Environ Biol Fish (2014) 97:865–873
DOI 10.1007/s10641-013-0185-8

Temperature preferences of hardhead *Mylopharodon conocephalus* and rainbow trout *Oncorhynchus mykiss* in an annular chamber

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Received: 27 February 2013 / Accepted: 23 September 2013 / Published online: 10 October 2013

Abstract To optimize habitat characteristics when managing resident and migratory stream fish populations in regulated systems, it is important to know a species' preferred temperatures. However, temperature-preference devices used in many laboratory studies often have design limitations (e.g., confounding variables such as differential light intensities or water depths, or perceived cover) limiting their usefulness. To overcome these design limitations, we constructed a 3-m-diameter, annular preference apparatus made of clear, acrylic plastic capable of presenting uniform light intensities, constant water depths and velocities, and stable vertical and horizontal temperature gradients for experimental fish. We determined preferred temperatures of hardhead *Mylopharodon conocephalus* (mean TL: 36.2 cm) and rainbow trout *Oncorhynchus mykiss* (mean TL: 35.4 cm) acclimated to 12, 15, and 18 °C and tested, individually, in the 12–24 °C annular gradient. All hardhead acclimation groups avoided waters <17 °C, whereas trout acclimated to 12 and 15 °C consistently avoided water >19 °C, and 18 °C acclimated trout avoided water temperatures <16 °C and >20 °C. Including all acclimation temperature groups, mean hardhead preferred water temperatures ranged from 19.6 °C to 21.0 °C (mean modal preferences were 20.2–21.5 °C), whereas trout preferred significantly cooler average water temperatures ranging from 16.0 °C to 18.4 °C (mean modal preferences were 15.8–18.5 °C). These temperature preference data can be used to guide regulation of stream systems for key fish species.

Keywords Hardhead · *Mylopharodon conocephalus* · Rainbow trout · *Oncorhynchus mykiss* · California streams · Temperature preference

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Introduction

In the South Fork of the American River (California), native fish and hydroelectric power regeneration dams occur together frequently, and these hydropower operations may have adverse or beneficial effects on resident and migratory fishes (reviewed in Young et al. 2011). Water temperatures in this watershed are influenced by headwater temperatures, seasonal flows, solar radiation (including influences of riparian cover), inputs from tributary streams and springs, air temperatures, and frequent anthropogenic water releases. These releases for power generation or white-water recreation frequently consist of cooler water from reservoirs during late-summer months (Young et al. 2011). Typical water releases have a base flow, a ramping stage, a peak stage, and a decreasing return to base stage (Cocherell et al. 2011;

Thompson et al. 2011). These staged releases often occur over the course of a day (5–10 h), involve releases of water that vary in magnitude from few $m^3 s^{-1}$ to over 120 $m^3 s^{-1}$ and may result in daily temperature excursions in excess of 3 °C (PGE 2005). There are no long-term temperature records for the South Fork of the American River, but we have observed seasonal temperatures ranging from 6 to 24 °C, and diurnal fluctuations of 8 °C during hydropower generation. Thus, these flows may introduce spatial and temporal water-temperature variation downstream that may affect habitat use and seasonal home ranges of native fishes.

The life histories of stream fishes in California's Sierra Nevada streams and rivers are influenced by multiple biotic and abiotic factors, and the rapid temperature changes brought about by staged water releases are of general concern. Moyle and Nichols (1973) and Moyle (2002) described elevation-related zones of different environmental properties and characteristic assemblages of native fishes. The effects of temperature and dissolved oxygen, two properties that structure fish communities in this region, have been studied (Cech et al. 1990). These authors measured the oxygen consumption (i.e., energy turnover or metabolic) rate responses to several temperatures and two dissolved oxygen levels in seven species. Myrick and Cech (2000) also described the physiological responses of two rainbow trout strains *Oncorhynchus mykiss* (Salmonidae) to a range of temperatures. Their data showed growth and metabolic homeostasis at optimal temperatures (14–19 °C), decreased growth and food-conversion rates at sub-optimal ones (<14 °C and >19 °C), and decreased survival at extremely warm (uninhabitable) temperatures of 25 °C. While these studies of physiological performance and limits have value in describing boundaries and thermal optima for fish distributions, they do not consider biotic variables such as predation, competition, and parasitism or the behavior of the fish in question (Cech et al. 1990). However, Jobling's review of thermal preference studies (1981) showed that when presented with a temperature gradient, fishes tend to select temperatures that are optimal for their growth. Further, Coutant (1987) predicted decreased survival for species in thermally degraded and altered waters. Thus, in managing and restoring stream fish communities, the temperature preferences of fishes should be considered, along with their physiological thermal limits.

