Comparative Thermal Preferences of Westslope Cutthroat Trout and Rainbow Trout

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Abstract

Remaining populations of westslope cutthroat trout *Oncorhynchus clarkii lewisi* are primarily confined to cool, headwater stream reaches whereas nonnative rainbow trout *Oncorhynchus mykiss* predominate in warmer, lower elevation stream sections historically occupied by westslope cutthroat trout. We assessed whether differing thermal preferences could account for the spatial segregation of these species in the field. Thermal preferences of age-1 westslope cutthroat trout and rainbow trout (125-150 mm total length) were assessed in the laboratory using a modified annular preference chamber at acclimation temperatures of 10, 12, 14, and 16ºC. Westslope cutthroat trout and rainbow trout had similar thermal preferences, with final preferred temperatures of 14.8-14.9ºC when tested in a thermal gradient of 11-17ºC. The similar thermal preferences parallel previous results showing the two species also have very similar optimum growth temperatures (13.1-13.6ºC). The high degree of overlap in physiological and behavioral responses to temperature indicates the two species have highly similar thermal niches and a high potential for competition. Temperature may play an important role in determining the degree of spatial overlap between the species and in predicting suitable habitat for westslope cutthroat trout reintroduction.

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Introduction

Three main metrics are used to define thermal requirements for fishes: upper and lower survival (tolerance) limits; growth range and optima; and thermal preference and avoidance (Fry 1947; McCullough 1999). The first two criteria are physiological measures of performance whereas thermal preference and avoidance represent temperature ranges fish behaviorally select or avoid through thermoregulatory movement. The preferred temperature of a species often corresponds closely to the optimal temperature range for growth and metabolism, thereby providing a behavioral mechanism to maximize survival and reproduction (Reynolds 1977; Jobling 1981; Sauter et al. 2001).

Temperatures in streams and lakes can vary markedly even over relatively small distances owing to such factors as groundwater or tributary inflows and vertical stratification (e.g., Cunjak and Power 1986; Bonneau and Scarnecchia 1996). Fish exhibit a remarkable ability to detect even small temperature differences and show strong orientation to particular temperatures when presented with thermal gradients (Bonneau and Scarnecchia 1996; Welch et al. 1998). Thermal preference information can help define optimal thermal habitat for a species as well as identify the potential for thermal niche overlap among competitors or predators (Edsall and Cleland 2000). In addition, thermal preference information can help define suitable or unsuitable temperatures for species restoration purposes.

Thermal preference can vary according to fish size (Kwain and McCauley 1978), season (Morgan and Metcalfe 2001), thermal history (Javaid and Anderson 1967; Konecki at al. 1995), food availability (Brett et al. 1969; Welch et al. 1998), and the presence of competitors and predators (Reynolds 1977). Thus, determination of thermal preference based on field observations of fish distribution in relation to temperature may not accurately depict true preference. Therefore, thermal preference has often been measured in the laboratory where preference can be examined under closely controlled conditions (Kwain and McCauley 1978).

The 'acute or short term preference method' has been commonly used to determine thermal preference relative to thermal history by acclimating fish to a certain temperature and then placing fish into a thermal gradient for a short (typically 2 h or less) time period (Fry 1947). Acute preference temperature is the average temperature occupied by fish based on multiple observations of location within the thermal gradient. Acute thermal preferences of fish acclimated to different temperatures are then plotted against the acclimation temperatures. The final preference temperature or 'final preferendum,' is defined as the point where the acute preference temperature is equal to the acclimation temperature (Fry 1947; McCauley 1977; Hofmann and Fischer 2002).

Traditional thermal preference testing has used horizontal gradient (Javaid and Anderson 1967; Peterson et al. 1979) and vertical gradient chambers (Kwain and McCauley 1978; Edsall and Cleland 2000), as well as shuttle boxes that produce a constantly varying horizontal gradient controlled by the organisms' movement (McCauley 1977; Konecki et al. 1995). However, these test systems may be limited by the presence of confounding variables inherent to their design such as varying water depth, cover, and light intensity that may mask or bias temperature preferences (Richards 1977; Myrick et al. 2004). To minimize the potential for such biases, an annular chamber with no corners or other cover and uniform illumination and water depth was recently developed for thermal preference studies of aquatic animals (Myrick et al. 2004). A modified version of this annular chamber was developed for use in this study.

