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Thermally Stratified Pools and Their Use by Steelhead in Northern California Streams

JENNIFER L. NIELSEN[1] AND THOMAS E. LISLE

U.S. Forest Service, Pacific Southwest Research Station
1700 Bayview Drive, Arcata, California 95521, USA

VICKI OZAKI

Redwood National Park
1125 Sixteenth Street, Arcata, California 95521, USA

Abstract. —Thermal stratification occurred in pools of three rivers in northern California when inflow of cold water was sufficiently great or currents were sufficiently weak to prevent thorough mixing of water of contrasting temperatures. Surface water temperatures in such pools were commonly 3–9°C higher than those at the bottom. Cold water entered pools from tributaries, intergravel flow through river bars, and streamside subsurface sources. In Redwood and Rancheria Creeks, cold water was protected where gravel bars encroached into pools that were scoured along bedrock banks, creating isolated backwaters. Sixty-five percent of the juvenile steelhead *Oncorhynchus mykiss* found in the Rancheria Creek study reaches moved into adjacent stratified pools during periods of high ambient stream temperatures (23-28°C). Fish showed a decline in forage behavior and increased agonistic activity just before movement into stratified pools. In the Middle Fork Eel River, pools deeper than 3 m stratified when surface flow decreased to less than 1 m^3/s. Summer-run steelhead adults were found in deep stratified pools on the Middle Fork Eel River throughout summer when midday ambient stream temperatures ranged from 26 to 29°C and coldwater pockets averaged 3.5°C cooler. Thermally stratified pools provided refuge habitat for significant numbers of young-of-the-year, yearling, and adult steelhead in marginal river habitats where stream temperatures reach upper incipient lethal levels.

In northern California many streams are characterized by high sediment loads, low summer flows, and elevated stream temperatures. During periods when ambient stream temperatures reach upper incipient lethal levels, available fish habitat may be considered marginal. Pools stratified vertically by temperature may provide salmonids important refuges from warm water during summer low flows.

Stream temperature plays a critical role in salmonid energy conversion by pacing the metabolic requirements for food and governing the rate of food processing (Brett 1952; Brett and Groves 1979; Pandian and Vivekanandan 1985). Rainbow trout *Oncorhynchus mykiss,* of which steelhead is the anadromous race, reach their physiological maximum at 17.2°C (Hokanson et al. 1977). Fish subjected to high water temperatures (20-24°C for rainbow trout; Hokanson et al. 1977) exhibit high metabolic demands, which can lead to growth suppression and early mortality (Brett 1979). Salmonids have been observed to actively seek cold water when ambient stream temperatures were high (Mantleman 1960; Gibson 1966; Kaya et al. 1977; Bennan and Quinn 1991; Keller et al., in press). Poikilothermic fish do not regulate their temperature physiologically, but do compensate for thermal conditions behaviorally by adjusting activity rates and metabolic demand in adverse thermal conditions (Coutant 1985; Priede 1985). Thermal refuges are known to be important for other species in unstable aquatic environments (Magnuson et al. 1979; Coutant 1985).

Temperature stratification in stream pools has been described previously (Neel 1951; Bilby 1984; Moses 1984; Keller et al., in press), but the relative importance of factors leading to stratification in different stream channels has not been evaluated. Thermal mixing can be inhibited by the buoyancy of warm water overlying cold water. This force, however, is extremely small. The difference in density between water that is 10°C and 20°C is only 0.15% and the corresponding buoyancy force equals 0.15 N/m^3. In comparison, a characteristic difference in density between fresh and sea water is 2.5%. This suggests that isolated bodies of cold water in stream pools can exist only where there are large influxes of cold water or where mixing is

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[1] Present address: Hopkins Marine Station, Stanford University, Department of Biological Sciences, Pacific Grove, California 93950-3094, USA.

FIGURE 1.—

severely limited. A large variety of structural features acting alone or in concert, including gravel bars and large woody debris, can shield portions of a pool from a jet of warm water entering the pool (Keller et al. 1983; Bilby 1984; Moses 1984).

California represents the southernmost range of anadromous salmonids along the west coast of North America, where the dryness and warmth of summers increase as one travels south. Because thermal compensation is bioenergetically expensive, diverting energy from other important processes such as growth and reproduction, it seems likely that high summer temperatures limit the range of salmonids in California (Bennett 1987).

Bilby (1984) detected no preference by fish for thermally stratified habitats as had Gibson (1966), Kaya et al. (1977), and Keller et al. (in press). But fish preference for different types of thermally stratified pools in California streams has been poorly described. We tested temporal preference for thermally stratified pools by adult and juvenile steelhead and looked at fish behavior in habitats considered marginal due to high ambient stream temperatures.

We studied the formation of thermally stratified pools in three contrasting northwestern California streams. In two of these streams, we quantified the temporal patterns of steelhead behavior and distribution that suggested preference for cold refuge habitats. We also investigated steelhead age-class distributions in relation to temperature gradients in thermally stratified habitats during periods of elevated stream temperatures.

Study Sites

The three contrasting stream channels surveyed for thermal stratification of pools were Redwood Creek, Rancheria Creek, and the Middle Fork Eel River (MFER; Figure 1). Redwood Creek, an aggraded, unstable, gravel bed stream with a 720-km² drainage area, was studied intermittently during 1981–1987 by Keller and his coworkers (Keller and Hofstra 1983; Moses 1984; Keller et al., in press) and by Ozaki (1988). Rancheria Creek, a bedrock-influence stream with large alluvial cobble bars, extensive intergravel flows, and a 590-km² drainage area, was studied by Nielsen during 1989–1991. The upper main stem and the Middle Fork of the Eel River, a steep river flowing through bedrock canyons with large deep pools, boulder-cobble substrate, and a 1,950-km² drainage area, was studied intermittently during 1986–1991 by W. Jones (California Department of Fish and Game, personal communication), M. Ward (University of Washington, unpublished data), and Nielsen and Lisle.

The channel of Redwood Creek has aggraded or filled in with sediment since 1964 in response to large floods and a landscape destabilized by extensive logging and road building (Nolan and Marron, in press). The lower third of Redwood Creek, where stratified pools were studied, has aggraded an average of 1.5 m since 1975 (Varnum and Ozaki 1986). As a result, the channel is unstable. Gravel bars shift from year to year and promote bank erosion. Pools are relatively small. The study reach has an average gradient of 0.18% and the bed is mantled predominantly by medium gravel, although bed load includes a large proportion of sand that partially fills pools. Minimum daily stream discharge recorded during the drought of 1985 was 0.8 m^3/s and maximum daily stream temperatures frequently exceeded 20°C during the summer.

Rancheria Creek, a tributary of the Navarro River, flows through a broad floodplain about 23 km from the California coast. The study reach where steelhead were observed to use stratified pools was in a low-gradient portion (<0.1%) near Big Canyon. Summer flows pass through deep cobble-mantled deposits (up to 28 m wide) bordered by steep bedrock cliffs and eroding hillslopes. Deep pools (maximum depth, 2-3 m) were sometimes found at the base of bedrock outcrops, but shallow pools (maximum depth, 20–80 cm) associated with long gravel bars at the channel margins were more common. Mean summer discharge was 2.1 m^3/s in Rancheria Creek. Little riparian vegetation lined the stream banks. During the summers of 1990 and 1991, maximum daily stream temperatures often exceeded 24°C during peak solar exposure.