Our model fishes, hardhead *Mylopharodon conocephalus* (Cyprindae) and rainbow trout, are both native species of interest found in many California streams. Hardhead are omnivores, occasionally reaching 1 m in length, and are typically found in deep clear pools and in runs with sand-gravel-boulder substrates in streams and rivers (Moyle 2002). However, hardhead populations may be declining throughout much of their range (Moyle 2002; Gard 2004), and thus are listed as a species of special concern by the California Department of Fish and Wildlife and the U.S. Forest Service. Rainbow trout are sympatric with hardhead in the American River watershed, typically found in cooler, waters (Cooper 1983), and are sought widely as game fish. To meet this angling demand, trout are reared in large numbers and regularly stocked by State-operated hatcheries.

The objective of this study was to determine the thermal preferences of hardhead minnow and rainbow trout. These fishes differ in their distributions in California watersheds (Moyle 2002), and we hypothesized that hardhead, which occupy lower elevations, would have warmer preferred temperatures than those of rainbow trout occupying higher elevations, with a narrow overlap of preferred temperatures. We conducted these studies using an annular thermal preference chamber, first conceived by Myrick et al. (2004). Our quantitative temperature preference data add to the relatively limited information regarding thermal influences on California native stream fishes in managed systems, particularly for the poorly-studied hardhead minnow. These data should aid resource managers in planning reservoir water releases that optimize favorable fish-habitat characteristics.

Methods

Fish collection and care

Hardhead were captured from April to June 2006 using rod and reel angling, in a 10-m-deep pool at the head of Slab Creek Reservoir, South Fork American River, California (El Dorado County). Fish were held in large, aerated ice-chests of river water and water temperatures were kept constant with additions of fresh river water throughout the day and prior to the ca. 2-h vehicular transport to the University of California, Davis' Center for Aquatic Biology and Aquaculture (CABA). At CABA fish were transferred to an aerated, 555-l tank held at 12 °C, with continuous flows of well water with a conductivity 670 μS cm^{-1}, level of dissolved oxygen >7.0 mg/l, and a pH of 8.1 until experimental acclimations. Our sample size (n=22) was limited by the allowable take of this species of special concern.

Forty one rainbow trout were obtained in April 2006 from the American River Hatchery of the California Department of Fish and Wildlife, where they were held at 11 °C. The trout were transported in a large, air-equilibrated aluminum transport tank to CABA and separated into two aerated 555-l tanks kept at 12 °C with continuous flows of well water, described above, until they were acclimated for the experiments. Wild fish were not used, due to frequent hatchery-sourced fish stockings in the South Fork of the American River.

Upon arrival at CABA both hardhead and trout were treated prophylactically with nitrofurazone at 10 g/l for 45 min, daily, over 10 days, to prevent bacterial infections associated with handling and transport. Hardhead were treated for ectoparasites with Chloramine-T (200 ppm) in a 4-h static bath three times from 4 May to 10 July 2006 and once for tapeworms with a 37 % formaldehyde solution at 200 ppm for 1 h. Hardhead and rainbow trout were trained to feed on commercial Silvercup™ salmonid feed and fed ad libitum daily.