Objective

Our previous work described the relative thermal tolerance and thermally-mediated growth performance of westslope cutthroat trout *Oncorhynchus clarkii lewisi* and rainbow trout *Oncorhynchus mykiss*, a nonnative potential competitor that now occupies many waters historically occupied by westslope cutthroat trout (Bear et al. 2005; Bear 2005). The objective of the study described in this report was to compare the relative thermal preference of westslope cutthroat trout and rainbow trout in the laboratory. Our overall goal was to assess to what degree differences in thermal preference could explain the observed spatial segregation of the species in the field, and to aid further development of criteria for identifying suitable thermal habitat for westslope cutthroat trout reintroduction.

Methods

Test fish

Westslope cutthroat trout were obtained as eyed eggs from a wild broodstock maintained at the Westslope Trout Company (Ronan, Montana) and rainbow trout eggs (Fish Lake strain) were obtained from the Ennis National Fish Hatchery (Ennis, Montana). About 100 fish of each species were separated into each of four separate 75-L flow-through acclimation tanks (3 L/min flow rate) in the thermal test facility at the Bozeman Fish Technology Center (BFTC)(Bear 2005). Fish used in trials were age01juveniles ranging in total length from 125-150 mm. Tank temperatures were originally 14°C but were adjusted at 1°C/d until acclimation temperatures of 10, 12, 14, and 16°C were reached. Test species were then reared in separate tanks at the four respective acclimation temperatures for two weeks prior to testing. Fish were fed to excess daily using pelleted trout food (Cutthroat Trout Grower; source: R. Barrows, BFTC) delivered over an 8-hr period with a belt feeder and tanks were cleaned daily. Fish were not fed for 24 h prior to testing.

Test apparatus

Preference testing was performed in an annular preference apparatus based on the design described by Myrick et al. (2004). We modified our apparatus from the original design in order to accommodate larger fish and higher flow rates. The diameter of the apparatus was 118 cm. Cross-sectional widths of the circular outer mixing and middle preference channels were 10 cm and 20 cm, respectively. The radius of the inner effluent channel with center drain was 29 cm. Water supplied from cold (8.5°C) and warm (22.4°C) constant temperature springs was mixed in four head tanks to achieve test temperatures of 8.4, 12.3, 17.0, and 22.3 ºC. Head tank temperatures were monitored with electronic thermographs and adjusted accordingly at the start of each trial. Aerated head tank water was supplied by 2-m-long, 1.25-cm-diameter hoses to eight separate mixing sections positioned around the outer edge of the test apparatus at a flow rate of 3 L/min, yielding a total flow-through rate of the apparatus of 24 L/min. A standpipe on the center drain maintained water depth at 10 cm. Dissolved oxygen concentrations measured in head tanks were greater than 7 mg/L (70% saturation) during the study. Unequal availability of temperatures and sharp temperature gradients within the preference channel were noted drawbacks to the original chamber design (Myrick et al. 2004). Therefore, to provide an equal area of available temperatures, water from each of the four head tanks was delivered to two separate mixing sections creating two equal areas of the four test temperatures. To minimize sharp temperature gradients and ensure laminar radial flow across the preference channel, 16 tubes (0.6-cm-diameter) were placed in a zig-zag pattern along the inner wall of each mixing chamber to achieve adequate mixing and uniform delivery to the preference channel. In addition, mixing sections were sequentially arranged as A, B, C, D, D, C, B, A, where A received head tank temperatures of 8.4ºC; B, 12.3ºC; C, 17.0ºC; and D, 22.3ºC. Dye testing showed that flow from each mixing section across the preference chamber was relatively uniform, with some eddy currents developing near transition areas. Temperatures in the annular preference chamber consistently produced a thermal gradient of about 6°C, with average temperatures ranging from 11 to 17°C (Figure 1). Temperatures varied from about 0.5 to 1.0°C between adjacent temperature measurement points positioned about 15 cm apart along the midline of the preference channel.