Thermally stratified pools were studied in the deep bedrock canyons of the upper channel of the main-stem Eel River and the MFER. Channels in these reaches are steep (gradients exceed 2%), bouldery, and confined between bedrock or eroding hillslopes. Deep pools are commonly carved along and within hard bedrock. Discharge in the MFER undergoes extreme seasonal variation. Peak winter flows near its confluence with the main-stem Eel River are thousands of cubic meters per second. In late summer during the drought of 1990, surface water discharge dwindled to 0.1 m^3/s or less. Flows in the main-stem Eel River are controlled by discharge from the Potter Valley Project, but summer releases are commensurate with natural runoff. Maximum daily water temperatures in the MFER below its confluence with Black Butte River usually begin to exceed 20°C by late June and exceed 25°C by late July (USGS 1965-1979).

Methods

Physical measurements. -- We surveyed cross sections and measured temperature profiles in five Redwood Creek pools and seven MFER pools during the summers of 1985 and 1986. An additional 12 pools in the lower MFER were mapped and surveyed for temperature (YSI model 2100, calibrated to 0.2°C) and dissolved oxygen (DO, mg/L; YSI model 54 temperature-compensating DO meter) during the summer of 1991. Seepage meters were used to measure inflow from different coldwater sources on Redwood Creek.

Topographic contours of 8 stratified and 16 nonstratified pools in Rancheria Creek were mapped and pools were surveyed for temperature and DO during the summers of 1990 and 1991. Recording thermographskept a continuous record of ambient stream and stratified pool temperatures in the MFER and Rancheria Creek from early June to late September 1991.

We evaluated the relative strength of mixing of cold and warm water within stratified pools of Redwood Creek and the MFER using residence time of water in pools, quantified as pool volume divided by discharge. Another measure of mixing

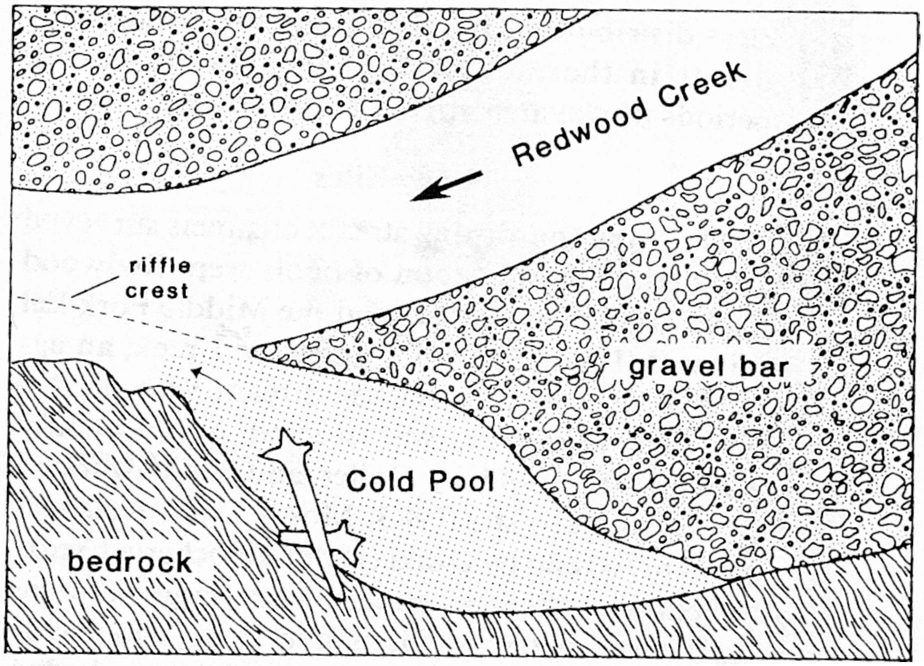


FIGURE 2.-Example of a gravel bar that protected a stratified pool from mixing in Redwood Creek. Cold water is derived from intergravel flow through the bar.

strength used, the Richardson number, is a dimensionless ratio of buoyancy forces to mixing forces:

$$R = (\Delta p/p)g \cdot Q/(W \cdot U^3);$$

p = water density, g = gravitational acceleration, Q = stream discharge, W = water surface width, and U = mean velocity in the pool. Evaluation of *R* was only appropriate for the MFER pools, where mean hydraulic variables could accurately quantify mixing strength.

Fish observations.--Steelhead use of thermally stratified pools was recorded by snorkelers along approximately 40 km of the MFER in late July and early August 1990. We compared fish counts made by two to six experienced snorkelers. Estimates of total counts were reconciled by methods outlined in Hankin and Reeves (1988). Surface and bottom pool temperatures were made with a handheld thermometer during this survey. The 12 stratified pools mapped in the MFER were similarly surveyed for summer-run adult and juvenile steelhead between July and September 1991.

Stratified pools on Rancheria Creek were surveyed by snorkeling and electrofishing (removal method) to determine fish distribution and abundance each summer from 1989 to 1991. Fish behavior was observed during summer 1990. Steelhead used for behavioral observation were captured in the study reach adjacent to eight stratified pools and marked as individuals with a Pan-Jet inoculator and acrylic paint according to methods described in Nielsen (1992a). Marked individuals were observed during 15-min intervals between the hours of 0600 and 1900 for three consecutive days at each pool. Observations were made during clear summer weather (June-September) when maximum ambient stream temperatures ranged between 21 and 28°C. Rates of forage activity (surface, midwater, and bottom foraging), agonistic acts (aggressive and submissive), and gill flaring were recorded for marked individuals. Gill flaring was assumed to be a response to increased environmental stress and oxygen demand (Parker and Dunson 1972: Heath 1987).

Analysis of variance (ANOVA, STATGRAPHICS V5.0) by habitat type was used to analyze the relationship between ambient stream temperature and fish density in stratified pools during two temperature regimes. Multifactor two-way ANOVA interactions were used to detect the effects of age-class and temperature category on the density of steelhead in stratified pools in the MFER and Rancheria Creek in August 1991.

Results

Formation of Stratified Pools

Coldwater sources found in this study included tributary inflow, seepage from groundwater sources along the channel bed, downstream intergravel flow. and thermal stratification of deep, still water. Circumstances for stratified pool formation contrasted strongly between Redwood Creek and the MFER due to differences in channel structure and

