

Thermal ecology of juvenile steelhead in a warm-water environment

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Abstract How salmonids adjust to the cost of chronic exposure to warm water in nature, particularly in habitats where areas of cold water are unavailable, is largely unknown. In the hot dry climate of southern California, oversummering juvenile steelhead, *Oncorhynchus mykiss*, can experience a continual warm-water environment. Studies were performed in three streams (34°N) during the summers of 2002–2004 to assess how steelhead (10–28 cm total length) exploit the thermal environment and to develop an understanding of how existing preference and heat tolerance information reported for the species relate to the actual temperatures the local population experiences. Analyses of achievable body temperatures, an index of observed body temperatures, and behavioral time budgets, indicate steelhead did not behaviorally thermoregulate. Findings from associated field surveys suggest areas of cold water were not available. Steelhead held focal points at temperatures (17.4–24.8°C) that were at times higher than the temperature preferences and heat tolerances reported for the species. Oversummering juvenile steelhead accept an elevated body temperature and remain active and forage throughout the day, apparently

as a means for coping with warm water at the southern extent of their range. The relatively high body temperatures that steelhead accept appear to represent a compromise in exchange for maintaining an expanded geographic (latitudinal) range.

Keywords Behavior · Habitat use · Temperature preference · Temperature tolerance

Introduction

When confronted with elevated temperatures during daily activities in summer, salmonids in streams adjust behavioral activity or microsite selection to reduce heat-load exposure (Nielsen et al. 1994; Ebersole et al. 2001), thereby promoting maintenance of body temperature. Because optimum performance of many physiological processes is tied to a narrow temperature range (Brett 1971; Myrick and Cech 2000) and temperatures far removed from preference can reduce feeding and activity and cause mortality (Johnstone and Rahel 2003), the maintenance of body temperature is considered favorable.

Behaviors for coping with the thermal environment can lead to compromise, especially in resources necessary for survival. Individuals tolerate low dissolved oxygen (Matthew and Berg 1997) and intraspecific interactions (Biro 1998) in

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exchange for cold water, endure lower food availability to experience lower daily maximum temperatures (Li et al. 1994), and accept higher body temperatures in exchange for an expanded foraging area (Grant 1990). Although past studies indicate temperature can influence the cost and benefit of body-temperature maintenance, how salmonids adjust to the cost of chronic exposure to elevated temperatures in nature is largely unknown. This is particularly true in habitats where areas of cold water are unavailable.

Juvenile steelhead, *Oncorhynchus mykiss*, overwintering in coastal streams of southern California can experience a continual warm-water environment. In many small coastal basins, streamflow is extremely low and clear during the summer and can lack areas of cold water. Daily maximum stream temperatures can begin exceeding 20°C in late spring, and daily temperatures can reach 21°C by mid morning and exceed 28°C in the afternoon during July and August. One purpose of this study was to assess how juvenile steelhead exploit the thermal environment during July and August. To this end, I measured temperatures that would be achievable (T_a) (i.e., available body temperatures) to steelhead in different mesohabitats within a single stream, quantified steelhead behavioral activities, estimated an index of observed steelhead body temperature (T_b) and compared T_b to T_a within the same habitat where steelhead are found, and

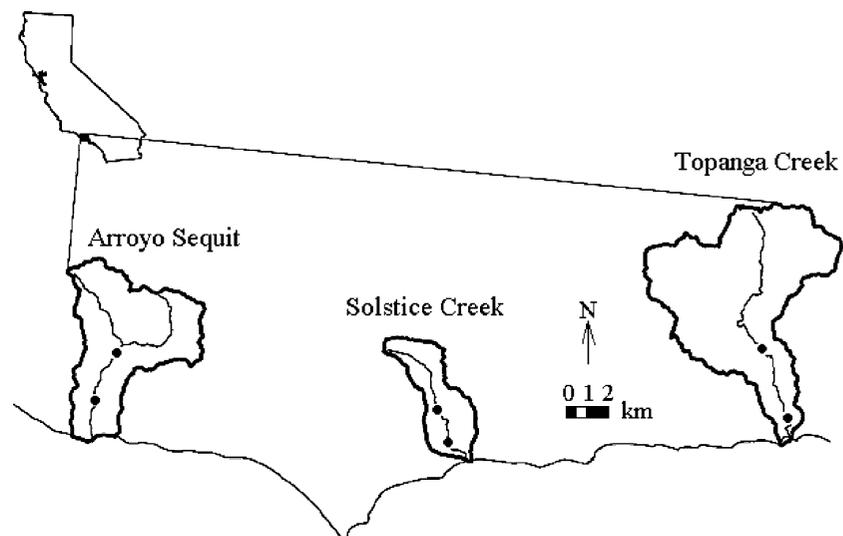
T_a between occupied and adjacent unoccupied habitats.