The test apparatus was covered with a shroud to minimize disturbance. Fish movement in the preference channel was recorded remotely with a Loligo Video Tracking System (Hobro, Denmark). The camera was mounted 2 m from the water surface to capture the complete field of view of the entire annular preference apparatus. White acetate sheets were mounted on the top of the shroud to provide diffuse, uniform lighting from overhead lights in the BFTC building.

Test protocol

A total of 24 trials was run, 12 with each species, with three replicates at each of the four acclimation temperatures. The sequence of the trials was chosen randomly prior to testing. To minimize the chance of preference of certain areas of the test apparatus independent of temperature, the positioning of the head tank delivery hoses was also randomly assigned prior to testing. Each head tank hose was labeled 1 through 8 and the position of hose 1 was randomly assigned to a mixing section and the remaining hoses were sequentially positioned as described above.

Following hose adjustment, water temperatures were allowed to equilibrate for 30 min. Temperature was then measured with a YSI meter (Yellow Springs, Ohio) 1 cm off the bottom in the middle of the preference channel corresponding to the middle and edges of each mixing section for a total of 16 measurements. Test fish were selected from the appropriate acclimation tank, measured, and introduced into the preference channel in a section most closely corresponding to their rearing (acclimation) temperature. The video system recorded fish position continuously for the next 3 h. At the end of a trial, fish were removed and temperatures re-measured. The test apparatus was then drained and hoses were repositioned as described above in preparation for the next trial.

Data analysis

Temperatures in the preference channel were calculated as the averages of pre- and post-trial temperatures. Temperatures between point measurements were calculated by interpolation of the averages of the two adjoining measurements. Fish locations (nose position) in relation to available temperatures were recorded from the video file every 1 min over the final 2 hr of the 3 hr test period for a total of 120 fish locations per trial; the first hour was deemed an acclimation period and fish locations were not recorded. Fish that failed to acclimate to the test apparatus, as evidenced by continuous swimming and lack of selection for any channel sections during the 2-h test period, were omitted from the data set. Final sample sizes for each acclimation temperature were 2 cutthroat trout and 3 rainbow trout at 10 ºC, 1 cutthroat trout and 3 rainbow trout at 12ºC, 1 cutthroat trout and 2 rainbow trout at 14ºC, and 2 cutthroat trout and 3 rainbow trout at 16ºC.

Acute preference temperature for each trial was calculated as the mean temperature of the individual fish locations. A frequency distribution of selected temperatures for each acclimation temperature was constructed for species comparisons (Richards et al. 1977; Edsall and Clelland 2000). Differences in acute preference temperature were compared among acclimation temperatures and between species using two-way analysis of variance. Relationships between preferred temperatures and acclimation temperatures were analyzed using linear and curvilinear regression. The final preferendum for each species was determined as the point where the preferred temperature was equal to the acclimation temperature on the preference-acclimation curve (Fry 1947; Richards et al. 1977; Hofmann and Fischer 2002).

Results

Temperature selection by westslope cutthroat trout and rainbow trout was similar at each acclimation temperature (Figure 2). At the lower acclimation temperatures of 10 and 12ºC, both species selected temperatures 2 to 4ºC warmer than acclimation temperatures. At 14ºC acclimation, temperature selection for both species was bimodal, with peaks in selected temperatures about 2ºC lower and higher than acclimation temperature. At the highest acclimation temperature (16ºC), both species showed a strong selection for temperatures below the acclimation temperature with westslope cutthroat trout selecting lower temperatures more frequently than rainbow trout.

Acute preference temperatures for westslope cutthroat trout and rainbow trout ranged from 14.5 to 15.8°C and varied only slightly (difference 0.17 to 0.29°C) between the two species at any acclimation temperature (Figure 3). Acute preference temperature was not significantly different among acclimation temperatures ($F = 2.61$, $P = 0.10$) or between species ($F = 0.27$, $P = 0.61$). The overall mean acute preference temperature for westslope cutthroat trout was 15.4 ± 0.2°C SE and 15.3 ± 0.2°C for rainbow trout.