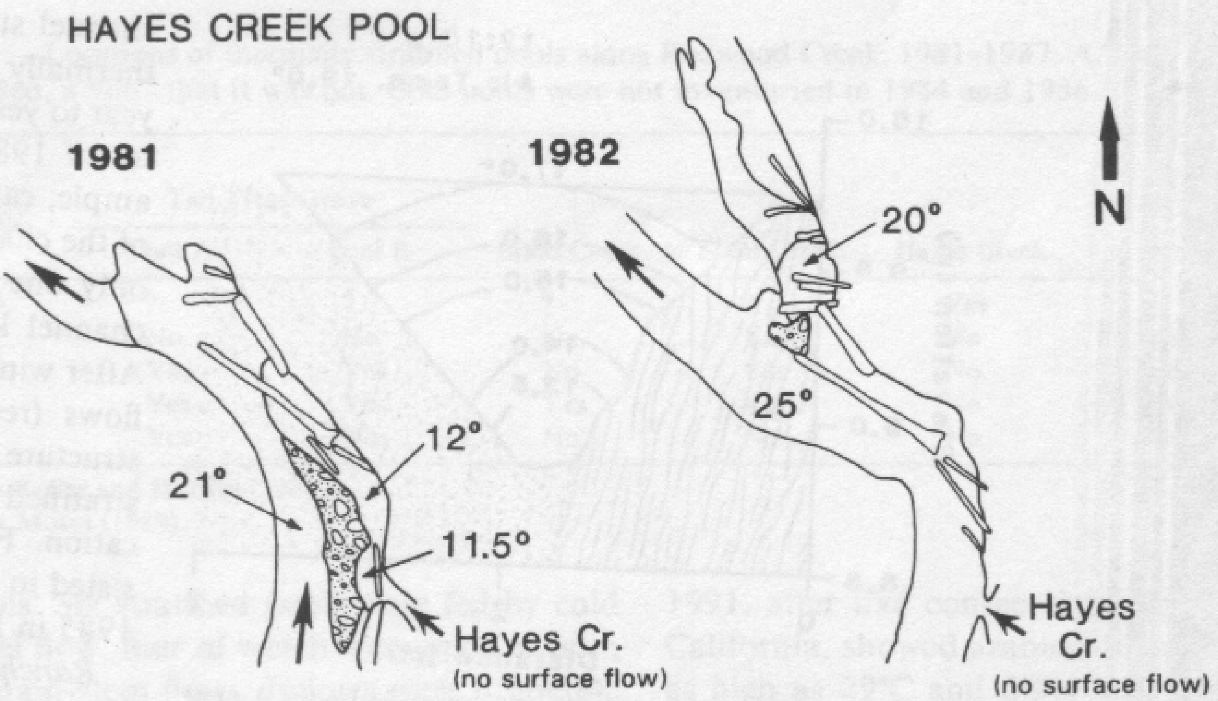


FIGURE 3.—Effects of changes in channel structure, principally shifts in the positions of gravel bars (stippled) and arge woody debris, on water temperatures in the thermally stratified pool at the mouth of Hayes Creek in Redwood Creek, 1981 and 1982.

coldwater sources. Rancheria Creek's thermally stratified pool formations were similar to those in Redwood Creek.

Redwood Creek. --In Redwood Creek, channel structure strongly influenced the development of thermally stratified pools. Stratified pools represented less than 9% of the total number of pools in lower Redwood Creek. Thermally stratified pools were formed most commonly where gravel bars encroached into pools that had been scoured along large bedrock projections or meander bends (Figure 2). These bars partially separated the pools from the main channel and inhibited thermal mixing of pool water with main-channel flow; the physical barriers concentrated and isolated coldwater inflows, which developed into large coldwater areas. In contrast, most main-stem pools were unstratified and uniform in temperature. Thermal stratification of pools in Redwood Creek was not a function of pool size. Linear regression analysis indicated no relationship between mean pool depth ($N = 5$; $r^2 = 0.14$), maximum depth ($r^2 = 0.06$), or volume ($r^2 = 0.28$) and temperature differencesbetween pools and main-stem flow.

Large woody debris in pools on Redwood Creek was not as effective as gravel bars in protecting influxes of cold water. In the Hayes Creek pool (Figure 3), for example, although cold water and large woody debris were present, a thermally stratified pool developed only in years when a gravel bar physically separated part of the pool from main-stem flows.

Coldwater sources for stratified pools in Redwood Creek were intergravel flow (water temperatures, 13-21°C), tributary flow (14–15°C), and hillslope groundwater seepage (11-12°C). Water that entered the pools from these sources was typically 3–9°C colder than the main-stem water. Mass balance calculations indicated that tributary surface inflow and upwelling intergravel flow were the primary coldwater sources. Coldwater inflow to pools from tributaries was as much as 0.016 m^3/s or approximately 2% of the surface water discharge of Redwood Creek. Pools were sustained by base-flow coldwater discharges that ranged from 0.008 to 0.020 m^3/s or 1-2.5% of surface water discharge. Measurements of inflow from different coldwater sources indicated that tributaries contributed 60-100% of the cold water to pools associated with tributaries, the rest coming from intergravel flow. Intergravel flow accounted for almost 100% of the coldwater inflow in pools not associated with a tributary. Groundwater was present in trace amounts.

Water at the bottom of stratified pools was as much as 7°C cooler than surface water and up to 11°C cooler than summer main-stem water. Subsurface flow of colder water into pools caused a distinct thermal gradient (Figure 4). Temperature profiles in stratified pools reflected the relative contribution and temperature of coldwater sources (Figure 5). The high rate of coldwater inflow at the head of the Elam Creek stratified pool kept pool temperatures low and uniform from top to bottom. In contrast, stratified pools A and B were maintained only by subsurface seepage and exhib-

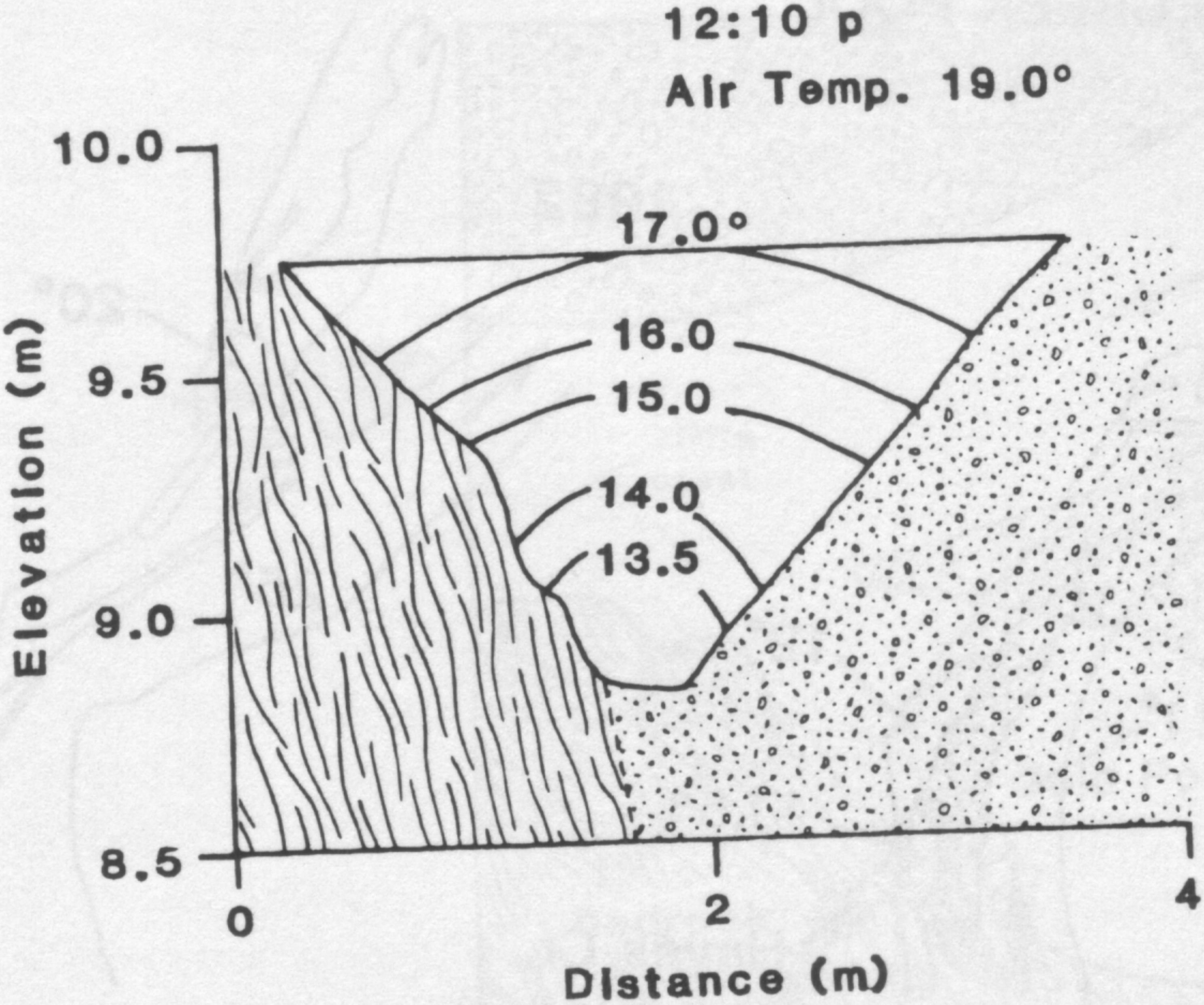


FIGURE 4.—Thermal gradient in stratified pool A near the Tall Trees Grove, Redwood Creek at 1210 hours.