Because thermal history contributes to shape temperature preference and tolerance (Cherry et al. 1977; Threader and Houston 1983), the local steelhead population may exhibit thermal-habitat associations that differ from preference and tolerance information reported for the species (e.g., Bjornn and Reiser 1991). The second purpose of this study was to develop a basic understanding of how existing temperature preference and heat-tolerance information relate to the actual temperatures the local population experiences. Such an understanding is needed, in part, to improve science-based conservation of steelhead in southern California, which are listed as endangered under the U.S. Endangered Species Act. I investigated the thermal regime of three southern California streams, measured water temperature at focal points of overwintering steelhead and compared these data to temperature preference and heat-tolerance information.

Study streams

Arroyo Sequit, Solstice Creek and Topanga Creek are small coastal streams originating in the Santa Monica Mountains, Los Angeles County, California (Fig. 1). White alder, *Alnus Rhombifolia*, California sycamore, *Platanus*

Fig. 1 The watersheds of Arroyo Sequit, Solstice Creek and Topanga Creek, and locations of temperature-monitoring stations for each stream (filled circles)



racemosa and willow, *Salix* spp., are common along each stream. Summer discharge was less than $0.04 \text{ m}^3 \text{ s}^{-1}$ in each stream, and water clarity in Topanga Creek (where steelhead-specific studies were performed) consistently exceed 3 m (determined by direct underwater observation and measuring the distance to an underwater object). Arroyo Sequit and Solstice Creek are within state and federal parklands; the portion of Topanga Creek considered in this study lies within state parklands. Only Topanga Creek contained a sufficient number of steelhead to provide statistically meaningful results. Although the frequency that adult steelhead return to study streams has not been assessed, adult steelhead (>50 cm total length) are typically observed in Topanga Creek. In this study, measurements were made on steelhead ranging from 10 cm to 28 cm in total length.

Methods

Thermal regime, temperatures at locations held and comparison with existing information

During 2002 and 2003, stream temperature was recorded during mid June to mid September using data loggers programmed to record time, date and temperature in 24-min intervals. Loggers were contained in protective housings (Spina 2005) and deployed at upstream and downstream reach boundaries of each stream (Fig. 1). Reach boundaries were delineated by natural waterfall barriers, extent of continuous surface flow and, in one case (upstream boundary at Arroyo Sequit), private property for which permission to pass was not granted.

To measure temperature at steelhead focal points, Topanga Creek was surveyed in July and August 2002 and 2003 during late morning and afternoon. An YSI model 85 water-quality meter and probe attached to a 1-m rod was used to measure water temperature at steelhead focal points. In some cases, multiple measurements of water temperature were averaged over the area covered by a moving steelhead. Because such fish were moving at a constant rate, calculating a weighted mean was unnecessary. A total of 11

habitats (i.e., habitats at different sites) were sampled in 2002 and 14 in 2003.

The daily maximum, median and minimum stream temperatures (obtained from the data loggers), and temperatures at steelhead focal points, were compared to published preference and heat-tolerance information (Table 1) (in making this comparison, I do not assume that the actual temperatures steelhead experience in southern California streams are 'stressful'). The comparison includes articles on rainbow trout (non-anadromous *O. mykiss*) because much of the literature is dedicated to rainbow trout, and the preference and tolerance of steelhead and rainbow trout generally appear similar. The highest average of the maximum daily temperature over any 7-day period and the highest average of the mean daily temperature over any 7-day period were also computed (Eaton et al. 1995; Welsh et al. 2001). Because the literature identifies 24°C as a heat-tolerance limit (Table 1; Eaton et al. 1995), the number of days and duration (h day^{-1}) that stream temperatures equaled or exceeded this criterion were calculated from the record of temperatures.

Habitat and microsite selection and behavioral activities

During summer 2004 at Topanga Creek, a physical model of steelhead was used to estimate an index T_b at locations held by individuals and to estimate T_a throughout randomly selected habitats (Bakken 1992). The physical model consisted of 23-cm long, 2-cm diameter (1-mm thick) copper tubing, which was filled with water and capped at each end with a 2-cm diameter copper plug. A calibrated temperature sensor connected to a digital display of real-time temperature was suspended at the center inside the model. To approximate the solar absorptivity of steelhead, the model was painted to match the coloration of steelhead in the creek. While physical models are commonly used to estimate body temperature of reptiles in nature (e.g., Hertz 1992; Brown and Weatherhead 2000), the use of such models to estimate fish body temperature was not apparent in the literature. In my study, I believed the use of a physical model was necessary to account for

Table 1 Summary of preferred (T_p), lethal maximum (T_{max}), and acclimation (T_{acc}) temperatures ($^{\circ}\text{C}$) of studies (source) assessing temperature preference and tolerance in *Oncorhynchus mykiss*