There was no significant relationship between acclimation temperature and acute preference temperature for westslope cutthroat trout (linear, $r^2 = 0.01$, $P= 0.89$; curvilinear, $r^2 = 0.12$, $P = 0.94$) or rainbow trout (linear, $r^2 = 0.10$, $P = 0.68$; curvilinear, $r^2 = 0.35$, $P = 0.81$). Therefore, the final preferendum of 14.9°C for westslope cutthroat trout and 14.8°C for rainbow trout was determined by plotting the relationship between acclimation and acute preference temperatures using a graphical smoothing function and interpolating where the two temperatures were equal on the curves.

Discussion

Juvenile westslope cutthroat trout and rainbow trout exhibited equivalent thermal preferences, with final preferred temperatures of 14.8-14.9°C when tested in a thermal gradient of 11-17°C. The similarities of thermal preferences parallels previous results showing the two species also have very similar optimum growth temperatures (13.6°C for westslope cutthroat trout and 13.1°C for rainbow trout; Bear 2005; Bear et al. 2005). Therefore, both species have nearly identical ‘physiological optimum temperatures,’ defined as the average of the optimum growth temperature and final temperature preferendum (McCullough et al. 2001), of 14.2ºC for westslope cutthroat trout and 14.0ºC for rainbow trout. The high degree of overlap in physiological and behavioral responses to temperature indicates the two species have similar thermal niches and a high potential for competition.

Westslope cutthroat trout and rainbow trout show little spatial overlap in the field despite similar physiological optima and behavioral preferences. Remaining populations of westslope cutthroat trout are primarily confined to cool, headwater stream reaches, and rainbow trout and other nonnative salmonids predominate in warmer, lower elevation stream reaches in the same drainages historically occupied by westslope cutthroat trout (Paul and Post 2001; Sloat 2001). The ability of rainbow trout to survive prolonged exposure to temperatures greater than 20°C and to grow over a wider range of temperatures than westslope cutthroat trout (Bear 2005; Bear et al. 2005), may account for the increased occurrence of rainbow trout at lower elevations and warmer temperatures. In contrast, the lower thermal tolerance and narrower growth range of westslope cutthroat trout (Bear 2005; Bear et al. 2005) may further explain their greater distribution in cooler, headwater streams, where colder water temperatures may allow them to remain more competitive with nonnative salmonids more tolerant of warmer temperatures. Although we found low selection of temperatures below 12ºC and above 16.5ºC by both species, assessing temperature preferences over a wider range than we examined would identify avoidance temperatures of each species and help elucidate if rainbow trout more strongly avoid colder, and westslope cutthroat trout warmer, temperatures. Because thermal preference can be strongly affected by food availability (Javaid and Anderson 1967; Despatie et al. 2001), and headwater streams where westslope cutthroat trout persist tend to have poor growing conditions because of low temperatures and low productivity (Sloat et al. 2005), examining thermal preferences under reduced rations would also be informative for gauging differing species distributions in response to elevational gradients in temperature (e.g., Welch et al. 1998). In particular, experiments comparing species performance in sympatry and allopatry (Taniguchi and Nakano 2000; Reese and Harvey 2002) are needed to fully assess the degree of temperature-mediated competition between the two species.

Preferred temperature of the Fish Lake strain rainbow trout in our study was about 2ºC lower than that reported for other strains in previous studies. Juvenile rainbow trout acclimated to 15ºC selected acute preference temperatures of 16.9ºC (Kwain and McCauley 1978), 17.5ºC (Javaid and Anderson 1967), and 18.4ºC (McCauley and Pond 1971) compared to an estimated 15.0ºC (Figure 3) in our study. Although differences in test equipment may account for some of the differences in preferred temperature of rainbow trout among studies (Myrick et al. 2004), rainbow trout used in our study also exhibited much lower optimum growth temperature than other rainbow trout, suggesting the possibility for stock differences in thermal requirements for this widely distributed species and the need for more extensive testing of thermal requirements using standardized methods (see also Myrick and Cech 2004). We found no reports in the literature on thermal preference testing of westslope cutthroat trout or other cutthroat trout subspecies thus precluding comparisons to our findings.