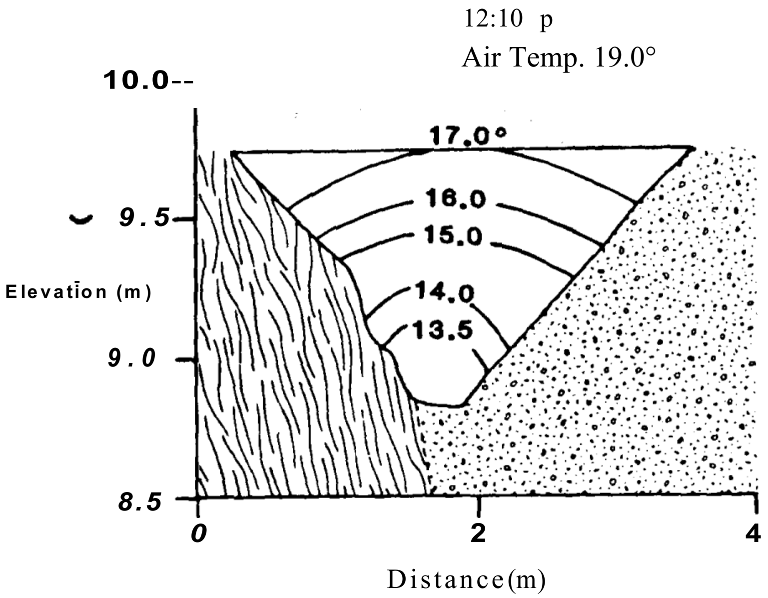


FIGURE 4.-Thermal gradient in stratified pool A near the Tall Trees Grove, Redwood Creek at 1210 hours.

ited well-developed thermoclines at depths of about 0.5 m. Greater shading and colder water flowing into stratified pool A than into stratified pool B accounted for the lower water temperatures observed in A. The Bond Creek stratified pool was shallow (<1 m deep) and completely exposed to solar radiation. Water temperatures at the bottom of the pool, however, were up to 4°C lower than main-stem temperatures. Small temperature differences in the Hayes Creek pool showed the ineffectiveness of woody debris in protecting influxes of cold water.

Channel shifting was common in the lower aggraded reaches of Redwood Creek; as a result, the channel structure important to the formation of thermally stratified pools was not reformed from year to year. Moderate peak flows during the winter of 1986 (5-year recurrence interval), for example, caused widespread shifting of the portion of the channel containing summer low flows, and only one stratified pool developed in the same channel location during the following summer. After winters (such as 1984–1985) with low peak flows (recurrence interval, </=3 years), channel structure was stable enough to cause thermally stratified pools to reform in the same channel location. For example, three stratified pools persisted in the same channel location from 1983 to 1985 in Redwood Creek (Table 1).

Rancheria Creek.—Stratified pools mapped in Rancheria Creek during the summers of 1990 and 1991 were similar in form and structure to the pools mapped in Redwood Creek in 1985 and 1986. Large sediment loads of mostly medium gravel and sand formed extensive gravel bars. In summer, the flow alternated from bank to bank across long lateral gravel bars into deep pools at bedrock outcrops or along stream meanders. During this study there was sufficient summer discharge to maintain mixing of warm surface waters throughout these large pools.

Eight stratified pools in Rancheria Creek were studied. They formed along the stream bank just downstream from large bedrock pools. These pools were separated from the main flow by large gravel bars that prevented mixing with cooler water at the stream margins. Intergravel and tributary inflows were the primary sources of cold water for

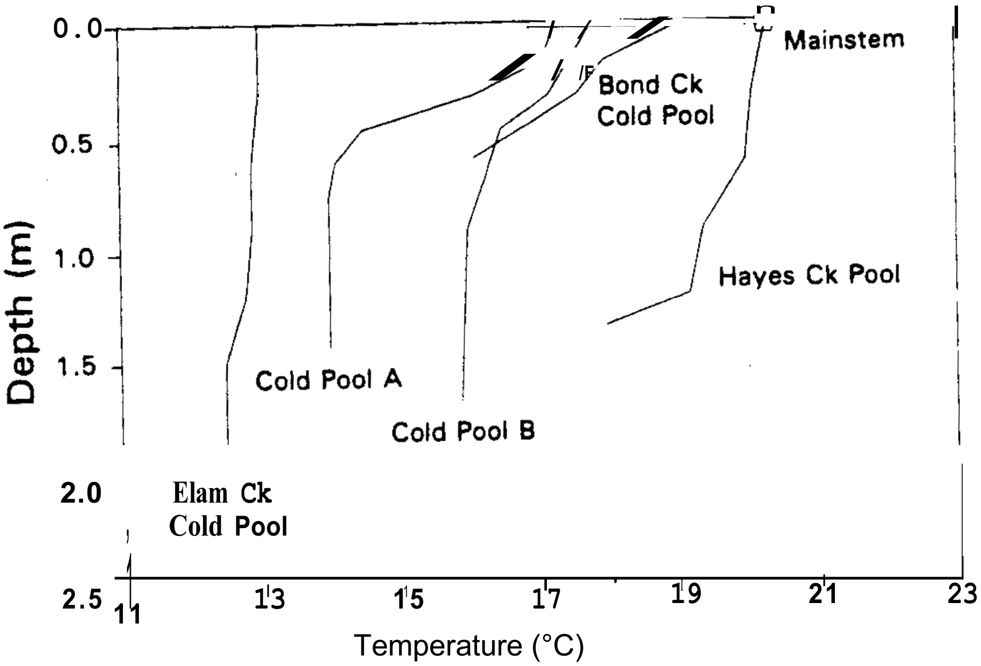


FIGURE 5.--Vertical temperature profiles in five pools in Creek during summer 1985 (Ck denotes creek).

TABLE 1.--Locations of thermally stratified pools along Redwood Creek, 1981-1987. A "yes" means that a pool was stratified, a "no" that it was not. Cold pools were not inventoried in 1984 and 1986.

Year	Tall Trees Grove		Bond Creek	Elam Creek	Hayes Creek	Other	Total number of stratified pools
	Pool A	Pool B					
1981[a]	?	?	?	?	Yes	?	1
1982[b]	No	No	No	Yes	No	Yes	2
1983[b]	Yes	Yes	No	Yes	No	Yes	5
1985	Yes	Yes	Yes	Yes	No	No	4
1987	Yes	No	No	No	No	No	1

[a] Data from Keller and Hofstra (1983).
[b] Data from Moses (1984).

these pools. Six stratified pools were fed by cold intergravel flow, four of which were open at both ends to main-stem flows. Inflows were negligible (<0.02 m^3/s), however, and the downstream opening was significantly larger and deeper than the upstream channel. In the remaining two intergravel pools only the downstream channel was open to main-stem flows, creating a cold backwater area. The other two stratified pools that were used to study steelhead were associated with small tributaries flowing into Rancheria Creek; gravel bars prevented mixing of the cold tributary flows with the warmer main-stem flows.

Middle Fork Eel River. —Temperature stratification in deep pools in the MFER occurred without the apparent influence of structural elements that isolate pool water from inflow (Figure 6). As the result of the extremely low summer discharge relative to the size of the channel, large pools that were scoured around bedrock outcrops in the steep channel during winter were left as essentially still bodies of water commonly exceeding 4 m in depth. This mode of stratification is well known for still bodies of water but had not been described in river pools.