T_p	T_{acc}	Source	T_{max}	T_{acc}	Source
11.8 ^a	5	McCauley et al. (1977)	27.6 ^d	9.8	Carline and Machung (2001)
12.7 ^a	10	McCauley et al. (1977)	28.1 ^d	9.8	Carline and Machung (2001)
10.4 ^a	15	McCauley et al. (1977)	28.4	10	Lee and Rinne (1980)
9.8 ^a	20	McCauley et al. (1977)	29.4	20	Lee and Rinne (1980)
12.0 ^a	25	McCauley et al. (1977)	25.6	16	Hokanson et al. (1977)
15.8 ^b	10	Javaid and Anderson (1967)	28	10	Currie et al. (1998)
17.5 ^b	15	Javaid and Anderson (1967)	29.1	15	Currie et al. (1998)
22.0 ^b	20	Javaid and Anderson (1967)	29.8	20	Currie et al. (1998)
18.4 ^a	18 ^c	McCauley and Pond (1971)	25	– ^h	Cherry et al. (1977)
18.4 ^a	18 ^c	McCauley and Pond (1971)	26.3	17	Grande and Andersen (1991)
11.6	6	Cherry et al. (1975)	24	11	Black (1953)
12.6	9	Cherry et al. (1975)	23.7, 25.0, 23.2 ^e	5	Kaya (1978)
14.4	12	Cherry et al. (1975)	24.2, 25.2, 24.7 ^e	9	Kaya (1978)
16.9	15	Cherry et al. (1975)	25.2, 25.2, 24.7 ^e	13	Kaya (1978)
18.1	18	Cherry et al. (1975)	25.7, 25.7, 25.2 ^e	17	Kaya (1978)
20.1	21	Cherry et al. (1975)	26.2, 26.2, 25.7 ^e	21	Kaya (1978)
22.0	24	Cherry et al. (1975)	26.2, 26.2, 26.2 ^e	24.5	Kaya (1978)
14.1	12	Cherry et al. (1977)	24 ^f	– ^h	Eaton et al. (1995)
17.1	15	Cherry et al. (1977)	25–26	15	Bidgood and Berst (1969)
18.6	18	Cherry et al. (1977)	22.8, 22.7, 22.6 ^g	4	Threader and Houston (1983)
20.2	21	Cherry et al. (1977)	24.1, 24.1, 24.0 ^g	8	Threader and Houston (1983)
22.2	24	Cherry et al. (1977)	24.6, 24.5, 24.5 ^g	12	Threader and Houston (1983)
14.3	12.7 ^c	Peterson et al. (1979)	25.4, 25.3, 25.1 ^g	16	Threader and Houston (1983)
14.7	12.1 ^c	Peterson et al. (1979)	25.9, 25.7, 25.5 ^g	20	Threader and Houston (1983)
			27.6, 27.7 ^l	10	Myrick and Cech (2000)
			28.6, 28.4 ^l	14	Myrick and Cech (2000)
			29.6, 29.3, 30.6, 30.0 ^l	19	Myrick and Cech (2000)
			31.0, 30.7 ^l	22	Myrick and Cech (2000)
			32.0, 31.5 ^l	25	Myrick and Cech (2000)

^a Mean occupied temperature for individual fish

^b Reported mean of individual modal temperatures fish selected in thermal gradient

^c Horizontal and vertical test gradients

^d Wild and cultured fish used in tests

^e Temperatures for three trout populations, or two different strains

^f Temperature is the 95th percentile of the highest 7-day mean temperature, based on field studies

^g Measured at 24, 48, and 96 h

^h Not reported

^l Two different strains used in tests

^j Two separate tests performed for each of the two strains

radiant heat, which I suspected could influence T_a and T_b due to the shallowness and transparency of the creek. Based on use of the model, values of T_a and T_b were typically lower in shaded locations than in adjacent locations exposed to sunlight.

The physical model was calibrated using dead rainbow trout obtained from a hatchery. The model and one trout were placed side-by-side in a shallow (15.2 cm) water-filled white tub (34.3×34.3 cm) on a wooden platform outdoors.

A temperature sensor was implanted in the trout anterior to the dorsal fin near the vertebral column. The tub was shaded for 10 min, after which the cover was removed and the model and trout were ‘sunned’ for at least 2 min before recording the temperature of the model and the trout. This trial was repeated 21 times, and for each trial the model was paired with a different trout and the water-bath temperature was varied. Least squares linear regression on the paired temperatures from

each side-by-side trial showed the physical model predicted an index of trout body temperature ($r^2=0.97$, $p < 0.0005$).

Between 1000 and 1600 hours during July, the physical model was used to estimate T_a in 32 randomly selected sample units consisting of 16 pools and 16 non-pools, which were paired in the same area to account for location effects. Depending on the length of the sample unit, T_a was measured at 10–30 randomly selected locations within each sample unit (3 cm from the channel bed, the typical focal height of steelhead). The model remained in a location for several seconds to several minutes until an equilibrium temperature was reached. Pairs of sample units were sampled on the same day within a few minutes of one another. The one-sample *t*-test was used to test the null hypothesis that the mean difference in unit-specific mean T_a between pools and non-pools was equal to zero (type I error rate = 0.05 for all tests). Multiple linear regression analysis related unit-specific mean T_a to time and habitat type, with habitat type treated as an indicator variable in the regression model.