Experimental apparatus

The temperature-preference apparatus was constructed of clear acrylic plastic and featured three concentric and perforated circular walls separating the receiving/mixing chambers, the swimming chamber, and the effluent chambers all within the 3-m-diameter, solid outer 1st wall (Fig. 1). The apparatus' base and sub frame was acrylic (3.05 m×3.05 m by 2 cm thick), blacked out with externally applied window tinting and mounted on a painted steel frame with large, leveling feet to prevent any chamber movements or vibration during experiments. Gräns et al. (2010) provides a brief description of a version of this apparatus. The area between the outermost two walls was divided into eight adjoining chambers for receiving and mixing the incoming water. Water was distributed to the receiving-mixing chambers via PVC manifolds and ball valves from 16, constant-head 17-l reservoirs containing either cooled (11.5 °C), ambient (18 °C), or warm (24 °C) water. The cool water was produced using two 15-horsepower chillers; the warm water was produced using two Mobius (model: T-M1 Takagi) on-demand tankless gas boilers. The heated well water was directed to two gas-equilibration columns, which prevented gas supersaturation, prior to its distribution into the receiving-mixing chambers. Both the chilled and heated water temperatures were controlled by motorized ball valves (Honeywell model: ML7984), controlled by a digital controller (Omrom model: E5AK). This system supplied ambient water to the ball valves to dampen temperature oscillations. The 30-cm-wide swimming channel, between the 2nd and 3rd outer-most walls, presented a large un-obstructed radial path for the fish and was kept at a constant 15.2-cm water depth. Temperature was measured at 64 positions, 48 of which were calibrated thermistors (YSI 400-series, accuracy ±0.1 °C) coupled to several YSI Telethermometers (model 46 TUC), and 16 calibrated digital thermometers (Fisher Traceable). The probes were positioned symmetrically around the inner (32 probes) and outer (32 probes) surfaces of the swimming channel at mid-water depth, and the temperature of each inside and outside probe pair was averaged to give a temperature for each of 32 positions. Temperature differences between probe pairs were always less than 0.1 °C. The annular thermal preference chamber was able to maintain a repeatable 12 °C thermal gradient, from 12 °C to 24 °C, verified on three separate experimental days (Fig. 2), and chamber temperatures during each fish experiment were manually taken. The radially inward-flowing water from the receiving-mixing chambers produced a negligible cross-swimming-channel velocity of 0.05 m/s (Marsh-McBirney model 201D current meter, ±0.02 m/s detection limit). As the water left the swimming channel, it passed into eight effluent chambers, directing it to the apparatus' center drain.

Experimental design

Due to limited fish numbers, the same hardhead were used for the 12, 15, and 18 °C acclimation groups. The hardhead were kept at 12 °C (field collection temperature) for 5 months before experimentation, during which they were trained to feed and prophylactically treated for infection and parasites as described above. Thermal preference experiments were performed on 12 °C-acclimated hardhead, before subsequent acclimations to 15 °C for 22 days, and 18 °C for 17 days. Because hardhead numbers were limited and their health and tolerance to warm acclimation temperatures was unknown, we did not randomize thermal acclimations. Rainbow trout were held for 4 months at 12 °C (hatchery temperature) before experimentation. Trout were not reused and were

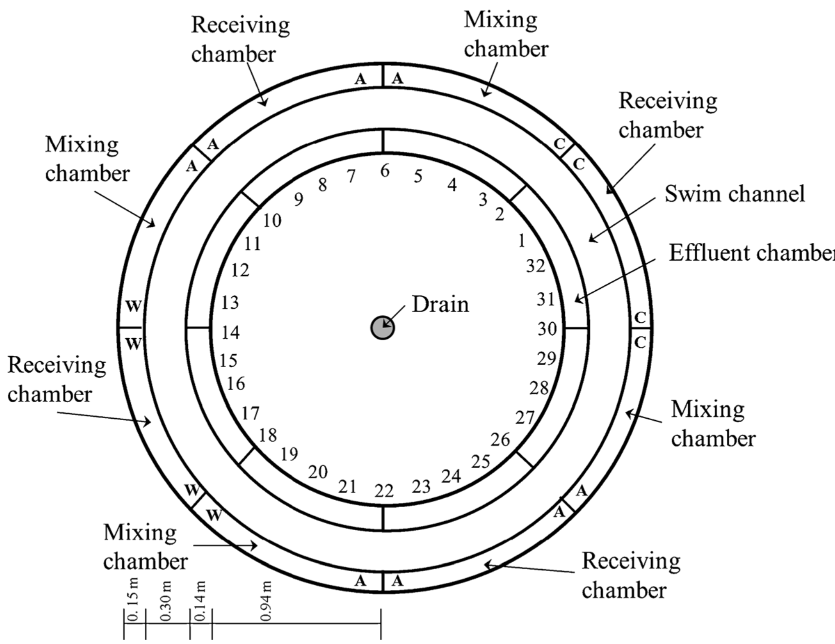

Fig. 1 Temperature-preference apparatus (overhead view) showing water (A = ambient (18 °C), C = cool (11.5 °C), and W = warm (24 °C)) flowing into each of the four receiving and four mixing chambers before moving through the perforated walls and into the concentric swimming channel, then to the effluent chambers and to the drain. The 32 temperature-measurement positions are shown, each encompassing an 11.5° arc of the apparatus' swimming-channel circle

separated into three acclimation groups: 12, 15, and 18 °C. The 15 °C fish were held for 15 days, and the 18 °C fish for 17 days before initiating experiments. The order of thermal preference experiments in trout was randomized. Acclimation temperatures were adjusted by no more than 0.5 °C d^{-1}, and variation in the temperature of acclimation never exceeded 1 °C d^{-1} for either species and was often only a 0.1–0.2 °C d^{-1}. Fish mean total length (cm), mass (g), and n values are presented in Table 1.