Water temperatures in pools were commonly uniform with depth in the morning and became stratified as throughflow water heated during the day and bottom water maintained a constant temperature (Figure 7). Although intergravel flow may have contributed cold water, these morning isothermal profiles suggest that the major source of cold water may have been surface water that was cooled each night and then settled to pool bottoms as surface water warmed in daytime. The steepest temperature gradient in all pools formed consistently at a depth of about 2 m. During our survey in 1986, maximum surface water temperatures reached 27°C and cold pockets were consistently about 3.5°C cooler than surface water (Table 2). Temperatures measured during the summer of 1991, after five consecutive years of drought in California, showed ambient stream temperatures as high as 29°C and differences between surface and bottom water as great as 7.8°C. Temperature differences between ambient streamflow and nonstratified pools in the MFER were typically 1.8°C.

Large pools in the MFER stratified by virtue of the low intensities of turbulence, the result of ex-

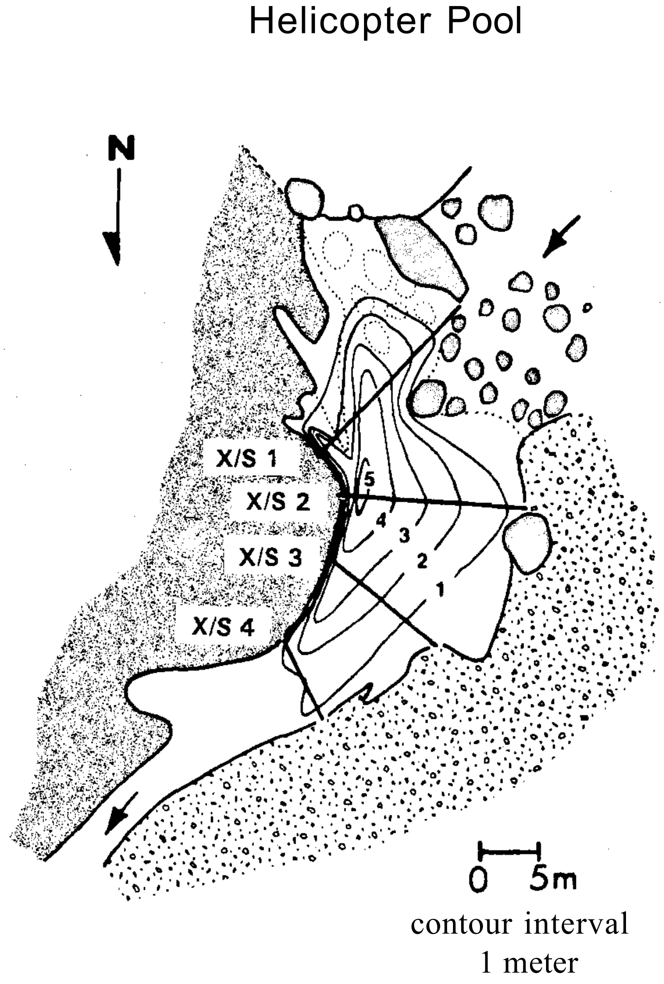


FIGURE 6.-Depth contours of the stratified Helicopter Pool in the Middle Fork Eel River, 1986 (x/s denotes cross section). Fine stippling denotes bedrock; coarse stippling indicates gravel.

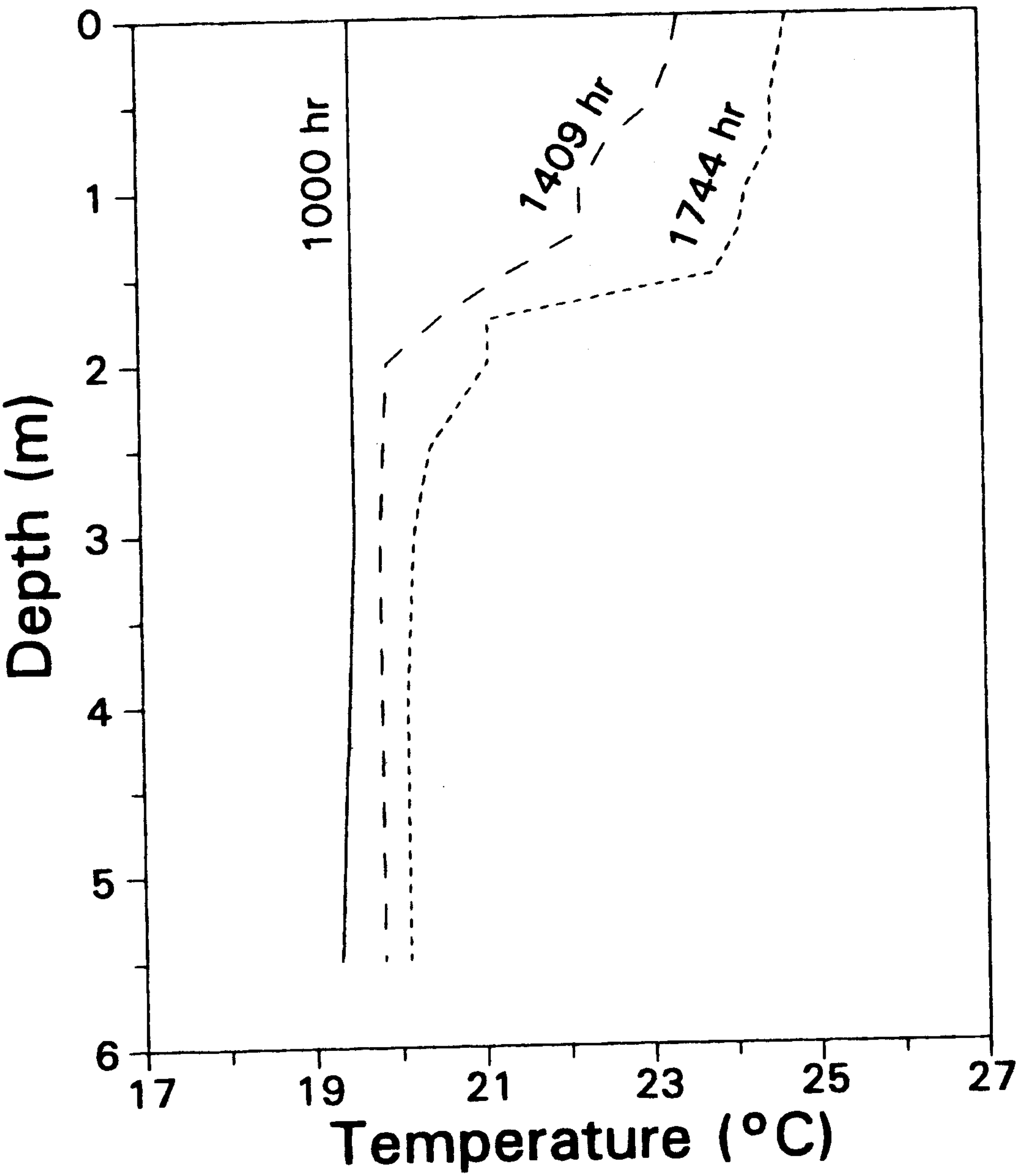
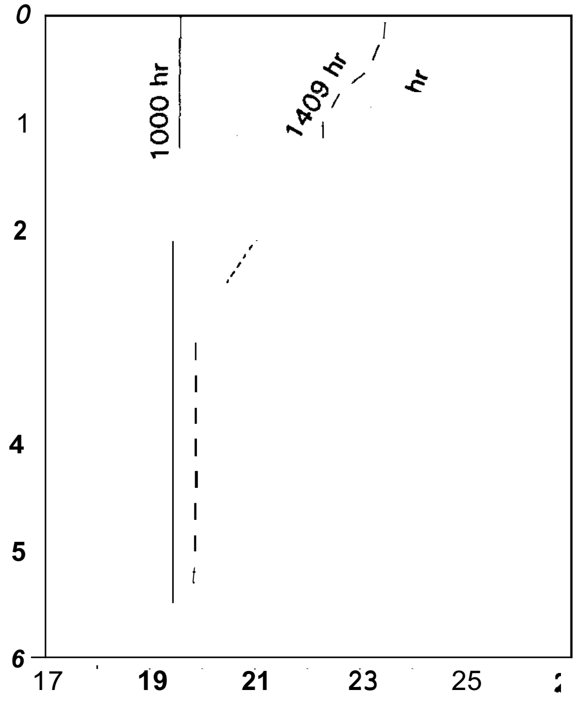