Overall, we found the annular chamber (Myrick et al. 2004) performed well for measuring temperature preference. Our modifications from the original prototype resulted in equal availability of temperatures and relatively gradual temperature gradients within the preference channel (Figure 1). Random assignment of temperature placement also precluded the need for testing whether fish preferred certain areas of the channel independent of temperature (Despatie et al. 2001; Hofmann and Fischer 2002). However, we did encounter several limitations in the study design. First, although we were able to establish a consistent thermal gradient, the gradient of 6°C (11-17°C) was narrower than we had planned, given head tank temperatures of 8-22°C. We originally tested the apparatus with higher flow rates, but the larger volumes of water created unstable and unpredictable thermal gradients in the preference channel. We were able to achieve a more stable, albeit narrower, thermal gradient by reducing inflow rates and allowing for more complete mixing in each mixing section by blocking off the inner wall of the mixing sections and inserting outflow tubes along the wall.

Another drawback to our apparatus design was uncertainty associated with the actual temperatures selected by the fish, as repeat temperature measurements at the same channel locations at the start and end of a trial sometimes varied by as much as 1°C. Placement of temperature sensors along the channel coupled with the video recording of position (e.g., Edsall and Clelland 2000; Hofmann and Fischer 2002; Myrick et al. 2004) would provide simultaneous measurement of water temperature and fish location and reduce ambiguity in the actual temperature fish were occupying.

The most significant drawback to our study was the difficulty of achieving consistent acclimation to the test apparatus with westslope cutthroat trout, which resulted in a diminished sample size. We do not believe this difficulty was related to the test apparatus as only one rainbow trout failed to show normal preference behavior in the test apparatus. For species of wild parentage such as westslope cutthroat trout, incorporating a pre-testing period longer than one hour may be required to enhance acclimatization to the annular chamber (Morgan and Metcalfe 2001).

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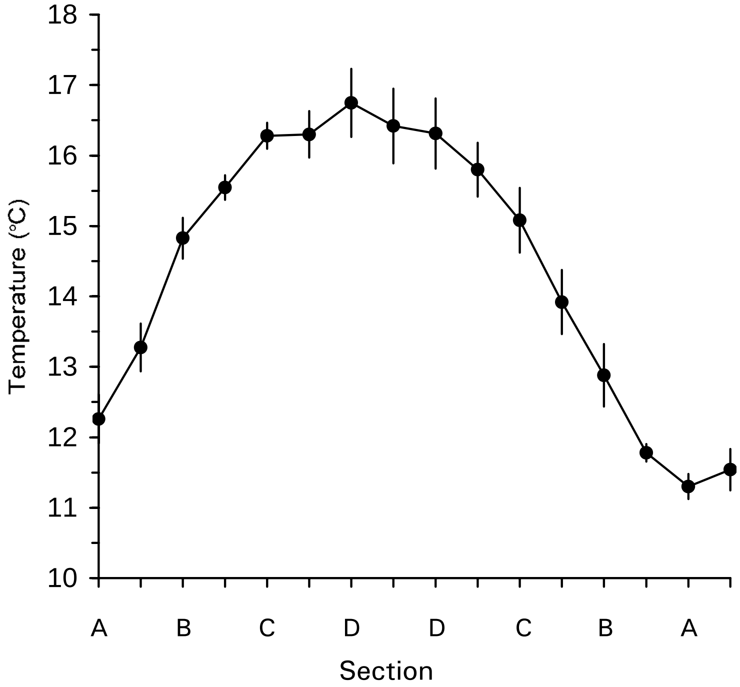

Figure 1. Water temperature (mean ± standard deviation from 15 randomly selected trials) measured at 16 equidistant points along the centerline of the annular preference channel. Letters in the x-axis refer to the eight different mixing sections arranged sequentially around the perimeter of the preference chamber receiving head tank water temperatures of 8.4°C (A), 12.3°C (B), 17.0°C (C), and 22.3°C (D).