The perimeter of the apparatus was surrounded by a 2.5-m-tall shade-cloth curtain, to diffuse the natural light from the building's translucent roof panels. A remote camera, coupled to a video monitor, was positioned overhead to observe the fish's position. Thirty-two areas, each encompassing an 11.25° arc of the swimming channel, were denoted by labels visible on the video monitor. During each daytime experiment an individual fish was released into the apparatus at one of four randomly selected locations, with the entire apparatus' temperature stabilized at the fish's acclimation temperature. After 20-min of acclimation, cooled, ambient, and warm water were supplied to the relevant receiving-mixing chambers for the 1-h experiment. The swimming channel's temperature gradient typically stabilized in <5 min. During the 1-h experimental period, fish snout location and the corresponding temperature were recorded every 2 min. Fish could easily swim around the entire swimming channel in <15 s, minimizing possible space and time autocorrelations. The number of fish per species and acclimation group used in thermal preference experiments ranged from 12 to 14 with variation due to equipment malfunction and fish jumping from the annular flume or out of acclimation tanks.

Statistical analysis

We calculated the mean temperature occupied by each fish over the entire experiment and used these preferred

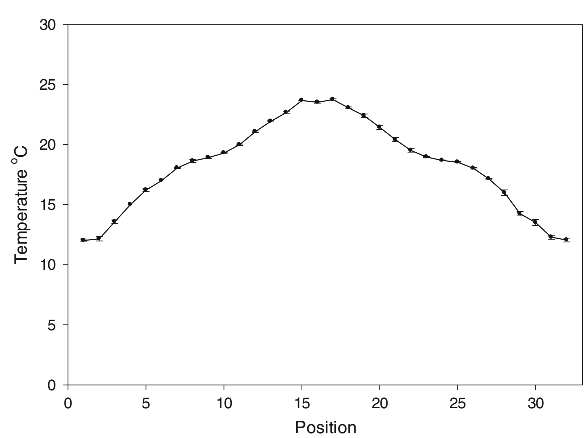

Fig. 2 Water temperatures (n=3 replicates; mean ± SE) monitored at 32 positions of the swimming chamber during non-organism tests. Positions refer to those shown in Fig. 1

Table 1 Mean (± SE) and modal (± SE) hardhead and rainbow trout preferred temperatures (°C) for each temperature-acclimation group

		Acclimation Temperature (°C)		
		12	15	18
Hardhead	Mean	20.0^{a,*} (±0.17)	21.0^{a,*} (±0.15)	19.6^{a} (±0.18)
	Mode	20.2^{a,*} (±0.91)	21.5^{a,*} (±0.73)	20.2^{a} (±0.99)
	n	13	13	12
	Total length (cm)	36.2 (±1.2)	35.9 (±1.0)	36.8 (±1.0)
	Mass (g)	528.8 (±42.3)	500.4 (±39.6)	548.3 (±39.8)
Rainbow trout	Mean	16.0^{a} (±0.12)	16.2^{a} (±0.14)	18.4^{b} (±0.10)
	Mode	15.8^{a} (±0.61)	15.9^{a} (±0.77)	18.5^{b} (±0.26)
	n	14	12	14
	Total length (cm)	34.7 (±0.7)	37.1 (±0.8)	34.6 (±0.8)
	Mass (g)	568.0 (±45.5)	644.2 (±44.6)	555.4 (±41.8)

Different superscript letters represent significantly different preferred temperatures between acclimation groups within fish species. An asterisk (*) indicates a significant difference in preferred temperature between species within an acclimation group (indicated on the hardhead data). Fish mean total length (± SE), mass (± SE), and n values are also presented

temperatures to compute the mean selected temperature for each species/acclimation group. We also determined modal preferred temperature of each fish (rounded to the nearest 0.5 °C) and calculated the mean modal temperature for each species/acclimation group (Fangue et al. 2009). Descriptive statistics and ANOVA on preferred temperatures between species and among acclimation groups were performed using Sigmastat 3.0™ software, Holm-Sidak post-hoc test. All data met the assumptions of normality and homogeneity of variance. Statistical significance was considered at α=0.05.