Steelhead behavior was observed from sheltered positions near the creek from 0800 to 1130 hours (water temperature ranged from 19.0 to 21.0°C) and from 1230 to 1600 hours (22.0–26.5°C) in July. The instantaneous sampling method (Martin and Bateson 1993) was used to quantify undisturbed steelhead behavior during a single 5-min recording session, divided into 10-s sample intervals. For each 10-s interval, exposure of steelhead to sun (full sun, filtered sun or shade) and behavior (foraging, stationary, roaming and agonistic, as defined in Table 2) were noted. The

two-sample *t*-test was used to test the null hypothesis of no difference in the mean percentage (%) time budget (the amount of time a behavior was observed divided by the duration of the entire observation period) for each behavioral activity between the morning ($n=15$) and the afternoon ($n=14$). The mean % time in full sun, filtered sun and shade was used in a second test. A simple correlation coefficient assessed the relationship between the unit-specific mean % time budget for each behavior and time of day.

Between 1130 and 1600 hours in July, T_a and T_b were measured in randomly selected pools ($n=17$). I carefully approached each pool and then noted the focal point of the steelhead. Beginning at the downstream end of each sample unit, I measured T_a (at randomly selected locations) and T_b (at steelhead focal points) concomitantly in an upstream direction while minimizing disturbance to the sample unit. In some cases, T_b was averaged over the area where a single steelhead was observed roaming. The one-sample *t*-test was used to test the null hypothesis that the average difference between the mean unit-specific T_b and T_a was equal to zero. Simple linear regression analysis was used to relate unit-specific values of T_b and T_a to one another.

Surveys were performed during July and August to measure T_a at randomly selected locations in occupied pools and in adjacent pools where steelhead were not observed (unoccupied pools) ($n=10$ for each pool type). Pool types were randomly selected and paired in the same general area to account for location effects. For each sample unit, I noted length and width (m), maximum depth (cm), area of riparian canopy

Table 2 Definition of terms describing the behavior of steelhead noted through the application of the instantaneous sampling method between 0800 and 1600 hours on 16, 19, 20 and 22 July 2004 within study reach at Topanga Creek

Term	Definition
Foraging	Movement while inspecting water column or surface, rocks, channel bed or accumulations of filamentous algae, which sometimes resulted in detection, approach and occasional feeding on an item. Brief burst swimming that sometimes resulted in capture of food item. Manipulation of food item in mouth.
Stationary	No apparent directional movement.
Roaming	Movement from one location to another with no apparent inspection of water column or surface, rocks, channel bed or accumulations of filamentous algae.
Agonistic	A steelhead chasing or fleeing conspecific, or one steelhead making 'lateral display' (Butler 1991) toward another.

(weighted by the area of the sample unit) and compass bearing of the thalweg referenced upstream. Pool pairs were surveyed on the same day within a few minutes of one another. Temperature data loggers were placed in each pool on 4 August 2004 and then retrieved on 10 September 2004. The one-sample *t*-test was used to test the null hypothesis that the mean difference in unit-specific mean T_a between occupied and unoccupied pools was equal to zero. Binary logistic regression assessed the contribution of physical and temperature characteristics of the sample units for predicting steelhead presence.

Results

Thermal regime, temperatures at locations held and comparison with existing information

During the summers of 2002 and 2003, temperatures in the three streams were elevated (Fig. 2) and exceeded the reported preferred temperatures (cf. Table 1). The average (across stations) daily maximum, median and minimum temperatures in Solstice Creek were consistently within the limits of reported preferred temperatures (9.8–22.2°C, Table 1). In Arroyo Sequit and Topanga Creek, the average daily maximum temperatures often exceeded the highest reported preferred temperature. Field surveys at Topanga Creek revealed steelhead held locations with temperatures ranging from 17.4 to 24.8°C (mean \pm 1 SE in 2002 and 2003 = 20.4 \pm 0.24 and 22.4 \pm 0.21°C, respectively). The temperatures at steelhead focal points were at times higher than some preferred temperatures (Fig. 3) including those based on high acclimation (cf. Table 1).

Steelhead were exposed to temperatures that are reported to be lethal. The highest single daily maximum temperature exceeded 25°C, whereas the highest average 7-day maximum temperature and the highest average 7-day mean temperature ranged (across stations and years) from 24.6 to 18.8°C and 22.0 to 17.4°C (Table 3). The highest average 7-day mean temperature never exceeded the 24°C criterion. The highest daily maximum temperature equaled or exceeded 24°C on 9 days at Arroyo Sequit up to 38 days at Topanga Creek.

