow trout (transmitters 190, 110, 150, 129) on August 12–14, 1992.

trolled the stratification phenomenon. A more comprehensive assessment of this linkage is necessary. No subsurface inflows to the main study pool were identified during an underwater search, but precise instrumentation was not available to exclude the possibility of such flows.

Study pool temperatures were lower than temperatures in shallower upstream pools in prior years (Berg, unpublished data). This difference suggests that the deep study pools may moderate elevated temperatures that otherwise could harm adult trout. Stratification may serve to lower the overall pool temperature and thereby reduce maximum water temperature during summer.

Coolwater zones in shallow, coastal stream pools typically result from tributary or groundwater inflow, rather than from thermal stratification influenced by depth (Ozaki 1988). Because depositional features like gravel bars are more common in low-gradient stream reaches, deep pools may be more common in higher-gradient, headwater reaches. Also, areas in our study pools that were deep enough to foster thermal stratification were relatively small, probably less than 10 m^3 in volume; their tendency to stratify varied with pool depth and bottom configuration. These areas were much smaller than the 8–60-m^3 zones influenced by groundwater or tributary inflows documented by Bilby (1984), Ozaki (1988), and Nielsen et al. (1994).

In bedrock pools, the location of the area of maximum depth may be a more important control on stratification than the presence of a waterfall or other sources of turbulence. Consistent stratification occurred in the main study pool that had a 4-m waterfall at its inflow point. The zone of stratification was at the deepest part of the pool, in a location that evidently was of sufficient depth and distance from the waterfall to allow stratification to overcome the waterfall's mixing effect.

Trout Behavior

Our rainbow and brown trout did not preferentially seek out and use cooler water (up to 5°C cooler) when ambient temperature was 19.3°C and below. In contrast, Berman and Quinn (1991) re-

ported that chinook salmon returning to spawn (and not feeding) were found in areas of the Yakima River that averaged 2.5°C cooler than ambient water of 12–19°C, similar to the temperatures experienced in our study. The different responses likely reflected differing temperature requirements and preferences among salmonid species. Reported temperature preferences are often contradictory and may depend upon whether a study was conducted in the laboratory or in different geographic areas. In laboratory experiments, rainbow trout thermoregulated and maintained a consistent 16.7°C in an experimental temperature gradient (14–19°C) by dividing their time between the two temperature extremes (McCauley and Huggins 1976). One California field study documented a temperature preference range of 16–18.2°C (Baltz et al. 1987), whereas the trout in our study occupied a broader temperature range (12.8°C–19.1°C).

The study pool's maximum water temperature during the day, a period of relative inactivity for trout, may not have been stressful enough to cause movement. This suggests that trout living in California's warmer climate may be more tolerant of elevated water temperatures than fish examined in other temperature preference studies (McCauley and Huggins 1976; Berman and Quinn 1991). Scott and Poynter (1991) found that rainbow trout in New Zealand, fish that originated in California, were found in water temperatures as high as 22.5°C, although cooler areas could be available. Rainbow trout can also extend into Mexican streams with higher water temperatures. In areas of warmer water, trout may be adapted to handle a wider range of temperatures than they tolerate in laboratory experiments or in other geographic areas.

Age may also be a confounding factor in temperature preferences. McCauley and Huggins (1976) speculated that rainbow trout have an age-dependent temperature preference such that younger fish prefer higher temperatures than older fish. Nielsen et al. (1994) also noted that juvenile steelhead did not use available cool water when temperatures were as high as 24°C.

Trout may have occupied the warmer temperatures in our study pool because the area of cool water was too small to accommodate all of the fish. Differences in water temperature between the two adjacent probe arrays suggested that the area of cool water was relatively small. During the period of maximum temperature, many fish were in the vicinity of cool water, yet we did not observe any fish (tagged or untagged) in the cool zone excluding others.

Jobling (1981) speculated that fish do not move into a given temperature and remain there, but instead make exploratory movements into water of both lower and higher temperatures. In our study, trout may have quickly moved into cooler water, but the thermistors may not have had sufficient time to register the change because of an equilibration time of about 5 min. However, we rarely saw fish moving during the day; they were mostly under rocks or in deep water.

Trout may prefer a fluctuating temperature. Hokanson et al. (1977) reported that growth of rainbow trout was accelerated when temperatures fluctuated ±3.8°C around the mean relative to growth at constant temperatures. The growth optimum for trout held at constant temperatures occurred at 17.2°C; in the fluctuating system, the optimum occurred at an average temperature of 15.5°C with daily highs and lows of 19.3°C and 11.7°C. Thus, growth may be enhanced by not using cool water areas.

Although temperature is an important abiotic factor for fish (Beitinger and Fitzpatrick 1979), there is undoubtedly a suite of biotic and abiotic factors that influence the distribution of fish throughout a pool. Many factors influence fish habitat use and distribution, such as proximity to competitors, predators, prey, cover, and habitat features. Possibly, our trout avoided the shallow, downstream portion of the pool during the day to reduce their vulnerability to avian predators or because no suitable hiding places (boulders and ledges) were there. But at night when their vulnerability was reduced, trout moved into the shallow end of the pool to feed.

During our study, both rainbow and brown trout were sometimes nocturnally active. Many studies have described brown trout as nocturnal (Jenkins 1969; Clapp et al. 1990); however, there is contradictory information regarding rainbow trout's nocturnal activities (Jenkins 1969; Jenkins et al. 1970; Bisson 1978; Angradi and Griffith 1990; Beauchamp 1990). From snorkeling observations, Campbell and Neuner (1985) reported that rainbow trout in Washington streams were relatively inactive during summer nights. On the other hand, there is evidence that nocturnal feeding occurs (Jenkins 1969; Jenkins et al. 1970; Bisson 1978; Beauchamp 1990). Jenkins (1969) speculated that both rainbow and brown trout are "in feeding readiness at nearly all hours of the day and night, at least in the summer months." Despite the con-

flicting information about the diel behavior of rainbow trout, our data demonstrated some rainbow trout were nocturnally active. We suspect that rainbow trout were feeding at night, but future research is necessary to support this hypothesis.

Conclusions

Stream temperature models and methodologies used to forecast effects of riparian vegetation removal or water diversion on water temperature generally do not consider temperature variation within a pool (Brown 1969; Beschta 1984). Because coolwater zones could act as thermal refugia for aquatic biota, models that lack a coolwater component may not be useful for predicting temperatures and inferring biotic responses to water temperature variation.

Streamside logging and grazing can lead to elevated stream temperatures and increased sedimentation from bank and upland erosion (Beschta et al. 1987; Marcus et al. 1990). The headwater basin of the North Fork of the American River is nearly pristine, which may contribute to the relatively low pool temperatures there. If riparian zone mismanagement results in filling of pools, reducing their potential to stratify, the coolwater zones may disappear and overall pool temperature may increase to a level stressful to fish.

Understanding temperature and habitat requirements of inland fish is important for predicting outcomes of management activities (logging, grazing, water diversions, etc.) that potentially alter water temperature. In our study, although trout did not use the coolest portions of the pool, the stratification may have reduced maximum water temperature during the summer. In addition, understanding temperature availability and use by fish is crucial in California, because periodic droughts and possible global warming increase air and water temperatures. Future work should determine how widespread these thermally stratified pools are in the Sierra Nevada and whether similar pools exist in areas that have been logged or grazed.

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