Results

Overall, there were significant differences in mean thermal preferences between species ($F_{1,75}$=67.65, P<0.001), and in response to thermal acclimation ($F_{2,75}$=2.26, P=0.112) with a significant interaction ($F_{2,75}$=7.13, P=0.001) (Table 1). Mean modal preferred temperatures showed the same patterns with a significant effect of species ($F_{1,75}$=53.20, P<0.001), thermal acclimation ($F_{2,75}$=2.05, P=0.136) and a significant interaction ($F_{2,75}$=5.80, P=0.005) Hardhead consistently avoided cool water <17 °C, and in the 12 and 15 °C acclimation groups rainbow trout preferred significantly cooler temperatures than did hardhead (p<0.001 for all comparisons). Hardhead were often observed milling and sitting on the bottom in the warmest sections of the annulus, while their movements through the coldest sections were relatively quick. The occupancy of hardhead in the warmer areas of the annular flume is apparent from the longer bars distributed at the bottom of the circular histograms in warmer water and the shorter bars at the top where annulus water

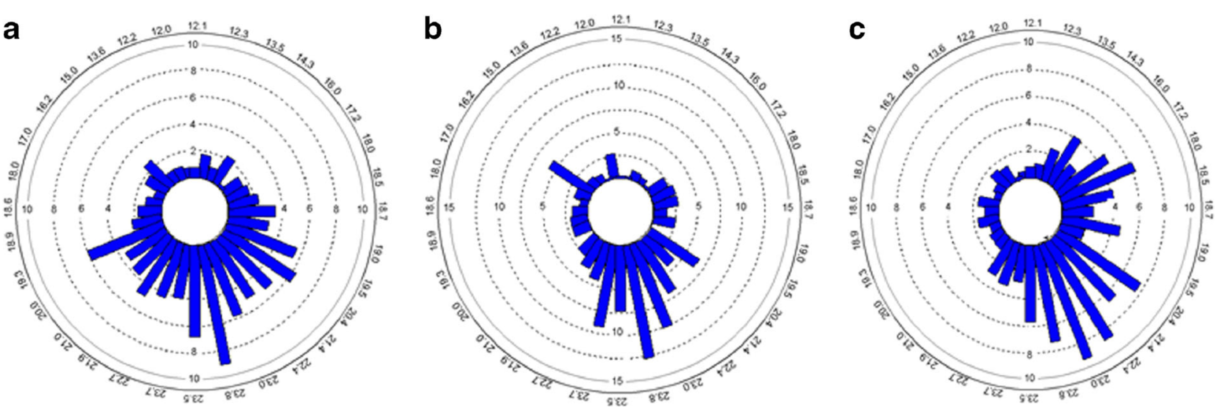

Fig. 3 The frequency of occurrence at selected temperatures of hardhead acclimated to 12 °C (**a**, n=13), 15 °C (**b**, n=13), and 18 °C (**c**, n=12) during the 1-h experiment. Temperatures are approximate for location, based on data shown in Fig. 2

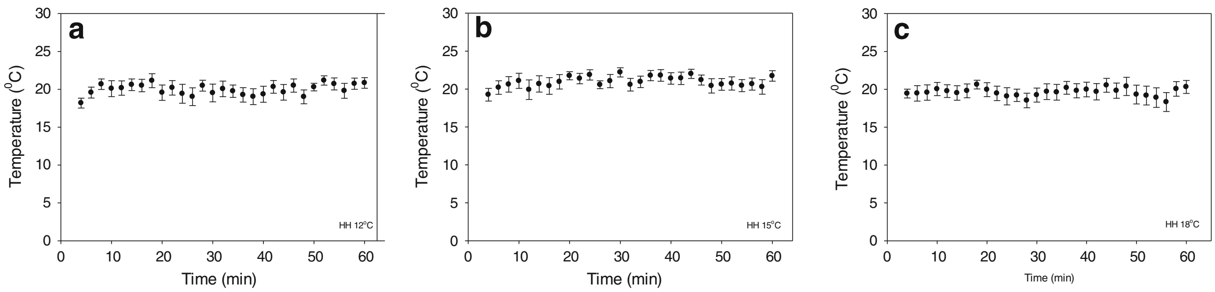

Fig. 4 Mean (±SE) selected water temperature of adult hardhead in a ca. 12–24 °C annular gradient apparatus at 2 min intervals over a 1-h experimental period. Hardhead were sequentially acclimated to one of three temperature groups: 12 (**a**, n=13), 15 (**b**, n=13), and 18 °C (**c**, n=12) before thermal preference experiments