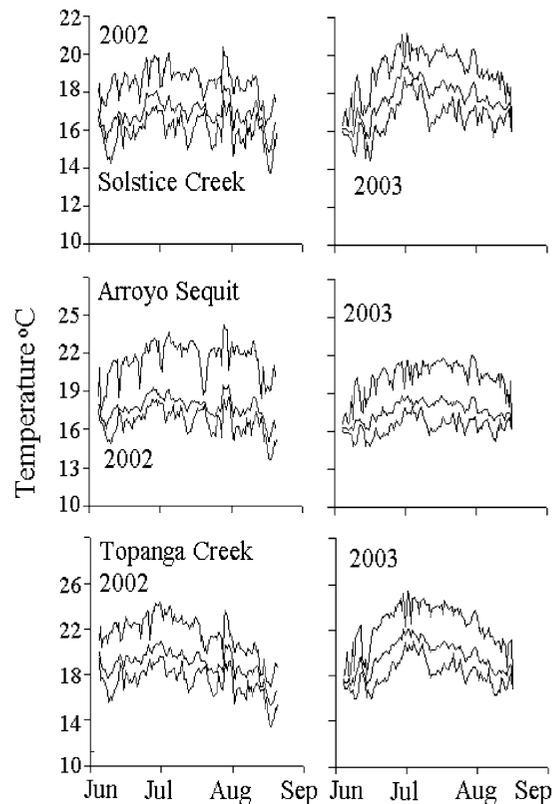


Fig. 2 Daily maximum, median and minimum water temperatures averaged across monitoring stations for the three study streams (mid June to mid September 2002 and 2003)

Diel temperature fluctuations ranged from 4.0 to 8.5°C, with the average duration of temperatures equal to or exceeding 24°C ranging from 1.8 (Arroyo Sequit) to 2.7 h day⁻¹ (Topanga Creek). Temperatures at steelhead focal points (Fig. 3) were within reported lethal limits; maximum focal temperatures were 22.9°C (2002) and 24.8°C (2003) (cf. Table 1).

Habitat and microsite selection and behavioral activities

During the summer of 2004 at Topanga Creek, the opportunities for steelhead to achieve a particular body temperature did not differ between pools and adjacent non-pools. Individual T_a varied throughout pools and non-pools (17.2–28.7°C), and differences between maximum and minimum temperatures within a given unit ranged from 0.1 to 9.4°C, with an average difference of 1.2°C.

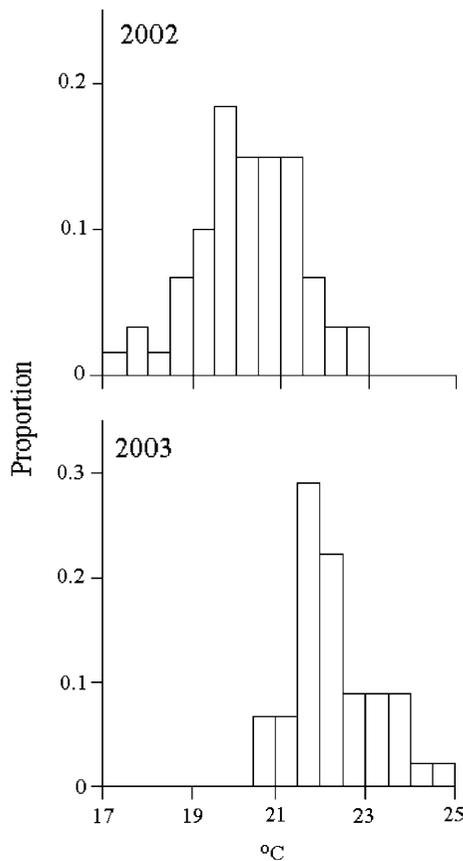


Fig. 3 Frequency of occurrence of water temperatures measured at steelhead focal points in Topanga Creek during the summers of 2002 ($n=60$) and 2003 ($n=43$) (cf. Table 1 for temperature preference and tolerance information on *Oncorhynchus mykiss*)

Unit-specific mean T_a was positively related to time ($R^2=0.7$, $p<0.0005$) with intercepts and slopes not depending on habitat type (both $p\geq 0.7$). The average difference between the mean (± 1 SE) T_a in pools ($21.3\pm 0.5^\circ\text{C}$) and non-pools ($21.3\pm 0.6^\circ\text{C}$) did not differ from zero ($t=0.6$, $df=15$, $p=0.6$).

Mean (± 1 SE) % time foraging and roaming did not differ between morning (foraging: $24.6\pm 10.2\%$; roaming: $15.8\pm 4.5\%$) and afternoon ($27.2\pm 9.1\%$; $31.7\pm 9.3\%$) (both $t\leq 1.6$, $df=27$, $p\geq 0.13$). Steelhead engaged in stationary behavior and agonistic bouts at similar average rates during the morning (stationary: $58.7\pm 9.8\%$; agonistic: $1.0\pm 0.5\%$) and afternoon ($39.7\pm 9.2\%$; $1.5\pm 0.7\%$) (both $t\leq 1.4$, $df=27$, $p\geq 0.17$). No trend was detected in the plots of % time budget for each behavior against time of day (Fig. 4). On average, steelhead spent a similar amount of time in filtered sunlight and shade between the morning (filtered: $20.0\pm 8.3\%$; shade: $61.5\pm 11.4\%$) and afternoon ($6.8\pm 2.6\%$; $47.3\pm 10.9\%$) (both $t\leq 1.5$, $df=27$, $p\geq 0.2$). The average amount of time steelhead spent in full sun was not different between the afternoon ($45.9\pm 10.2\%$) and morning ($18.5\pm 8.9\%$) ($t=2.0$, $df=27$, $p=0.053$).