FIGURE 7.—Vertical temperature profiles of Helicopter Pool in the Middle Fork Eel River at midday on August 13, 1986.



tremely slow flows in the pools. Although we lack data for comparison of nonstratified pools in the Middle Fork, we used residence time to evaluate the relative strength of mixing in stratified pools. Residence time ranged from 2.5 to 9.3 h in the study pools. In comparison, residence times in large unstratified pools during minimum flow in Redwood Creek were less than 1 h.

Values of R, the ratio of buoyancy to mixing forces, for stratified pools in the MFER exceeded 500,000, confirming the observed tendency for stratification. Fischer et al. (1979) estimated that the transition from well-mixed to strongly stratified flow in an estuary occurs in the range $0.08 < R < 0.8$. Using by analogy a threshold value of $R = 1$, we can estimate corresponding threshold Values of velocity at which mixing will occur. We can assume that width and depth vary little with discharge in large pools during low flows because any incremental increase in discharge would cause a negligible increase in depth. Using characteristic values of width (12 m), depth (3 m), and $\square p = 0.1$ g/m^3 in stratified pools, we computed a maximum threshold velocity for mixing of 0.05 m/s. This value corresponded to a discharge of 2 m^3/s. Flow near the mouth of the MFER usually drops below 2 m^3/s in late June to early July (USGS 1965-1979).

Stratified Pools Used by Steelhead

Steelhead were observed in stratified pools in Rancheria Creek and the MFER. Studies along the MFER focused on adult summer-run and juvenile steelhead use of stratified pools during late summer. Rancheria Creek studies focused on juvenile steelhead behavior and stratified pool use throughout summer low-flow conditions. No fish surveys were made during this study in Redwood Creek. Stratified pools used as thermal refugesby steelhead varied significantly in size and microhabitat characteristics (Table 3). Coldwater areas (3.5°C cooler than ambient stream temperature) used by steelhead during periods of elevated stream temperatures (>23°C) made up 22-74% of the total pool volume in stratified habitats. They represented a much smaller proportion, however, of the total available summer pool volume (stratified and unstratified) measured in Rancheria Creek (2.3%) and the MFER (12.2%). Summer cold areas were not significantly different in volume between 1990 and 1991 (Student's t-test, $P < 0.05$). During this study, mean dissolved oxygen (DO) levels in coldwater habitats exceeded 7.0 mg/L, well above the plateau of concentration critical for maximum salmonid growth (5 mg/L; Herrmann et al. 1962; Brett 1979). The lowest DO levels (6.4

TABLE 2.-Comparison of physical and water quality variables in thermally stratified pools of the Middle Fork Eel River, summer 1986.

Pool	Volume (m^3)	Maximum depth (m)	Depth to cold water (m)	Water temperature (°C)		Discharge (m^3/s)	Mean velocity (cm/s)	Residence time (h)
				Bottom	Surface			
Rattlesnake	2,220	5.1	1.0	20.5	24.0	0.066	0.013	9.3
Helicopter	1,190	5.5	2.1	20.1	24.5	0.055	0.008	6.0
Goforth	1,080	3.6	2.0	22.1	26.5	0.12	0.015	2.5
Eel River	1,780	4.3	1.8	23.5	27.0	0.19	0.028	2.6
Pothole		3.1	1.5	19.0	22.8			
Bear Creek		4.9	1.8	19.6	23.0			
Bedrock		5.5	2.1	20.0	23.0			

TABLE 3.-Stratified pool microhabitats used by adult and juvenile steelhead in the Middle Fork Eel River (MF) and by juvenile steelhead in Rancheria Creek (RC), 1990-1991. Standard deviations are in parentheses.

Thermally stratified pool	N	Mean size (m^2)	% of volume cold	Mean maximum depth (m)	Mean temperature difference (°C)	Mean dissolved oxygen[a] (mg/L)	% of total oxygen saturation[a]
Groundwater seep (MF, RC)	4	18.3 (7.0)	22.1	1.8 (0.6)	4.2 (0.4)	7.1 (0.4)	73.1
Intergravel flow (RC)	6	20.8 (9.6)	42.5	0.8 (0.7)	6.3 (0.9)	7.4 (0.7)	75.9
Tributary flow (MF, RC)	5	149.5 (88)	61.2	2.5 (0.4)	4.8 (0.7)	8.2 (0.6)	85.7
Low-inflow pool (MF)	5	929 (404)	73.5	3.7 (0.5)	6.8 (0.3)	7.7 (0.3)	78.2

[a] In the cold portion of the pool.

mg/L) were recorded in two areas within 25 cm of groundwater inflows in the MFER. Percent total saturation remained above *70%* in all coldwater areas throughout the summer, and DO was not considered limiting to steelhead (Moyle 1976; Brett 1979).

Middle Fork Eel River. —Adult summer-run steelhead were observed only in pools stratified at depth in the MFER. Summer-run steelhead typically enter the MFER during spring and early summer (March–June) as 3- and 4-year-old, reproductively immature adults (Jones 1980). These large fish *(60–80* cm fork length) mature in deep holding pools through the summer (Shapovalov and Taft 1954).

Adult steelhead in the MFER (N = 449) were found in three types of pools: large pools thermally stratified at depth with low-velocity inflows and limited mixing *(76%),* stratified pools fed by cold tributary flows (13%), and deep pools fed with cold groundwater seeps (11 %). The distribution of summer-run steelhead into stratified pools was significantly different from a hypothetical chance distribution wherein fish would be evenly distributed into all large pools (>2 m deep) within the study reach (chi-square goodness-of-fit test, $P < 0.01$). Summer temperature differences between cold pockets used by adult steelhead and ambient stream temperatures recorded in MFER pools ranged from 4.1 to 8.2°C. The average overall temperature difference between pools and ambient flows in the MFER was 1.8°C.

During the summers of 1990 and 1991, juvenile steelhead were observed in pools and many riffle habitats throughout most of the study reaches. Juveniles have been observed to hug the stream bottom along upwelling cold seeps in the main-stem Eel River, presumably to take advantage of colder temperatures (R. E. Geary, Pacific Gas and Electric Company, personal communication). During this study, however, juvenile steelhead were seen actively feeding in surface waters with ambient temperatures up to 24°C. Young-of-the-year (age-0) steelhead density in coldwater habitats (Table 4) did not increase significantly when stream temperatures rose above 23°C in the MFER (ANOVA: in all habitat types, $P > 0.05$). Surprisingly, the density of age-1 steelhead in stratified groundwater pools dropped when ambient stream temperatures increased to 23°C (ANOVA, $F = 32.4$; df = 1,2; $P < 0.01$). These groundwater seep pools had the lowest mean DO level (7.1 mg/L) recorded in this study. No significant change in age-2 steelhead density was documented at higher temperatures in any stratified habitat type in the MFER.