temperatures were cool (Fig. 3). Mean preferred temperatures of hardhead did not differ between acclimation groups (p>0.202 for all comparisons), and similar to mean preferred temperatures, modal preferred temperatures ranged from 20.2 °C to 21.5 °C and did not differ with thermal acclimation (p>0.389 for all comparisons) (Table 1). Figure 4 shows the mean selected temperatures of each hardhead acclimation group at 2 min intervals during the 1-h experiment. Regardless of acclimation temperature, hardhead quickly (within the first 6 min of the experiment) and consistently selected temperatures very close to their preferred temperature of ca. 20–21 °C over the 1-h experiment.

Rainbow trout preferred cooler temperatures than did hardhead, except in 18 °C acclimated fish where mean and modal preferences were similar between species (p=0.090, p=0.094, respectively), and this is apparent from the general clustering of the bars toward the top of the circular diagram, (cooler water, Fig. 5). In the case of rainbow trout, the use of the annular thermal preference flume revealed several important insights. Rainbow trout acclimated to 18 °C had thermal preference peaks corresponding to 18.5 and 18.9 °C (Fig. 5c). These fish displayed an obvious diametrically bimodal frequency distribution (axial) of preferred temperatures reflecting the two zones of (preferred) ambient (18 °C) water available on opposite sides of the apparatus. The 18 °C acclimated rainbow trout preferred significantly warmer temperatures than did the 12 °C and 15 °C acclimated trout (p<0.013 for all comparisons) (Table 1; Fig. 5a-c). In trout acclimated to 12 °C and 15 °C, the modes (longest bars) of the curved distribution peaked at 15.0 °C and 17.2 °C, indicating an avoidance of both lower and higher water temperatures (Fig. 5a, b). These trout actively avoided water >19 °C, by either abruptly reversing direction or bursting through the warmest section of the flume. While trout acclimated to 12 °C and 15 °C had very similar mean and modal thermal preferences, there were subtle differences in their distribution in the

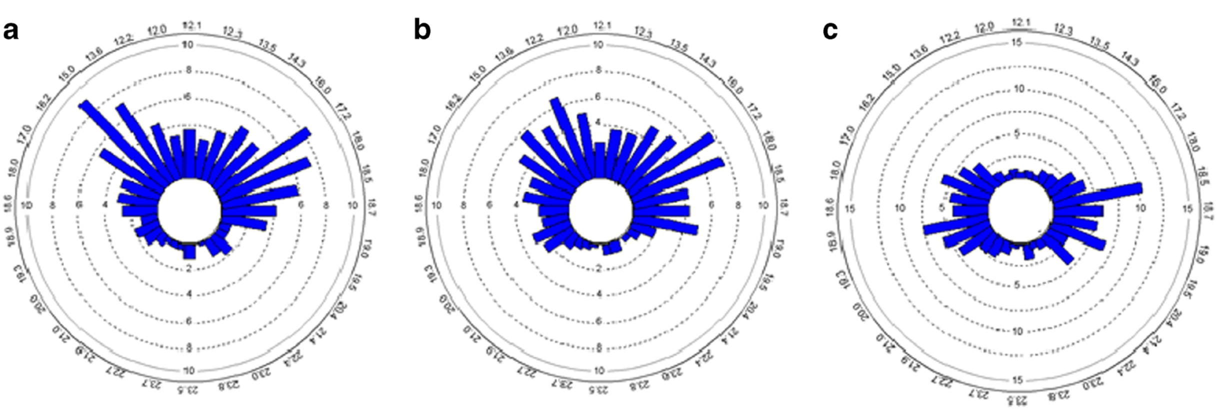

Fig. 5 The frequency of occurrence at selected temperatures of rainbow trout acclimated to 12 °C (**a**, n=14), 15 °C (**b**, n=12), and 18 °C (**c**, n=14) during the 1-h experiment. Temperatures are approximate for location, based on Fig. 2