Steelhead did not have the option of exploiting areas of cold water. Individual minimum and maximum values of T_b and T_a were identical, ranging from 18.7 to 24.5°C (Fig. 5). While the mean difference between grand means (± 1 SE) of

Table 3 Maximum temperatures (Max), highest averaged 7-day daily maximum temperature (M_{max}), highest averaged 7-day daily mean temperatures (Mean t), number of days and average duration (h day⁻¹) when water temperature was $\geq 24^\circ\text{C}$ and the maximum diel temperature fluctuation (Δt) documented at upstream (u) and downstream (d) monitoring stations in three streams during the summers of 2002 and 2003

	Year	Station	Max	M_{max}	Mean t ($^\circ\text{C}$)	Number of days $\geq 24^\circ\text{C}$	Hours $\geq 24^\circ\text{C}^a$	Δt ($^\circ\text{C}$)
Topanga Ck	2003	u	25.1	24.4	22.0	18	2.4 (4.4)	5.3
		d	25.7	24.5	21.9	38	2.7 (6.4)	6.8
	2002	u	23.2	22.7	20.6	0	0	4.3
		d	25.4	24.6	21.0	29	2.3 (4.4)	7.9
Solstice Ck	2003	u	21.1	20.4	19.3	0	0	4.0
		d	21.1	20.5	19.3	0	0	4.5
	2002	u	21.1	20.2	18.7	0	0	4.3
		d	19.5	18.8	17.4	0	0	4.0
Arroyo Sequit	2003	u	21.2	20.7	18.2	0	0	5.0
		d	22.9	22.2	19.5	0	0	6.3
	2002	u	23.5	22.2	19.2	0	0	5.8
		d	24.9	23.8	20.0	9	1.8 (2.8)	8.5

^a Maximum is given in parenthesis

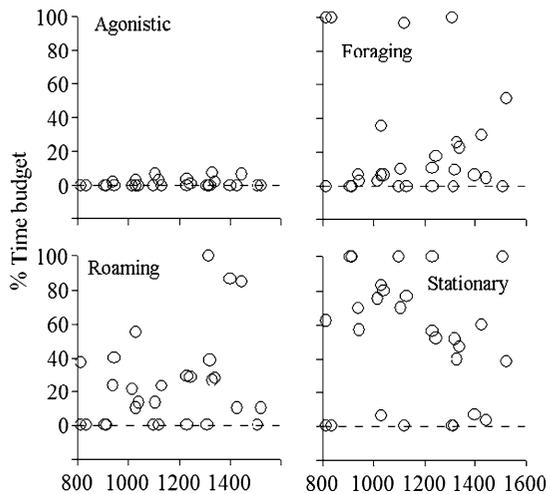


Fig. 4 Relationship between unit-specific % time budget and time of day for steelhead agonistic ($r=0.18$, $p>0.5$), foraging ($r=-0.04$, $p>0.5$), roaming ($r=0.27$, $0.1 < p < 0.2$) and stationary ($r=-0.17$, $p>0.5$) behaviors observed at Topanga Creek on 16, 19, 20, and 22 July 2004 ($n=29$ for each behavior type). Because discrete habitats (e.g., pools) are treated as the statistical unit (rather than individual steelhead), an individual circle represents the average % behavioral time budget of steelhead for a particular habitat

T_b ($21.5 \pm 0.3^\circ\text{C}$) and T_a ($21.7 \pm 0.3^\circ\text{C}$) differed from zero ($t=2.1$, $df=16$, $p=0.047$), the mean difference was slight (0.2°C). Unit-specific mean T_b increased as T_a increased ($r^2=0.9$, $p < 0.0005$), both of which were consistently elevated throughout the day (Fig. 6).

Opportunities for juvenile steelhead to achieve a certain body temperature did not differ between occupied and adjacent unoccupied pools. The magnitude of individual T_a in occupied and unoccupied pools showed considerable overlap (Fig. 7). The mean difference in the unit-specific mean T_a between occupied (21.9°C) and unoccupied (21.8°C) pools did not differ from zero ($t=0.3$, $df=9$, $p=0.7$). None of the sample unit characteristics considered in the logistic-regression model predicted steelhead presence (Table 4).

Discussion

The findings are in large not consistent with those of other investigators reporting on the habitat use and behavior of salmonids experiencing elevated

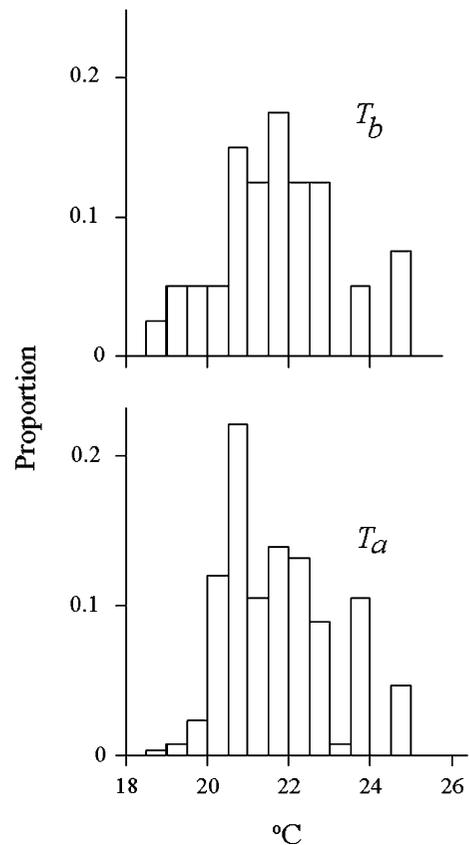


Fig. 5 Proportional frequency of occurrence of individual T_b ($n=54$) and T_a ($n=338$) in pools of Topanga Creek measured during surveys conducted on 23, 26, and 27 July 2004