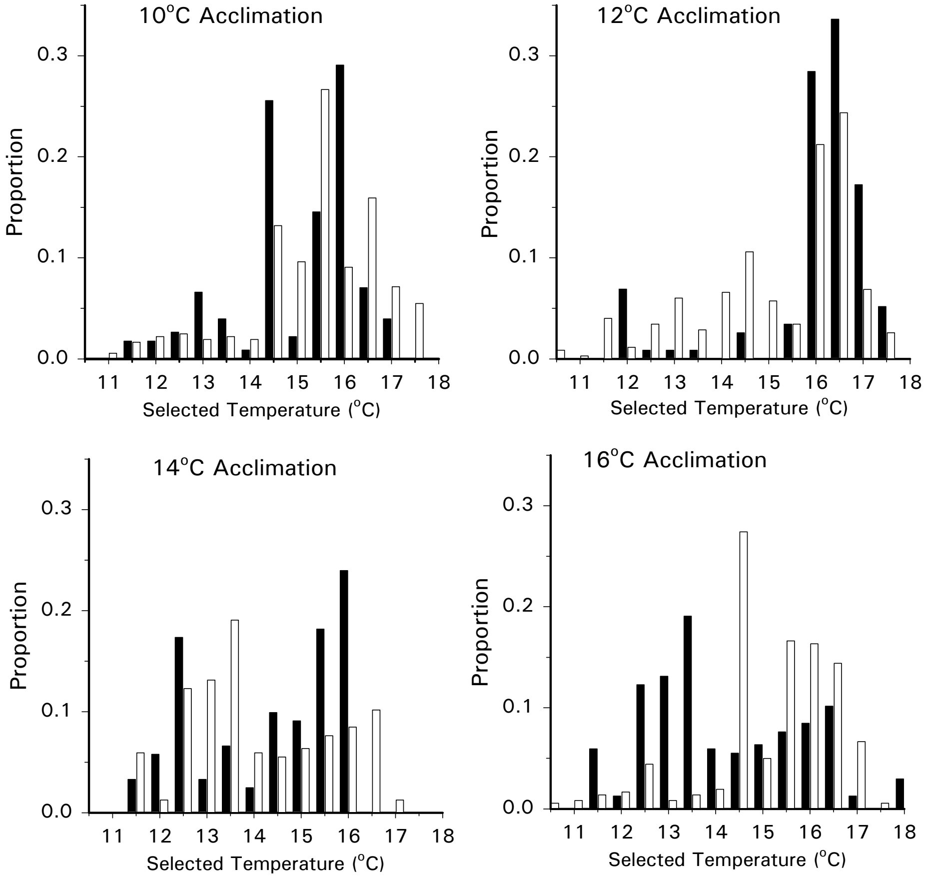

Figure 2. Frequency (shown as proportion of total observations) of temperatures selected by juvenile westslope cutthroat trout (black bar) and rainbow trout (open bar) acclimated to 10, 12, 14, and 16°C.

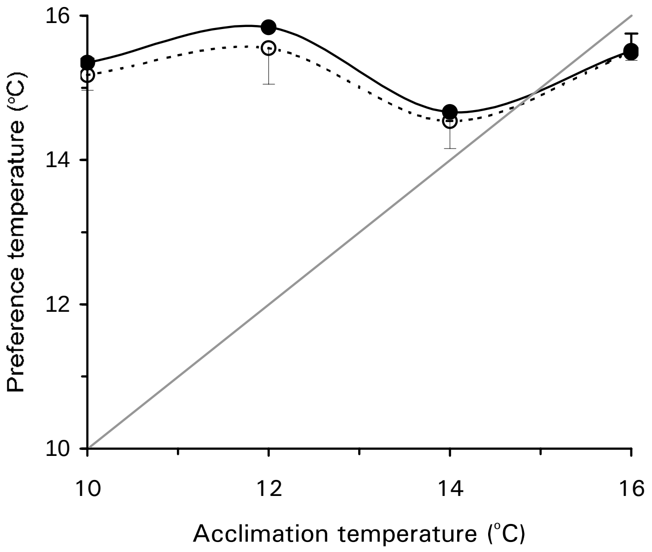

Figure 3. Acute temperature preferenda of juvenile westslope cutthroat trout (solid line; mean + SD) and rainbow trout (dotted line; mean - SD) in relation to acclimation temperature. Gray line denotes 1:1 preference to acclimation line. The final temperature preferendum was calculated as the point at which the preferred temperature equals the acclimation temperature (westslope cutthroat trout, 14.9°C; rainbow trout 14.8°C). SD = standard deviation.