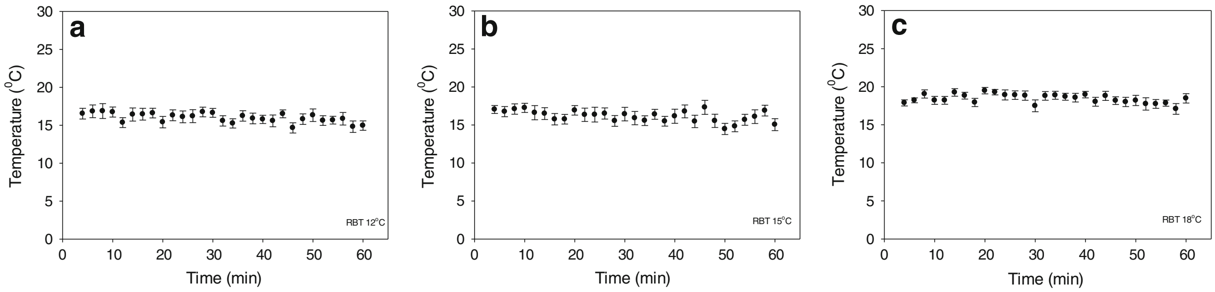

Fig. 6 Mean (±SE) selected water temperature of adult rainbow trout in a ca. 12–24 °C annular gradient apparatus at 2 min intervals over a 1-h experimental period. Trout were acclimated to one of three temperature groups: 12 (**a**, n=14), 15 (**b**, n=12), and 18 °C (**c**, n=14) before thermal preference experiments

flume. 12 °C acclimated fish showed two approximate peaks, one at 15 °C and one at 17.2 °C. In 15 °C acclimated fish, rather than distinct peaks, there are two clusters encompassing temperatures of ca. 12–16 °C and 13–18 °C. Similar to the pattern seen in hardhead, rainbow trout also quickly selected their preferred temperatures (Fig. 6).

Discussion

Mean and modal temperatures selected by adult hardhead were within a rather narrow range of 19.6–21.5 °C and were not correlated with acclimation temperature. The distribution of selected temperatures in Fig. 3 indicates that the hardhead's temperature preference was actually broader than the narrow range of means might imply. Baltz et al. (1987) observed, in the Pit River watershed, hardhead adults primarily in water ranging from 16.6 to 20.2 °C, which were similar temperatures to those found in our laboratory tests. In contrast, Knight (1985) found a positive relationship between acclimation temperature and mean preferred temperature range of 15.3–28.6 °C for juveniles <100 mm TL using a wider acclimation temperature range (10–30 °C, Table 2). This temperature range was somewhat similar to the 15–28 °C water where hardhead were found along the western edge of California's Sierra Nevada Range during the summer. The juveniles' smaller body sizes may restrict their distributions to shallower habitats characterized by greater temperature extremes. Adult hardhead would be less vulnerable to aquatic predators such as pike minnows and bass (Moyle 2002), and the preferred, warm temperatures are probably associated with faster growth and gametic development rates (Jobling 1994). The lack of a positive relationship between acclimation temperature and mean preferred temperature in our hardhead could have been confounded by repeated exposures to the chamber. The shorter acclimation times for the 15 and 18 °C hardhead and trout, however, exceeded the 2-week acclimation period of rainbow trout used by McMahon et al. (2008) in their temperature-preference experiments.

Other factors, besides their temperature preferences, may influence hardhead distribution in the South Fork of the American River. For example, we readily captured hardhead in 8 °C water, ca. 12 °C cooler than their preferred temperature in our laboratory. Previous field studies found very few hardhead in the warmer, lower reach of the South Fork below Chili Bar Dam (Klimley et al. 2006). This distributional pattern may have resulted from the hardheads' competition with non-native fish, disease, or river management practices

Table 2 Laboratory-derived mean (± SE) temperature preferences for adult (present study) and juvenile (Knight 1985) hardhead

Life stage	Acclimation temperature (°C)						
	10	12	15	18	20	25	30
Juvenile	15.26 (±0.96)	–	19.27 (±2.35)	–	24 (±1.96)	26.28 (±0.98)	28.63 (±0.45)
Adult	–	20 (±0.17)	21 (±0.15)	19.6 (±0.18)	–	–	–

(Moyle 2002). For example, Gard (2004) found that non-native smallmouth bass *Micropterus dolomieu* limited the abundance of their prey, native cyprinids, in the South Yuba River.