temperatures in nature. In a study on a single southern California stream pool, *O. mykiss* generally avoided microsites where water temperatures were greater than 20.3°C (Matthews and Berg 1997), which is in contrast to steelhead in Topanga Creek, which showed a T_b frequently exceeding 20°C . Findings noted for steelhead in northern California streams generally indicate changes in behavioral activity and habitat use at elevated temperatures ($>22^\circ\text{C}$) (Nielsen et al. 1994), although juveniles have been observed feeding in surface water of 24°C . Observations of *O. mykiss* in Oregon streams indicated that individuals moved into areas of cool water when ambient temperature ranged from 18 to 25°C (Ebersole et al. 2001).

The fact that the present findings differ in some ways from those of earlier investigations may be

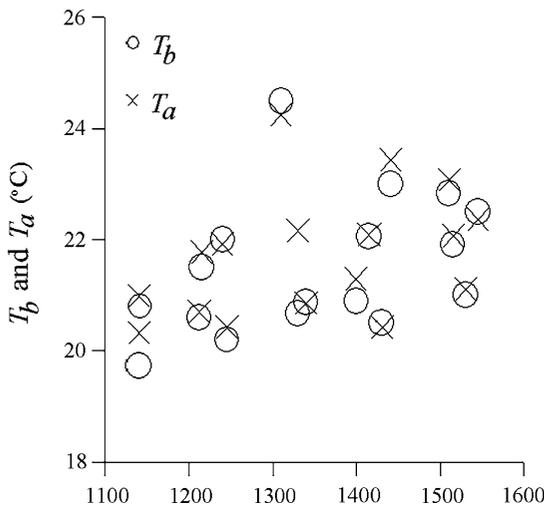


Fig. 6 Pool-specific means ($n=17$) of T_b and T_a measured during surveys conducted on 23, 26, and 27 July 2004 in Topanga Creek. Pool pairs of T_b and T_a are arranged vertically according to the time of measurement

related, in part, to the recent thermal history of the fish considered and the characteristics of the thermal environment. Two of the previous studies included measurements on ‘summer-run’ adult steelhead (Nielsen et al. 1994) or large individuals that were likely adults (Matthews and Berg 1997). Steelhead that recently migrate into a stream after a relatively long stay in the ocean might exhibit different temperature preferences or heat tolerances than juveniles that have been reared in the stream. While the populations of *O. mykiss* considered in the previous studies had the option of exploiting areas of cold water, the findings for Topanga Creek indicate that the opportunities for juvenile steelhead to achieve a particular body temperature (T_a) did not differ between occupied and unoccupied pools (and non-pools).

Whether the lack of detectable behavioral thermoregulation in Topanga Creek steelhead is related to the cost of adopting such behavior, or to the absence of cold water, is unclear. Steelhead were active over a broad range of T_b and showed evidence of conforming to T_a , which appears to be consistent with cost-benefit expectations for individuals living in a thermally taxing environment (Huey and Slatkin 1976). However, water temperatures appeared to be spatially homogenous, and steelhead did not seem to have the option of exploiting areas of cold water during the day.

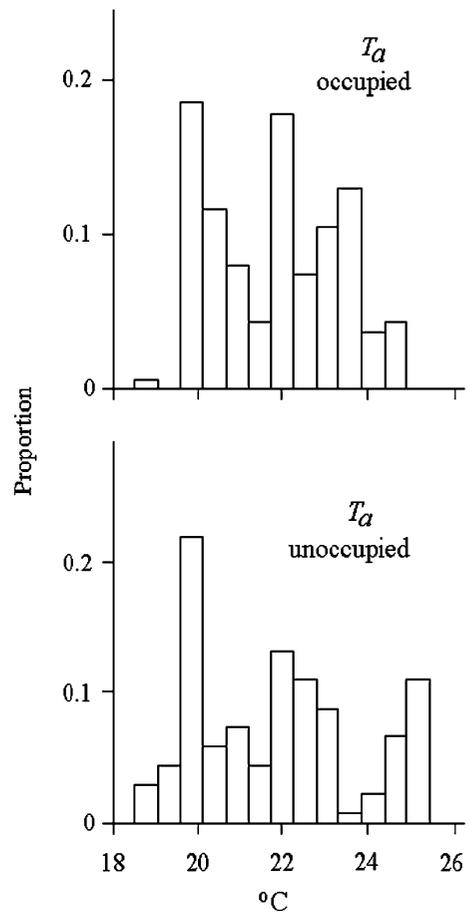


Fig. 7 Proportional frequency of occurrence of T_a in occupied ($n=162$) and unoccupied ($n=137$) pools of Topanga Creek during surveys conducted on 28 July and 2, 3, and 4 August 2004. Minimum and maximum values ranged from 18.7 to 24.7°C (T_a occupied pools), and 18.7 to 25.4°C (T_a unoccupied pools)

The thermal environment may require steelhead to accept a higher body temperature as T_a increased, and either remain active into the afternoon or become inactive. Perhaps the temperatures steelhead experienced during the field studies were not sufficiently high to prompt behavioral adjustments.