Rancheria Creek. —Stratified pools in Ranche-

TABLE 4.--Densities of juvenile steelhead (number/m^2 of surface area) in three age-classes calculated for peak ambient stream temperatures (23–28°C)and low ambient stream temperatures (<23°C) in the Middle Fork Eel River and Rancheria Creek, August 1991. Asterisks denqte significant differences (ANOVA; $P < 0.05$) between densities in the two temperature categories for a specific age-class.

		Density at 23–28°C			Density at <23°C		
Cold pool	*N*	Age 0	Age 1	Age 2	Age 0	Age 1	Age 2
Groundwater deep	4	0.23	0.02*	0.11	0.17	0.13*	0.1
Intergravel flow	6	1.02*	0.24*	0.09	0.47"	0.11*	0.07
Tributary flow	5	0.44	0.31	0.1	0.48	0.37	0.16
Low-inflow pool	5	0.64	0.38	0.08	0.59	0.29	0.05

TABLE 5.-Foraging activity, agonistic activity, gill flaring, and movement (cumulative %) of juvenile steelhead into stratified pools, July–August 1990 ($N = 65$). Data are based on 15-min observationsof focal animals in three warm pools near cold pools fed by intergravel flow in RancheriaCreek (adapted from Nielsen 1992b).

Time of day (hours)	Mean temperature (°C)	Mean (per fish) number of actions per minute			Number (%) of fish moving to cold pools
		Foraging	Agonism	Gill flare	
0600	16.5	1.77	0.42	0	0
0830	18.3	3.30	0.18	0.41	0
1100	20.5	2.69	0.38	0.47	0
1230	22.4	0.78	0.73	0.63	2 (3%)
1400	23.2	0.14	0.78	0.59	16 (28%)
1500	24.5	0.03	0.02	0.82	24 (65%)
1630	23.5	0.60	0.33	0.33	0
1830	21.1	2.44	0.28	0.18	0

ria Creek contained age-0, age-1, and age-2 steelhead during most of the daylight hours. During periods of elevated ambient stream temperatures (23-28°C), however, there was a significant increase in the density of age-0 steelhead (ANOVA: $F = 215.09$; df = 2, 3; $P < 0.001$) and age-1 steelhead ($F = 37.2$; df = 1, 2; $P = 0.038$) in intergravel-fed stratified pools. Two-factor interaction effects between age-class and temperature category were significant only in intergravel-fed pools ($F = 107.67$; $P < 0.001$) in Rancheria Creek. No significant increase in density was found for steelhead of any age-class in other stratified pool types in Rancheria Creek.

The behavior of steelhead found in pools within 30 m of three intergravel-flow stratified pools suggested some of the physiological mechanisms underlying this selection for thermal refugia (Table 5). Mean rates of foraging began to decline for individual steelhead when stream temperatures reached approximately 22°C. At the same time agonistic activity increased. This activity consisted of numerous aggressive exchanges and nipping bouts between individual steelhead in the observation pools. The rate of gill flaring by marked steelhead was directly correlated with temperature in these pools (Kendall's $\tau = 0.4$, $P < 0.05$). Between noon and 1400 hours fish began to leave the observation pools and move into adjacent stratified pools, where all forage and agonistic activities ceased. Fish moving into stratified pools mixed freely with any resident fish but tended to remain in discrete age-groups.

Twenty-four marked steelhead (65%) were observed leaving their holding habitats to take up positions in adjacent stratified pools. Steelhead moved primarily downstream into intergravel-fed stratified pools from forage positions as far away as 28 m (mean, 15.4 ± 0.4 m). The marked fish held position in the stratified pool for up to 4 h and then returned to their original holding habitats as ambient stream temperatures fell to about 23°C. Marked individuals were observed repeatedly using the same thermally stratified pool on different days during periods of thermal stress. No movement into stratified pools was observed on days when ambient stream temperatures remained at or below 22°C.

Intergravel-flow stratified pools in Rancheria Creek usually had sandy bottoms with little or no cover within or above the pools. During their stay in the stratified pools, steelhead frequently held positions distributed throughout the cold pocket of the pool. Many steelhead were clearly visible from the bank and appeared extremely vulnerable to predation. However, no predation was observed in this study during the time of elevated ambient stream temperatures. Fish within the pools remained quite still, often close to each other with little agonistic interaction. Very little activity was observed along the creek during these periods.

Discussion and Conclusions

Conceptual Model of Stream Pool Stratification

The tendency of stream pools to thermally stratify can be evaluated qualitatively by considering the two factors mentioned previously: protection from mixing and source of cold water (Figure 8). The volume and temperature differentials of coldwater pockets tend to increase as coldwater flows increase and mixing weakens. Several protective mechanisms inhibit mixing of coldwater inflow with the warmer main-stem flow, Small pockets of cold water may form at the streambed surface from seeps or intergravel flow entering along a bar front at the upstream margin of a pool. The only inhibition of mixing of cold water is the vertical velocity gradient or some channel feature that separates flows. Bilby (1984) observed large woody debris to be an effective bamer to mixing, but such cases probably depend upon the build-up of enough debris to form an impervious barrieror upon contributions from other inhibiting factors such as gravel deposition along the woody debris. Gravel bar barriers that create backwater areas reduce velocities nearly to zero and are extremely effective at inhibiting mixing. Large, deep pools receiving little discharge can be equally effective due to the

THERMAL REFUGES FOR STEELHEAD

Q X ΔT OF COLDWATER SOURCE

COLD WATER SOURCE:	Flow separation	LWD	Bar barrier	Large pool ratio
Tributary inflow		Redwood Rancheria	Redwood Rancheria	
Bar and bank seepage	MF Eel	Redwood Rancheria	Redwood Rancheria	MF Eel
Thermal stratification				MF Eel

PROTECTIVE MECHANISM:

WEAKNESS OF MIXING

FIGURE 8. -Conceptual model of factors influencing the volume and temperature differences of coldwater volumes in stratified pools. The vertical axis represents main-stem flow (Q) multiplied by the temperature difference between streamflow and the coldwater source *(❒ T).* Combinations typical of Redwood Creek, Rancheria Creek, and the Middle Fork (MF) Eel River are identified by river name (LWD is large woody debris).

high volume-to-discharge ratio. Stratified pools of this type do not require special channel configurations or influxes of cold water and can be common in channels such as the Eel River, where scour is deep and summertime flows are extremely low.

Influxes of cold water that are protected from mixing may be a dominant factor in creating stratified pools. Seeps from intergravel flow through bars are common sources of cold water for pools, but their small flows rarely provide temperature differences greater than a few degrees. Tributaries may discharge so much cold water that, by virtue of their sheer discharge, the inflow can maintain large volumes of cold water before being thoroughly mixed with the main-stem flow. Thus tributary-inflow stratification may occur despite the presence of relatively high main-stem velocities.

Redwood Creek, Rancheria Creek, and the MFER differ with respect to the factors that combine to form stratified pools. Study reaches along Redwood and Rancheria Creeks had low gradients, mostly unconfined channels, and large gravel bars. At these sites, maintenance of cold water in pools depended on an influx of cold water directly into pools and specific channel structures that prevented mixing. The principal structures were large gravel bars that formed backwaters in pools. In contrast, the MFER had a steep gradient and a confined channel, which created a high potential for scour. Scour pools were commonly large and deep and stratification could occur without large influxes of cold water and special channel configurations that inhibit mixing. As a result, stratified pools were more frequent and cold water more voluminous in the MFER than in the other creeks.

Flow augmentation from increased reservoir releases in summer can have adverse effects on critical temperature conditions in rivers downstream. By increasing mixing in thermally stratified pools, increased flow can destroy coldwater refuges. Recognizing this potential, the California Department of Water Resources has recommended limitations on summer releases from Van Arsdale Dam (California Department of Water Resources 1976).