In our experiments, rainbow trout preferred cool water, which typifies many fast-moving stream and river sections in California. Schurmann et al. (1991) and Myrick et al. (2004) found results similar to ours for 18 °C-acclimated rainbow trout where these fish preferred waters of 18.1 °C (±0.10 SE) and 16.1 °C (±1.1 SE), respectively. The 12 and 15 °C acclimation groups' preferred temperature coincides with an optimal temperature of 16 °C for congeneric Chinook salmon *O. tshawytscha* (Salinger and Anderson 2006). Baltz et al. (1987) commonly found rainbow trout in 16 °C water in the Pit River except in July when they were found in 18 °C water. Because our rainbow trout acclimation groups' preferred temperatures coincide with those ranging from 14 to 19 °C described by Myrick and Cech (2000) regarding optimal temperatures for rainbow trout growth, they support Joblings' (1981) relationship between preferred temperatures and those of maximal growth. Our 18 °C acclimated fish may have been selecting warmer water for reproduction. Rainbow trout typically spawn in the spring, although lower water temperatures can delay spawning to mid-summer (Moyle 2002).

The annular temperature-preference apparatus used here avoids drawbacks inherent in traditional thermal preference devices and also improved upon the smaller (1-m diameter) annular chamber described by Myrick et al. (2004). The strengths of this apparatus have been discussed in detail elsewhere (McMahon et al. 2008; Behrens et al. 2012), but in brief the annular design presents fish with uniform light intensity and water depth, eliminates fish-perceived cover (due to corner or edge effects), and limits the possibility of the fish becoming distracted or disoriented by the influence of the thermal gradient, as often occurs in nature (Reynolds 1977) as well as in some laboratory studies (Beitinger and Magnuson 1976; Fangue et al. 2009). In comparison to Myrick et al. (2004), we provided a more uniform temperature gradient, by using digital mixing valves to control the water temperature and by using a smaller temperature gradient. We were able to use large fish (ca. 550 g), and we increased the number of fish position observations to every 2 min over the 1-h experiment resulting in 30, rather than six, temperature observations increasing temperature-preference resolution.

The histograms presenting the distributions of selected temperatures (Figs. 3 and 5) of both hardhead and rainbow trout show distinct positions/temperatures of preference and avoidance in both species. Temperature avoidance, the negative aspect of thermal behavior (Reynolds 1977), was observed in both species. All three hardhead groups showed active avoidance of the coldest section of the apparatus (Fig. 3), and the 12 and 15 °C-acclimated rainbow trout actively made 180° turns in the apparatus to avoid the warmer section (Fig. 5a, b). The 18 °C trout group showed this same avoidance of the warmest and the coldest areas (Fig. 5c), occupying the available 17–19 °C water. The flume use shown by 18 °C-acclimated rainbow trout (Fig. 4c), where the preferred temperature of 18.5–18.9 °C was accessible in two separate areas of the swimming channel, strongly argues for temperature, rather than some other variable in the laboratory, to be the primary driver of the fishes' position in the apparatus lending further validation to the use of annular chambers in the study of thermal preference in fishes.

Our description of the preferred and avoidance temperatures in hardhead and rainbow trout should facilitate the maintenance and management of stream and river conditions conducive to the growth and sustainability of populations of these two important native species, especially in California's highly-regulated stream systems. Our results also point the way towards interesting future research. For example, the relationship between preferred temperatures and metabolic enzyme activities (sensu Licht et al. 1969) or reproductive vs. non-reproductive physiological states (sensu Pankhurst and Thomas 1998) may reveal more concerning the biological significance of these findings. Because both hardhead and rainbow trout live in complex stream systems with managed hydrographs, these data improve our ability to predict and mitigate the effects of stream temperature alterations on hardhead and rainbow trout.

Acknowledgments We thank S. Hamilton for project coordination and fish collection. T. Reid, C. Myrick, S. Chun, M. Fish, D. Kratville, C. Woodley, G. Soyster, N. Pham, and R. Kaufman for advice and technical support; A. Kay for extensive laboratory assistance; P. Lutes and E. Hallen from the UC Davis Center for Aquatic Biology and Aquaculture for technical assistance; V. de Vlaming for manuscript review; California Department of Fish and Game's American River Trout Hatchery for trout; the Pulsed-Flow Program Management, Team especially J. O'Hagan, J. Canaday, D. Conklin, and P. Young for guidance; and the Public Interest Energy Research Program of the California Energy

Commission (Contract No. 500-01-044) and the UC Davis Agricultural Experiment Station (grant no. 2098-H to NAF) for financial support. All handling, care and experimental procedures used were reviewed and approved by the UC Davis Institutional Animal Care and Use Committee (IACUC Protocol 16832).

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