Although the thermal environment does not appear to be ecologically problematic for juvenile steelhead, temperature has physiological implications. Optimal growth of *O. mykiss* in the laboratory varies among investigations but is often reported to be between 14 and 19°C (e.g., Hokanson et al. 1977), whereas T_b of steelhead in Topanga Creek often exceeded 20°C and approached 25°C. The distribution of T_a

Table 4 Means (range) and results of binary logistic regression on characteristics of occupied and unoccupied pools in the study reach of Topanga Creek, July and August 2004

Creek characteristics ^a	Occupied	Unoccupied	Odds ratio	Upper and lower (95%) limits	<i>p</i>
Maximum depth (cm)	86.8 (47.0–135.0)	60.3 (25.0–81.0)	1.05	1.11–0.99	0.08
Unit orientation ^b	15.5 (1–45)	16.7 (0–42)	0.97	1.07–0.88	0.6
Riparian canopy ^b	0.3 (0–0.9)	0.4 (0–1)	5.99	312–0.12	0.4
Maximum temp (°C)	22.6 (21.6–24.5)	23.1 (21.3–24.9)	0.88	32.69–0.02	0.9
7-day max temp (°C)	21.9 (21.2–23.7)	22.2 (21.0–23.7)	0.72	43.88–0.01	0.9

^a The degrees of freedom = 9 except for temperature variables (*df*=8) due to a malfunctioning temperature-data logger

^b Response variables for unit orientation and riparian canopy are compass bearing of the thalweg and fractional proportion of riparian canopy over sample unit

throughout the creek indicated few daytime opportunities for steelhead to achieve T_b that are considered optimal, although such temperatures exist during the night and morning. In the laboratory, *O. mykiss* can experience reduced food intake and growth at elevated temperatures, with the greatest reductions observed at 22–25°C (Myrick and Cech 2000), but increased feeding may compensate for the sometimes negative influence of high temperatures on steelhead growth (Wurtsbaugh and Davis 1977). In Topanga Creek, the rates of feeding in juvenile steelhead did not differ between the morning and afternoon, and were unrelated to time of day (i.e., over the range of hours considered).

The present findings provide a clue that steelhead in southern California streams might possess the thermal preferences and tolerances of fish acclimated to higher temperatures. Steelhead in southern California experience elevated temperatures, and exposure to elevated temperatures can impart a higher temperature preference and heat tolerance (Cherry et al. 1977; Threader and Houston 1983; Hawkins 1996). Studies conducted on California strains of *O. mykiss* report thermal tolerances (27.6–32.0°C) that exceed tolerances reported for other strains (Myrick and Cech 2000; Myrick and Cech 2004). In the present study, temperatures at steelhead focal points were higher than reported preferred and lethal temperatures, including those based on high acclimation. The lower preferred temperatures reported for the species appeared to be unavailable.

While steelhead are exposed to temperatures to be considered lethal, the duration of the exposure is short-lived, a feature believed to be critical for salmonids to survive elevated

temperatures. In nature, fluvial Arctic grayling, *Thymallus arcticus*, living at the extreme southern extent of their historical geographic distribution can experience temperatures exceeding their upper incipient lethal temperature (25.0°C), but the exposure is infrequent and brief (Lohr et al. 1996). In the laboratory, cutthroat trout, *O. clarki*, did not die when experiencing a 7-day daily temperature cycle of 20–26°C, even though chronic exposure to 26°C resulted in mortality (Dickerson and Vinyard 1999). Johnstone and Rahel (2003) observed no mortality of cutthroat trout experiencing a 7-day daily temperature cycle of 16–26°C despite a daily 6-h exposure to temperature exceeding the upper incipient lethal limit (24.2°C).

The factors enabling juvenile steelhead to tolerate the local thermal environment are not known, but they might involve acclimatization, diel temperature fluctuations or natural selection for certain enzymes that promote heat tolerance. While the findings give a hint that juvenile steelhead might be adapted to the temperatures, evolutionary hypotheses regarding acclimatization (including research on the physiological consequences of the temperatures for the local steelhead genotype) require testing before conclusions can be made in this regard. Overwintering juvenile steelhead accept an elevated body temperature and remain active and forage throughout the day, apparently as a means for coping with warm water at the southern extent of their geographic range. The relatively high body temperatures that steelhead accept appear to represent a compromise in exchange for maintaining an expanded geographic (latitudinal) range.

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