Steelhead Use of Stratified Pools

Steelhead use of thermally stratified pools may be unique to warmer climates. Summer steelhead use of deep, stratified pools in the MFER has been documented by the California Department of Fish and Game for the last 26 years (Jones 1980). Summer steelhead in more northern rivers, however, use pools where stratification was not recorded. For example, the New River in northern California maintains sufficiently cool summer flows to support summer-run steelhead without stratification (R., Nakamoto, U.S. Forest Service, personal communication). Use of stratified summer pools, although important for the adult summer steelhead populations in this California study, may be largely a function of the high ambient stream temperatures and low summer flows found in the MFER.

As flows dwindle seasonally to a trace in small tributaries, juvenile trout have been shown to move downstream from their natal streams to larger creeks and rivers (Erman and Leidy 1975). Erman and Leidy documented that some trout fry remained in isolated pools with high ambient stream temperatures (22.4°C) and suggested that highly oxygenated seepage of groundwater into these pools may mitigate thermal effects. In our study significant numbers of large juvenile steelhead (age 1) left cold pockets near groundwater seeps when ambient stream temperature reached 23°C, whereas age-0 steelhead did not. The groundwater sources creating these cold pockets were poorly oxygenated compared with ambient flows. This suggests groundwater sources are not all the same, and biochemical properties may not be specific to different stratified pool types. It also suggests an ontogenetic shift in the trade-offs made by steelhead between oxygen demand and thermal stress.

The only positive association found in this study between stratified pools and juvenile steelhead density was in intergravel-fed pools in Rancheria Creek. These pools were used as thermal refugia during periods of high ambient stream temperatures by age-0 and age-1 steelhead. Physiological stress from high stream temperatures was demonstrated by the direct correlation between gill flare rates and increasing stream temperatures. Increased agonistic activity and a decrease in forage activity in juvenile steelhead indicated a conflict in maintenance requirements and resource needs after ambient stream temperatures exceeded 22°C.

The threshold at which the benefits of behavioral thermal regulation outweighed the costs was not the same for all individuals. There was no mass movement of fish into the stratified pools, suggesting physiological thresholds were not uniform throughout the population. Constraints of social behavior may affect the trade-off values for individual steelhead moving from warmer to cooler water. Some individuals repeatedly used the same stratified pool environment during periods of thermal stress, suggesting a learning component in this behavior. Once in the pool, fish uniquely positioned themselves in small groups without agonistic exchange, suggesting once again that experience was a critical component of this behavior. Possible long-term implications of this behavior on age-specific interactions among juvenile steelhead outside the stratified pool, such as the development of cooperative forage or migration groupings, have not been studied.

The importance of thermally stratified pool refugia to steelhead appears unique within different California streams and tends to serve different fish life history stages. The general distribution of thermally stratified habitats in northern California streams and the role they play in sustaining fish populations need more study. What types of management actions have the greatest influence on the formation and persistence of thermally stratified habitats remain unknown. However, the potential loss of cold habitat that can sustain fish during periods of critical thermal stress—loss due to pool filling, decreased groundwater flows, changes in the geomorphic structure in streams, or other factors—may become ever more important to the freshwater fish assemblage as the long-term drought continues in California and as air temperatures increase with climatic warming (Meisner 1990). Field surveys of fish habitat made at one time of the year under one thermal condition ignore the critical temporal element that we have shown thermally stratified pools to play in streams. The results of this study suggest a long-term temporal scale is necessary to understand and analyze the geomorphic conditions leading to the formation of stratified pools and the role such pools may play in fish communities that experience marginal habitat conditions due to thermal stress.

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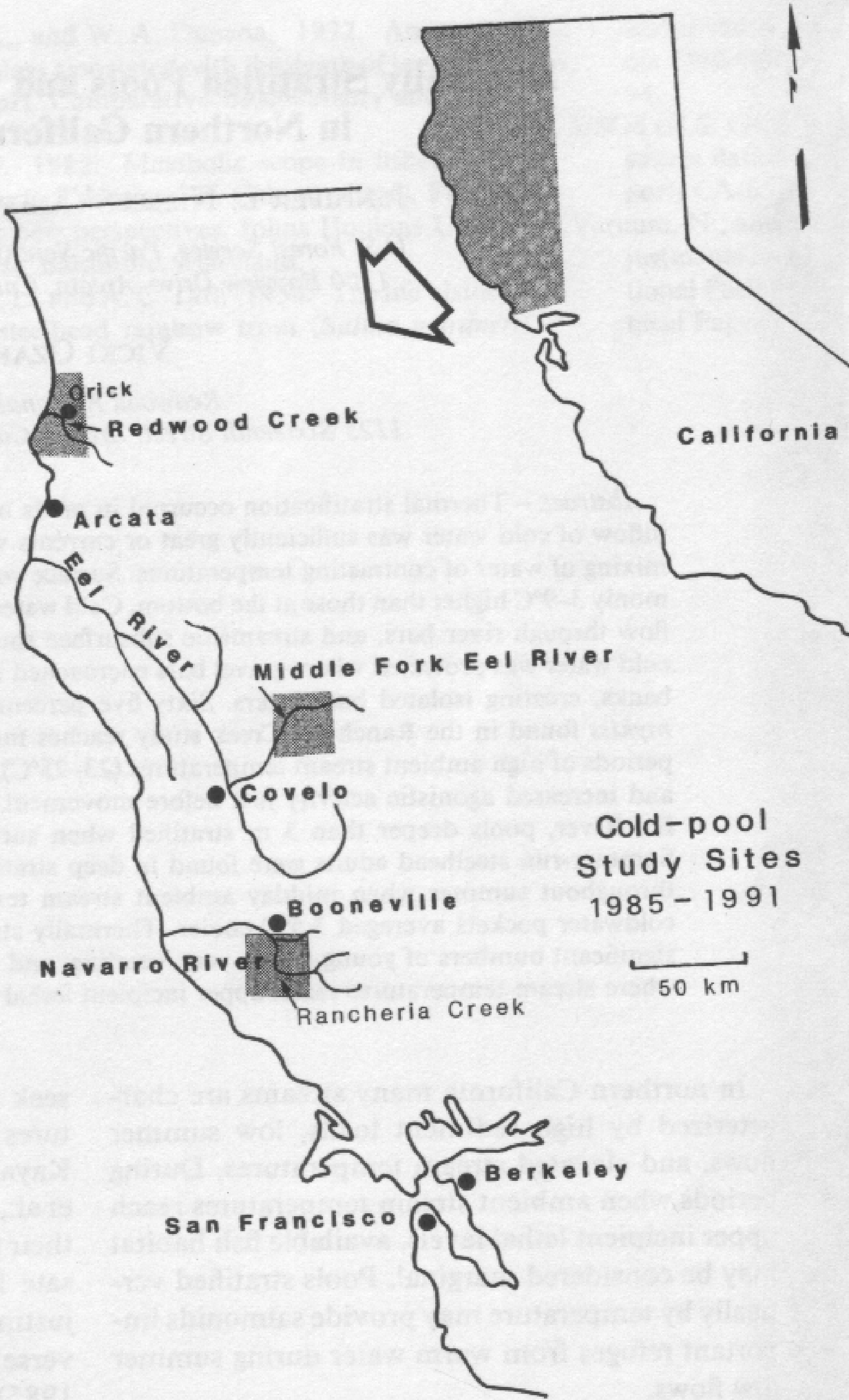

FIGURE 1.—Locations of three study reaches (shaded) with thermally stratified pools in northern California.

thermally stratified habitats as had Gibson (1966),